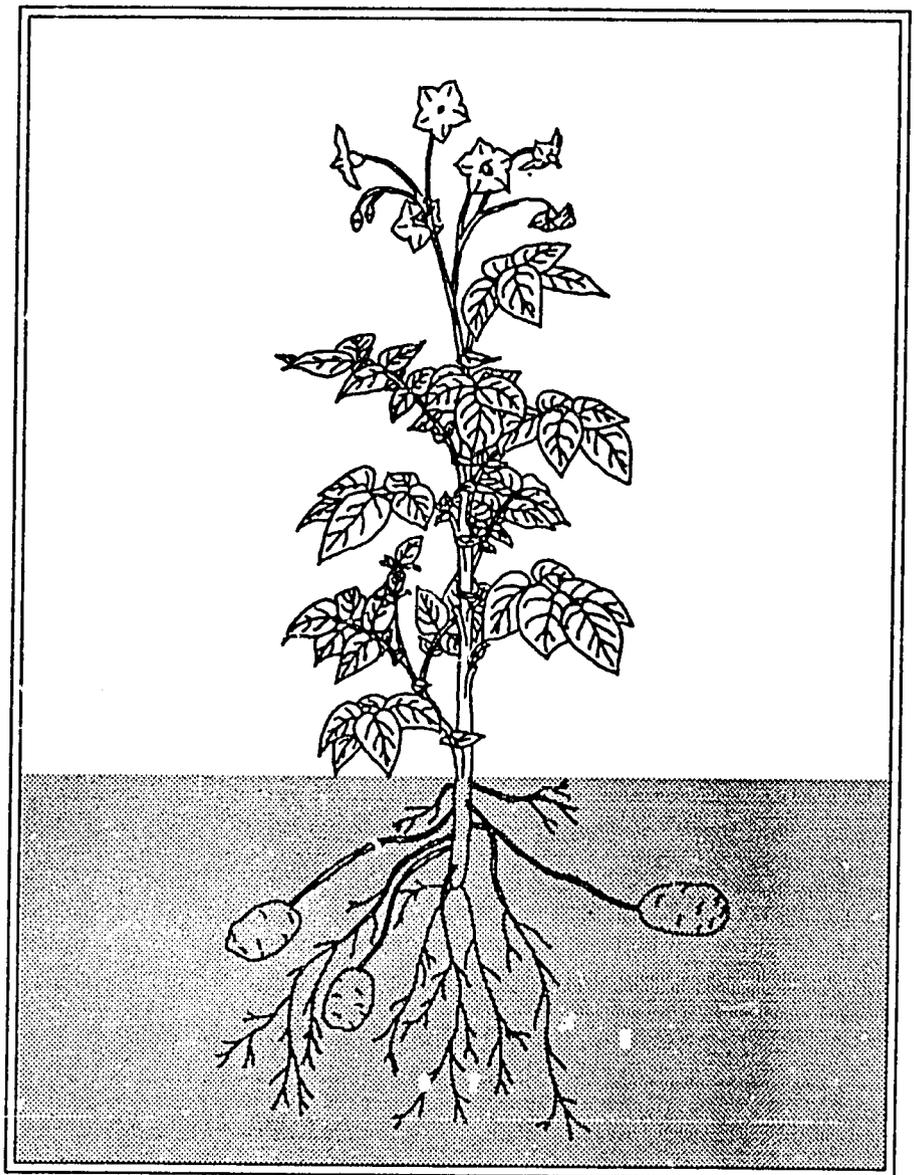# A Simulation Model for Potato Growth and Development: SUBSTOR-Potato Version 2.0

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A Simulation Model for Potato Growth and Development: SUBSTOR-Potato Version 2.0

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Introduction

The accumulation and partitioning of biomass and the phenological development of a potato (*Solanum tuberosum* L.) crop are influenced by many factors. Individually or in combination, the most important are the environmental variables temperature (Snyder and Ewing, 1989; Prange et al., 1990), photoperiod or daylength (Ewing, 1981; Wheeler and Tibbetts, 1986) and intercepted radiation (MacKerron and Waister, 1985). The simulation of potato growth across diverse environments and different cultivars must take each of these variables into account. Numerous efforts have been made to simulate potato growth, ranging from simple regression or correlative models based on temperature (e.g., Iritani, 1963; Manrique and Bartholomew, 1991) to the mechanistic, organ-level model of Ng and Loomis (1984). A common feature of these models is that they are location- (and usually cultivar-) specific. By limiting the application of the model to a specific geographical region, the number of environmental inputs required to run the model is effectively reduced. Temperature response functions (i.e., thermal time or growing degree days (GDD)) are most commonly used to simulate both growth and development. Manrique and Bartholomew (1991) demonstrated that changes in biomass partitioning of cvs. Kennebec and Desiree in Hawaii were strongly related to a single environmental factor; minimum daily temperature. The model of Ingram and McCloud (1984), for cv. Sebago in Florida, depends almost entirely on temperature response to determine potential growth rate, but is rather unique in using different functions for the growth of roots, tops, and tubers. Hartz and Moore (1978), and Sands et al. (1979) use temperature as the primary factor in estimating potential biomass accumulation and adjust these estimates based on intercepted radiation. MacKerron and Waister (1985) were able to accurately predict the growth of cv. Maris Piper in Scotland using total intercepted radiation, not temperature, as the primary factor, presumably because daily temperatures in this region are near the optimum for potato growth (i.e., 17 to 20°C) during tuber initiation and bulking.

The effect of photoperiod is ignored in most potato models, although tuber initiation is sensitive to photoperiod and wide differences in photoperiod response between cultivars have been demonstrated (e.g., Ben Khedher and Ewing, 1985; Snyder and Ewing 1989). There are two potential reasons for this omission. First, the aforementioned geographic and cultivar specificity makes it unnecessary to quantify the effects of different photoperiods (vs. predictable seasonal shifts in photoperiod) on each cultivar. And second, unlike temperature response where cardinal values are reasonably well documented, the quantification of photoperiod effects has been less rigorous. For most cultivars, a threshold photoperiod beyond which tuber initiation is adversely affected has not been firmly established.

This paper presents the development and performance of a new potato model, SUBSTOR-Potato Version 2.0, which is intended to be used over a wide geographical range and for different cultivars. SUBSTOR-Potato was developed as a CERES-type crop model, and thus uses capacity type models of soil water and soil N dynamics that are used in other CERES-type models (e.g., Jones and Kiniry, 1986). The effects of soil water and plant N deficit are simulated in SUBSTOR-Potato and are used to modify rates of growth and phenological development, but the details of these calculations are not presented in this paper. Instead, this paper focuses on the effects of temperature, photoperiod, and light interception on development, and biomass accumulation and partitioning by potato. The input files for soil, climatic, and cultural data required as input to run the model are similar to those for other CERES-type models and are described in IBSNAT Technical Report 5 (IBSNAT, 1986), Thornton et al. (1991), and Ritchie et al. (1992). The following discussion includes: I. prediction of phenology; II. prediction of biomass accumulation and partitioning; and III. model performance.

Model Development

Relative Temperature Functions (subroutine THTIME)

SUBSTOR-Potato uses zero-to-one relative temperature functions based on mean daily air temperature (XTEMP; variable descriptions in Table 1) or soil temperature (ST(LO)) to simulate the response of different plant organs and processes over a wide temperature range. The relative temperature factors (RTF) increase from zero at some base temperature (TB; from 2 to 5°C), to a plateau value of one, then decrease to zero at temperatures of 33 to 35°C, depending on the function. Manrique and Hodges (1989) demonstrated that this type of function was preferable to a linear temperature function because it accounted for the obvious detrimental effect of high temperatures on potato growth and development.

The relative temperature factors for vine growth (RTFVINE) and tuber and root growth (RTFSOIL) are illustrated in Figure 1. The RTFSOIL function (Equation 1) is adapted from the seed piece substrate availability function of Ingram and McCloud (1984) and is used in the model for substrate mobilization from the seed piece, root growth and tuber growth. The RTFVINE function (Equation 2) is generalized using cardinal values from numerous literature sources (e.g., Yamaguchi et al., 1964; Epstein, 1966; Marinus and Bodleander, 1975; Moorby and Milthorpe, 1975; Prange et al., 1990). This function is used to calculate daily leaf expansion and vegetative biomass accumulation. We agree with the Ingram and

Table 1. *Summary of simulated and state variables In SUBSTOR-Potato.*

Variable name	Units	Description
Subroutine PHENOL (Phenological development)		
CTII	none	Cumulative tuber induction index (TII)
GRORT	g plant^{-1} d^{-1}	Daily root growth
PHPER	hr	Length of photoperiod
RDLFTI	none	Relative daylength factor for tuber initiation
RTFTI	none	Relative temperature factor for tuber initiation
SEEDAV	g plant^{-1}	Available seed reserve, 0.8*seed weight at planting
ST(L0)	degree C	Mean daily soil temperature (surface)
TEMPM	degree C	Weighted mean daily air temperature; 0.75*TEMPMN+0.25*TEMPMX
TEMPMN	degree C	Minimum daily air temperature (input)
TEMPMX	degree C	Maximum daily air temperature (input)
TII	none	Tuber induction index; strength of induction to tuberize
Subroutine THTIME (Calculation of relative thermal time)		
RTFSOIL	none	Relative temperature factor, for tuber & root growth
RTFVINE	none	Relative temperature factor, for vine growth
XTEMP	degree C	Mean daily air temperature
Subroutine GROSUB (Carbon assimilation and partitioning)		
CARBO	g plant^{-1} d^{-1}	Actual daily carbon assimilation
DDEADLF	g plant^{-1}	Weight of daily leaf loss from senescence
DEVEFF	none	Developmental effect, for partitioning during transition from ISTAGE1 to ISTAGE 2

GROLF	g plant^{-1} d^{-1}	Daily leaf growth
GROPLNT	g plant^{-1} d^{-1}	Daily total plant growth
GRORT	g plant^{-1} d^{-1}	Daily root growth
GROSTM	g plant^{-1} d^{-1}	Daily stem growth
GROTUB	g plant^{-1} d^{-1}	Daily tuber growth
LAI	m^{2}m^{-2}	Leaf area index
LALWR	270 cm^2 g^{-1}	Leaf area to leaf weight
PAR	MJ m^{-2}	Photosynthetically active radiation
PCARB	g plant^{-1} d^{-1}	Potential carbon assimilation from photosynthesis
PLA	cm^2 plant^{-1}	Plant leaf area
PLAG	cm^2 plant^{-1}	Daily plant leaf area growth
PLAS	cm^2 plant^{-1}	Daily plant leaf area senesced, due to stress
PRFT	none	Photosynthetic reduction factor, for temperature
PTUBGR	g plant^{-1} d^{-1}	Maximum potential daily tuber growth
RLGR	none	Relative leaf growth rate
RVCHO	g plant^{-1}	Reserve soluble carbohydrate pool
TIND	none	Proportion of PTUBGR receiving first priority

Subroutine NFACTO (Nitrogen deficit factors)

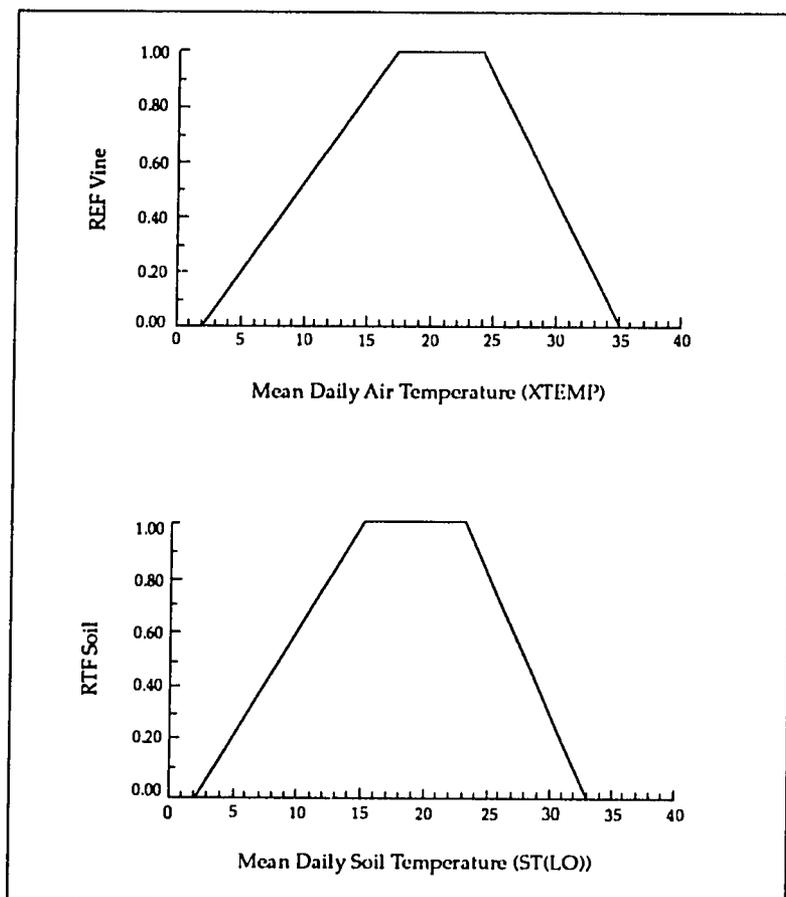| NDEF1 | none | Relative N deficit effect on photosynthesis |
NDEF2	none	Relative N deficit effect on growth
NFAC	none	Leaf N concentration, relative to TCNP and TMNC
TANC	%	Actual N concentration in vines
TCNP	%	Critical vine N concentration
TMNC	%	Minimum vine N concentration, below which growth ceases

Figure 1.
Relative
thermal time
functions for
vine growth
(RTFVINE)
and for tuber
and root
growth
(RTFSOIL).

McCloud (1984) conclusions that potato leaves, tubers and roots have different temperature response functions. However, there are insufficient data to distinguish separate temperature response functions for growth rate and development rate (Sands et al., 1979). Thus, RTFVINE is also used to calculate the rate of phenological development.

$$
\begin{aligned}
\text{RTFSOIL} &= 0 \text{ if ST} <=2 \text{ or ST}>33 \\
&= 0.079 \text{ (ST-2) if } 2<\text{ST}<=15 \\
&= 1 \text{ if } 15<\text{ST}<=23 \\
&= 1 - 0.1 \text{ (ST-23) if } 23<\text{ST}<=33
\end{aligned}
\tag{1}
$$

$$
\begin{aligned}
\text{RTFVINE} &= 0 \text{ if XTEMP}<=2 \text{ or XTEMP}>35 \\
&= 0.0667 \text{ (XTEMP-2) if } 2<\text{XTEMP}<=17 \\
&= 1 \text{ IF } 17<\text{XTEMP}<=24 \\
&= 1 - 0.0909 \text{ (XTEMP-24) if } 24<\text{XTEMP}<=35
\end{aligned}
\tag{2}
$$

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Phenological Development (subroutine PHENOL)

Growth Stages
Potato growth is divided into five phenological stages (variable ISTAGE) within SUBSTOR-Potato, as follows:

> ISTAGE 5: pre-planting
> ISTAGE 6: planting to sprout germination
> ISTAGE 7: sprout germination to emergence
> ISTAGE 1: emergence to tuber initiation
> ISTAGE 2: tuber initiation to maturity.

The variable XSTAGE is used to mark progression through each ISTAGE. It is calculated as a function of accumulated RTFVINE during ISTAGES 5, 6, 7 and 2 and as a function of RTFVINE and photoperiod during ISTAGE 1.

Sprout Germination and Emergence
In SUBSTOR-Potato, preference is given to observed emergence dates (IEMERG) to be included in the appropriate input file, rather than simulation of sprout germination and emergence. We based this decision on the paucity of reliable calibration data for pre-emergent development and, more importantly, the inherent difficulty in obtaining accurate assessments of seed piece physiological age that affects the rate at which potato reaches both of these phenological events (Greenwood et al., 1985a; Van der Zaag and Van Loon, 1987). If IEMERG is not input, germination of unsprouted seed and sprout elongation of both sprouted and unsprouted seed are simulated using RTFSOIL. For both unsprouted and sprouted seed, emergence occurs when cumulative sprout length (SPRLEN) > depth of planting (SDEPTH).

Tuber Initiation
Mechanistic simulation models for potato (e.g., Ng and Loomis, 1984) have attempted to model the timing, rate and duration of tuber initiation. Because of the multitude of factors affecting tuber initiation and the lack of understanding of how these factors affect initiation at the physiological level, we have taken an approach suggested by Sands et al. (1979) to estimate the timing of tuber initiation; that is, extrapolation of linear tuber bulking rate back to the time axis (zero tuber weight). This approach makes tuber initiation an instantaneous event, like emergence, rather than a distinct growth stage. Because the initial lag phase of tuber growth is not directly simulated in SUBSTOR-Potato, the estimated date of tuber initiation will, by necessity, be later than the observed date.

Tuber initiation effectively divides the post-emergence growing season into vegetative and tuber-bearing stages and an accurate estimation of when initiation occurs is critical. Plant

leaf area at initiation, and thus the plant's ability to intercept radiation during tuber bulking, strongly influences end-of-season tuber yield when nutrients and water are not limiting during bulking (Moorby and Milthorpe, 1975; MacKerron and Waister, 1985). In SUBSTOR-Potato, the timing of tuber initiation is a function of cultivar response to both temperature and photoperiod, with these responses modified by plant N status and soil water status. In developing the theoretical framework for predicting tuber initiation, we have relied heavily on the theory, put forth by Ewing (1981), Wheeler and Tibbetts (1986) and others, that tuber initiation by "early" cultivars is less sensitive to non-optimal conditions (i.e., high temperatures and/or long photoperiods) than initiation by "late" cultivars.

Researchers have established that (*i*) cultivars differ in the threshold temperature above which tuber initiation is inhibited (Ingram and McCloud, 1984; Ben Khedher and Ewing, 1985; Snyder and Ewing, 1989), and (*ii*) tuber initiation is influenced more strongly by daily minimum temperature than by daily mean or maximum temperature (Slater, 1968; Manrique and Bartholomew, 1991). We developed a dimensionless cultivar-specific relative temperature factor (RTFTI; range of 0 to 1) to simulate the effect of high temperatures on tuber initiation. This function is similar in shape to the RTFVINE function. Cultivars are assigned a coefficient for critical temperature (TC; Table 2), above which tuber initiation is inhibited to some degree. Cultivar TC corresponds roughly to "early" versus "late," with early cultivars having a higher value for TC. The RTFTI value above TC is

Table 2. Genetic coefficients in SUBSTOR-Potato for leaf expansion rate (G2), tuber growth rate (G3), determinacy (PD), and sensitivity of tuber initiation to photoperiod (P2) and temperature.

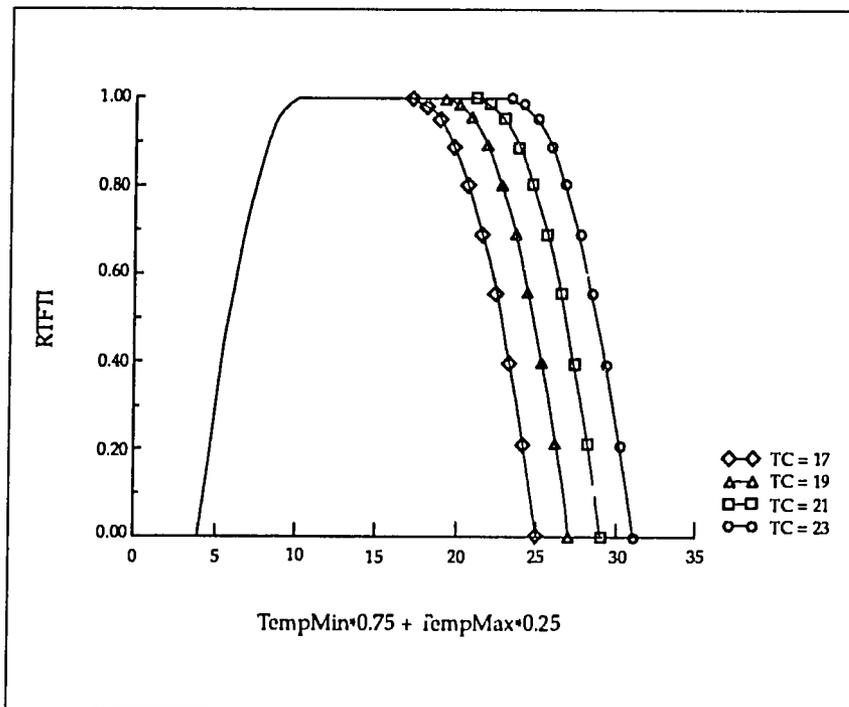| Cultivar	G2	G3	PD	P2	TC
Units	$cm^2m^{-2} d^{-1}$	$gm^{-2} d^{-1}$			C
Segago	2000.0	22.5	0.7	0.8	15.0
Russet Burbank	2000.0	22.5	0.6	0.6	17.0
Katahdin	2000.0	25.0	0.7	0.6	19.0
Maris Piper	2000.0	25.0	0.8	0.4	17.0
Desiree	2000.0	25.0	0.9	0.6	17.0
Norchip	2000.0	25.0	1.0	0.4	17.0

Figure 2.
Relative thermal time function for effect of temperature on tuber initiation. (RTFTI is the relative temperature factor for tuber initiation; TC is the cultivar-specific critical temperature above which tuber initiation is inhibited. TEMPMIN and TEMPMAX are minimum and maximum daily air temperatures.)

calculated as:

$$RTFTI = 1.0-0.0156*(TEMPM-TC)^2, \quad TC<TEMPM<TC+8 \qquad [3]$$
$$RTFTI = 0 \quad TEMPM>TC+8, \qquad where$$
$$TEMPM = 0.75*TEMPMN+0.25*TEMPMX \qquad [4]$$

where TEMPMN and TEMPMX are daily minimum and maximum temperatures, respectively. The result (Figure 2) is a family of identical, decreasing curves dependent on a single coefficient, TC.

The calculation of a relative daylength factor (RDLFTI) is similar to that for RTFTI. When the photoperiod is less than 12 hr, RDLFTI equals 1.0 for all cultivars. This common photoperiod insensitive phase was demonstrated by Rasco et al. (1980), who showed that different cultivars initiate tubers at about the same time under favorable (i.e., short) photoperiod. Differences in time to tuber initiation become apparent under long photoperiods, or as discussed above, under high temperatures.

For photoperiods greater than 12 hr, early and late cultivars are differentially sensitive to increasing photoperiod, with early cultivars being less sensitive than late cultivars (Ewing,

1981; Wheeler and Tibbetts, 1986; Snyder and Ewing, 1989). Thus, early cultivars should have a higher RDLFTI under long (16 to 20 hr) photoperiods. To accommodate these differences, each cultivar is assigned a dimensionless genetic coefficient (P2) indicating sensitivity of tuber initiation to photoperiod. This coefficient, effectively ranging from 0.2 to 0.8, defines the shape of the RDLFTI curve by:

$$RDLFTI = (1.0\text{-}P2) + 0.00694 * P2 * (24.0\text{-}PHPER)^2 \qquad [5]$$

where PHPER is photoperiod (in hrs). The resultant family of RDLFTI curves is shown in Figure 3. Examples of the upper- and lowermost RDLFTI curves are 'Norland' and *Andigena*, respectively (Wheeler and Tibbetts, 1986; Rasco et al., 1980).

A tuber induction index (TII) is calculated daily as:

$$TII = (RTFTI * RDLFTI) + 0.5 * (1.0\text{-}AMIN1(SWDF2,NDEF2)) \qquad [6]$$

and is used as a measure of the relative strength of the induction to tuberize. AMIN1 is the FORTRAN command for selecting the minimum value from a list of numerical values. The modifiers SWDF2 and NDEF2 are factors for soil water and N stress, on expansion growth. These factors, through their effect on TII, hasten tuber initiation under stress conditions.
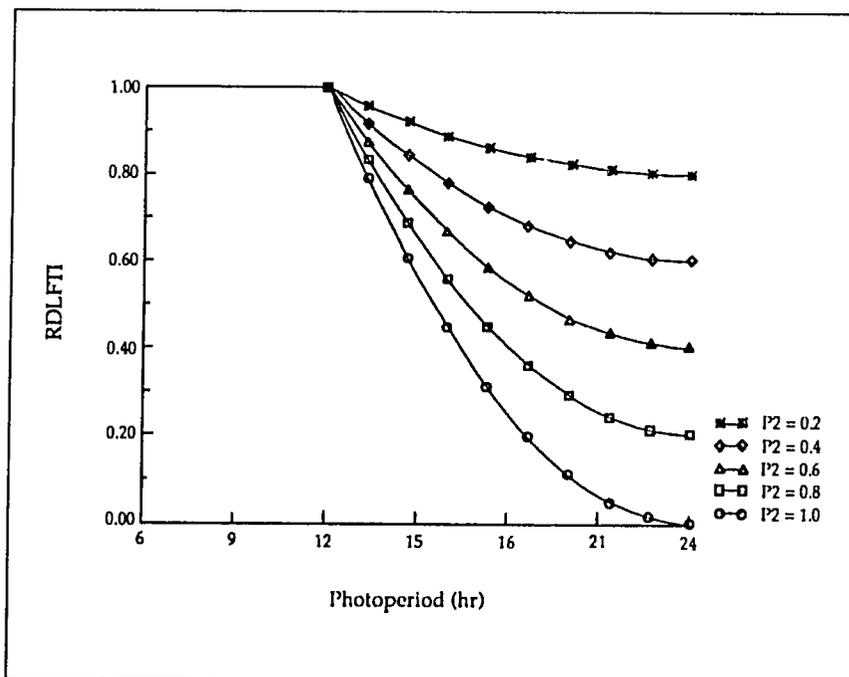

Figure 3. Function for relative effect of photoperiod on tuber initiation. (RDLFTI is the relative daylength factor for tuber initiation; P2 is the cultivar-specific genetic coefficient.)

The multiplicative function of RTFTI and RDLFTI is necessary because long photoperiods and high temperature act synergistically in inhibiting tuber initiation (Snyder and Ewing, 1989; Ewing et al., 1990).

From the daily calculation of TII (beginning at emergence), a cumulative tuber induction index (CTII) is calculated as:

$$CTII = \Sigma TII \tag{7}$$

Available calibration data sets indicate that zero tuber weight, obtained by extrapolation of linear bulking back to the time axis, corresponds to a CTII value of approximately 20. Thus, this value is used to flag tuber initiation in SUBSTOR-Potato.

Biomass Accumulation and Partitioning (subroutine GROSUB)

Pre-emergent Growth (ISTAGE 7)
The seed piece represents the only carbon (C) source to support growth from sprout germination to emergence. Growth during this stage is simulated only if IEMERG is not supplied by the user. Maximum availability of seed piece C (SEEDAV) for growth is adapted from Ingram and McCloud (1984) and pre-emergent sprout growth (SPRWT) is a linear function of RTFSOIL. Daily root growth (GRORT) is assumed to equal daily SPRWT. If the sum of sprout and root growth exceeds SEEDAV, the growth of both components is reduced by the fraction SEEDAV/(SPRWT + GRORT).

Vegetative Growth (ISTAGE 1)
Post-emergent growth is supported by three C sources: seed reserves, current photosynthetic assimilate, and reserve carbohydrate. Immediately following emergence, growth is supported primarily by seed reserves. As in Ng and Loomis (1984), the availability of seed reserve decreases as plant leaf area (PLA) increases. This is accounted for in the model by calculating SEEDAV as a function of PLA up to 400 cm^2plant^{-1}, after which SEEDAV is zero.

Potential photosynthetic C assimilation (PCARB) is calculated as:

$$PCARB = 3.5*PAR/PLANTS*(1.0*EXP(-0.55*LAI)) \tag{8}$$

where PAR is photosynthetically active radiation (MJ m^{-2}), EXP is the FORTRAN command for an exponential function, and LAI is leaf area index (m^2m^{-2}). The radiation use efficiency (RUE) of 3.5 g MJ^{-1} PAR is adapted from literature values (Sale, 1973; Allen and

Scott, 1980; Jeffries and MacKerron, 1989; Manrique et al., 1991), as is the extinction coefficient, k, of -0.55 (Allen and Scott, 1980). The above calculation estimates net C assimilation assuming that nutrients and soil water are non-limiting. Actual C assimilation (CARBO) is calculated by:

$$CARBO = PCARB*AMIN1(PRFT,SWDF1,NDEF1))+0.5*DDEADLF \quad [9]$$

The unitless modifiers are for temperature (PRFT), soil water (SWDF1), and N stress (NDEF1) effects, on photosynthetic efficiency. One-half of the C in senesced leaves (DDEADLF) is translocated prior to abscission (Johnson et al., 1986). If CARBO is greater than daily growth demand, excess C enters a soluble carbohydrate pool (RVCHO), limited to 10 percent of haulm dry weight (Ng and Loomis, 1984).

The following priorities for C use are used in SUBSTOR-Potato. Photosynthetic assimilate is always used first. If additional C is needed to meet growth demand, either seed reserves or carbohydrate reserves may be used according to the criteria described above. The use of seed reserves and carbohydrate reserves are mutually exclusive in the model, because the carbohydrate reserve is allowed to accumulate when PLA > 400 cm^2 plant^{-1}, when seed reserve is no longer available.

During vegetative growth, potential leaf expansion (PLAG) is calculated first as:

$$PLAG = EXP(RLGR)*PLA-PLA \quad [10]$$
$$RLGR = 0.50*RTFVINE \quad [11]$$
$$GROLF = PLAG (1/LALWR) \quad [12]$$

where RLGR is the relative leaf growth rate (Ingram and McCloud, 1984). This estimate of leaf expansion may be modified for N stress and soil water stress effects on expansion growth (NDEF2 and SWDF2), and is then used to calculate daily biomass addition to leaves (GROLF), based on a leaf area to leaf weight ratio (LAWLR) of 270 cm^2 g^{-1}. Daily stem growth (GROSTM) is assumed to equal GROLF, while partitioning of biomass for root growth (GRORT) changes with phenological stage. Growth of all organs are given equal priority during ISTAGE 1 (e.g., Munns and Pearson, 1974). Thus, a shortage of C for growth results in all organ growth potentials being reduced by the fraction CARBO/ GROPLNT, where GROPLNT is the summation of GROLF, GROSTM, and GRORT.

Tuber-bulking (ISTAGE 2)
The initiation of tubers elicits several fundamental changes in the growth of the potato plant. First, as shown by Sale (1973), radiation use efficiency (RUE) *may* increase by 50

percent or more. Sale attributed this increase in RUE to the presence of the tubers, which represented a large, rapidly growing 'sink' for photosynthetic assimilate. Rather than attempting to dynamically simulate the effect of sink size on RUE, SUBSTOR-Potato calculates PCARB during tuber bulking using [8], with the RUE increased to 4.0 g MJ^{-1} PAR. Actual carbon assimilation (CARBO) is calculated as in [9].

The second change in growth after tuber initiation, involves biomass partitioning to competing organs or sinks. Unlike growth during ISTAGE 1, when the proportion of total assimilate partitioned to each organ remains relatively constant under stressed vs. non-limiting conditions, partitioning during ISTAGE 2 is a dynamic process potentially influenced by many factors. For example, partitioning to tubers is favored (i.e., a greater proportion of the total is allocated to tubers) by low temperature, short photoperiod, and low to moderate soil water or N level. Because these same factors hasten tuber initiation, Ewing (1981) suggested that the "tuberization stimulus" influences *both* initiation and partitioning of biomass after initiation. To make this partitioning response operational in SUBSTOR-Potato, we assume that tubers are given first priority on available assimilate (from both current photosynthesis and the soluble reserve carbohydrate pool), thereby eliminating the need to directly estimate partitioning coefficients to allocate C. When the tuber sink is small or conditions are non-limiting, this assumption is not critical because nearly all daily growth demands can be met. However, when stress reduces the amount of assimilate available or the tuber sink is very large, growth of vines and roots can be greatly reduced by imposing this priority. This was demonstrated experimentally by Munns and Pearson (1974), who found that drought during tuber bulking could cause a very rapid cessation of vine growth while tubers continued to grow.

Environmental and soil factors are used in SUBSTOR-Potato to modify potential tuber growth demand. The estimation of tuber growth demand is a two-step process. The first step is to estimate the proportion of maximum potential tuber growth that will receive first priority on assimilate (variable TIND). TIND is independent of the size of the tuber sink and is based on the concept that tuber sink strength is analogous to tuber induction strength. TIND is calculated as:

$$TIND = (\Sigma DTII/3)^*(1/NFAC)^*DEVEFF, \qquad \text{when NFAC>1} \qquad [13]$$
$$TIND = (\Sigma DTII/3)^*DEVEFF, \qquad \text{when NFAC<1}$$

where

$$DTII = RTFTI+0.5^*((1.0-AMIN1(SWDF2,NDEF2,1.0)) \qquad [14]$$
$$DEVEFF = AMIN1((XSTAGE-2.0)^*10^*PD,1.0)$$

DTII estimates the daily tuber sink strength as a function of temperature, and nutrient and soil water status. A three-day moving average of DTII is used because the partitioning response to changing conditions is not instantaneous (Ewing, 1981), and serves to buffer against excessive fluctuations in partitioning. NFAC, which is used to calculate N deficit factors, is included only when greater than one, indicating the promotion of vegetative growth by excessive N. DEVEFF is an artificial variable that alters partitioning during the transition from vegetative to tuber-bearing stages. For example, for determinate cultivars (PD = 1), DEVEFF equals 1.0 when XSTAGE equals 2.1 (i.e., approximately one week after initiation).

Estimation of potential and actual tuber growth rate (PTUBGR and GROTUB) is the second step. PTUBGR is a function of maximum tuber growth rate (genetic coefficient G3) and temperature, in the form:

$$PTUBGR = G3*RFTSOIL/PLANTS \qquad [15]$$

Tuber growth, potential leaf expansion (PLAG), and leaf, stem, and root growth (GROLF, GROSTM, and GRORT) are then calculated as:

$$GROTUB = PTUBGR*AMIN1(SWDF2,NDEF2,1.0)*TIND \qquad [16]$$
$$PLAG = (G2*RFTVINE/PLANTS)*AMIN1(SWDF2,NDEF2,1.0)$$
$$GROLF = PLAG/LALWR$$
$$GROSTM = GROLF*0.75$$
$$GRORT = (GROLF+GROSTM)*0.2$$

G2 is a genetic coefficient for maximum leaf expansion rate, currently equal to 2000 $cm^2 m^{-2} d^{-1}$ for all cultivars because of the lack of evidence to the contrary. After calculating potential growth, actual daily growth of each organ is determined within an hierarchical routine, where assimilated C becomes increasingly limiting in relation to potential growth. The structure of this routine is briefly illustrated below.

1. If CARBO > GROTUB, CARBO is updated as CARBO = CARBO-GROTUB to reflect the priority given to tuber growth.
2. If CARBO or CARBO+RVCHO > GROLF+GROSTM+GRORT, all organs grow at the estimated rate. The reserve carbohydrate pool is adjusted accordingly.
3. If CARBO+RVCHO < GROLF+GROSTM+GRORT, all reserve carbohydrate is used and the growth of leaves, stems and roots is reduced by a growth reduction factor (GRF)

$$GRF = (CARBO+RVCHO)/(GROLF+GROSTM+GRORT) \qquad [17]$$

4. If CARBO+RVCHO < GROTUB, tuber growth is reduced by (CARBO+RVCHO)/GROTUB, and growth of all other organs is set to zero.

Stress Factors

Soil Water Deficit Factor (SWDF)

The effects of soil water deficit (SWD) on potato were reviewed by Van Loon (1981), and include reduced expansion growth and photosynthetic rates, increased allocation of biomass to tubers, and increased rate of phenological development. The manner in which these effects are simulated in SUBSTOR-Potato were discussed previously. Two generalized SWD factors are used in this model: SWDF1 and SWDF2 simulate the effects of SWD on photosynthesis and growth, respectively. SWDF2 is also used in various capacities as a modifier for developmental rates and partitioning of biomass.

Leaf and soil water potentials are not directly estimated in the model. Thus, SWDF1 and SWDF2 can be viewed as the relative deficiency between potential water uptake by roots and transpiration from the leaf surface. Both deficit factors are calculated as a ratio of total root water uptake potential (TRWU) and transpiration (EP1). TRWU is a function of rooting depth, root length density, and soil water content and distribution. The greater sensitivity of leaf expansion to SWD was demonstrated by Munns and Pearson (1974) and Jeffries and MacKerron (1987, 1989), attributable to the loss of leaf cell turgor under deficit conditions. The use of linear SWDFs is supported by Jeffries (1989), who found that leaf extension rate was directly proportional to leaf water potential and leaf turgor. In addition, Vos and Oyarzain (1987) observed a linear relationship between leaf water potential and photosynthetic rate.

Nitrogen Deficit Factor (NDEF; subroutine NFACTO)

The N concentration of potato vines is a much more sensitive indicator to transient changes in N fertility than is the concentration in either roots or tubers. Vine N concentration also generally declines with advancing maturity, even under N sufficient conditions. For these reasons, the estimation of N deficiency or excess in SUBSTOR-Potato is based solely on vine N concentration.

Critical N concentration in the vines or "tops" (TCNP) is the concentration required to maintain maximum growth and photosynthetic rates. Minimum N concentration (TMNC) is the concentration below which growth and photosynthesis cease. The values for TCNP are approximated from Saffigna and Keeney (1977) and Greenwood et al. (1985). In SUBSTOR-Potato, the N concentration in roots and tubers (that have a critical N concentration, TUBCNP, of 1.4 percent regardless of growth stage) is maintained at or slightly above

the respective critical values, reflecting the lack of fertility effects on these organs (e.g., Carter and Bosma, 1974; Saffigna and Keeney, 1977; Kleinkopf et al., 1981).

The extent of N deficiency (NFAC) is measured on a linear scale relative to the minimum and critical concentrations by:

$$NFAC = (TCNP-TANC)/(TCNP-TMNC)$$ [18]

where TANC is the actual N concentration in the vines. NFAC is then used to calculate NDEF1 and NDEF2, for photosynthesis and growth, respectively:

$$NDEF1 = NFAC$$ [19]
$$NDEF2 = 0.95*NFAC$$

Under conditions of excess N, NFAC is allowed to exceed 1.0 and is used to delay development of the plant.

Performance of Substor-Potato

The validation data set for SUBSTOR-Potato (Table 3) includes a wide range of geographical regions, cultivars, and management intensities (e.g., irrigation, N fertilization). Because of the diversity of these data, we have intentionally limited our presentation of model validation in several ways. First, we chose not to conduct a formal sensitivity analysis in our evaluation. The inclusion of diverse data in the validation set seemed to us to make such analyses redundant. For example, within the validation set climatic conditions range from cool temperature/short photoperiod to high temperature/short photoperiod (both from Hawaii; Manrique and Bartholomew, 1991) to cool temperature/ long photoperiod (Scotland; Jeffries and MacKerron, 1987, 1989). Likewise, early, intermediate, and late cultivars (e.g., Norchip, Katahdin, and Russett Burbank) were included in the validation set.

The second limitation is the scope of validation specifically for plant stress factors. Although the validation set inherently addresses the effects of N and soil water stresses on development, growth and yield, we have not included validation statistics on plant-soil N (or water) balance. This decision was based on the fact that most data sets did not include sufficient soil and plant N analyses to adequately evaluate the nitrogen subroutines in the model.

Table 3. *Description of validation data for SUBSTOR-Potato V2.0.*

Location	Latitude	Cultivar(s)	Year(s)	Reference(s)
Murrumbridge, Australia	35.0 S'	Sebago	1970, 1971	Sale (1973)
Olinda, HA (1097 m)	20.5 N	Katahdin, Desiree	1986	Manrique & Bartholomew (1991)
Hamakuapoko, HA (91 m)	20.6 N	Katahdin, Desiree	1986	Manrique & Bartholomew (1991)
Haleakala, HA (640 m)	23.0 N	Katahdin, Desiree	1986	Manrique & Bartholomew (1991)
Ithaca, NY		Katahdin	1980, 1981, 1982, 1985, 1986	Ewing et al. (1990)
Kimberly, ID	42.3 N	Russet Burbank	1978	Ritchie (unpublished)
Aberdeen, ID	43.0 N	Russet Burbank	1978	Ritchie (unpublished)
Entrican, MI	43.2 N	Russet Burbank	1985, 1986, 1987, 1988	Ritchie (unpublished)
Hermiston, OR	45.8 N	Russet Burbank	1988	English (unpublished)
Grand Forks, ND	47.9 N	Russet Burbank Norchip	1985, 1986, 1987	Ritchie (unpublished)
Invergowrie, Scotland	56.5 N	Maris Piper	1984, 1985, 1986, 1987	Jeffries & MacKerron (1987, 1989)

To demonstrate the performance of SUBSTOR-Potato, we have included two distinct approaches in the following discussion. First, the traditional approach showing the relationship between simulated and observed values using all available validation data. And second (where appropriate), simulated versus observed values for a single growing season at a specific location (i.e., seasonal growth pattern).

Simulation of Tuber Initiation Date

Tuber initiation (TI) represents the critical phenological event of potato during the growing season, and unlike grain crops for example, is the only distinct phenological event after emergence. Simulation of the timing of this event is made more difficult by the indeterminate growth habit of some potato cultivars. For these reasons, we put considerable effort into developing a framework for simulating this event that would be useful across environments and cultivars. Within our validation data set, a strong linear relationship was apparent between simulated and observed time to TI (Figure 4), demonstrating the utility of our approach to simulating TI. Despite unknown differences in seed piece physiological age, SUBSTOR-Potato accurately simulated TI under conditions highly conducive for initiation (30 to 40 DAP) and under conditions that delayed initiation until mid-season (80 to 90 DAP). The intercept (a) of the regression of simulated on observed values was 19.35,
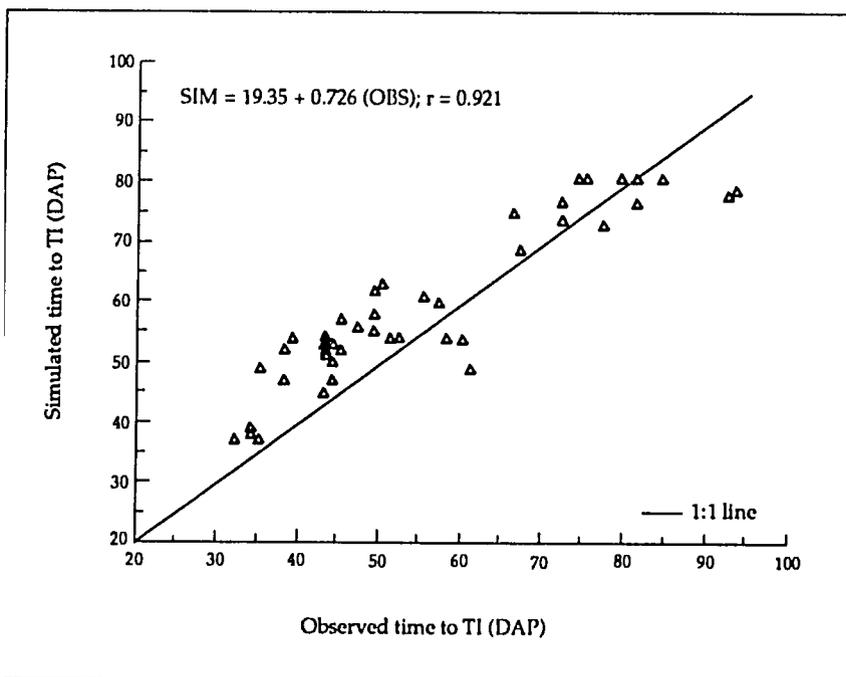

Figure 4.
Simulated
versus
observed
time to tuber
initiation.
n = 41.

indicating that the initiation occurred earlier than the model simulated. This was expected because the model does not simulate the discrete lag phase of tuber growth that occurs immediately after initiation.

The general approach we have taken to simulate phenological development, incorporating both temperature and photoperiod effects, is not unique to SUBSTOR-Potato or potato simulation models in general. Hammer et al. (1989) analyzed grain sorghum (Sorghum bicolor (L.) Moench.) development in diverse environments and developed functions for temperature and photoperiod response very similar to those reported here. They also recognized that cultivars (or cultivar groups) differ in their response to these factors. Russell and Stuber (1985) demonstrated that tassel initiation in maize (Zea mays L.) involved an interaction of temperature and photoperiod effects, and that the effect of photoperiod was minimal after tassel initiation. Similar relationships have been shown for the rate of development by soybean [Glycine max (L.) Merr.] (Major et al., 1975).

The integration of climatic effects, the extrapolation of linear tuber bulking to define tuber initiation, and the recognition of cultivar differences, which are features unique to this model, represent a new approach to modeling potato development. Compared to previous models, this approach may be preferable for several reasons. First, compared to simulation based solely on temperature, this approach takes into account the obvious effects of photoperiod on delaying or hastening TI. Second, although we realize that refinement of the cultivar-specific genetic coefficients (Table 2) are likely, this approach recognizes that cultivars are distinctly different in their response to climate. And third, compared to mechanistic models, this approach greatly simplifies the simulation of TI. This may change as the physiological basis and control factors for TI are clarified.

Simulation of Leaf Growth

Carbon assimilation by potato is directly related to the ability of the plant to intercept solar radiation, which is in turn a function of photosynthetically active leaf area. SUBSTOR-Potato does not simulate the development of individual leaves as in Ng and Loomis (1984), but rather the development of the entire canopy. The model's ability to simulate leaf area expansion or leaf biomass was evaluated in two ways. First, we compared simulated and observed maximum LAI values (Figure 5). Essentially, this evaluates the model equations for potential leaf growth given prevailing climatic and fertility conditions. Compared to observed values, the model performance was poorer than that for tuber initiation, with a correlation coefficient (r) of 0.47. For maximum LAI between 4 and 6, the model tended to overestimate leaf area. Most likely, this was due to the lack of disease and(or) insect defoliation subroutines within the model, which would serve to constrain leaf area. The potential for coupling pathogen submodels with CERES-type crop models was discussed by
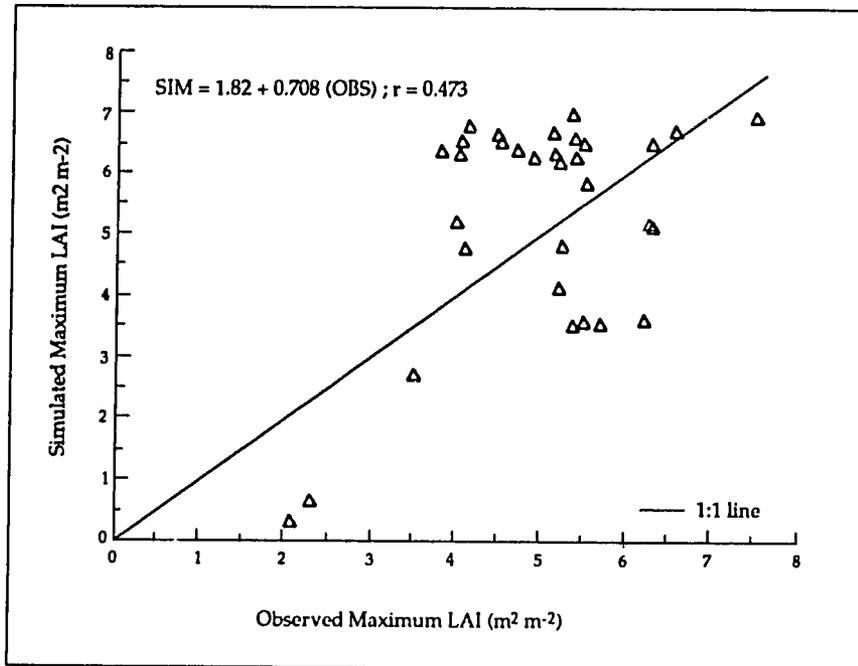
Figure 5. Simulated versus observed maximum leaf area index (LAI) during growing season. n = 32.

Rickman and Klepper (1991), and should represent a major goal of plant simulation modeling. At very low observed maximum LAI, the model underestimated leaf area, suggesting that the model may be overly sensitive to severe environmental conditions (e.g., drought, N stress). As pointed out by Greenwood et al. (1985b) and Jones and Kiniry (1986), crop growth simulation is more difficult under extreme conditions because small differences in initial soil water and soil N levels have disproportionally dramatic effects on simulated plant growth. The designation of tubers as having first priority on assimilated C may also play a role; under extreme conditions that result in less leaf area being produced, this priority may cause leaf growth to cease completely.

To further evaluate discrepancies in the simulation of leaf growth by the model, we present seasonal leaf growth patterns for three location-years: Oregon, 1988; Scotland, 1984; and North Dakota, 1987. These data represent very high, moderately high, and low tuber yield potentials. Simulated leaf growth under long photoperiod and irrigated conditions of Oregon was nearly identical to the observed leaf growth pattern (Figure 6A). This indicates that the functions to estimate leaf growth in the nearly complete absence of plant stress were appropriate. Under conditions slightly less favorable for canopy growth (Scotland), simulation of initial leaf development followed the growth patterns observed i the field (Figure 6B). However, observed leaf growth essentially ceased at about 40 g plant^{-1}, while
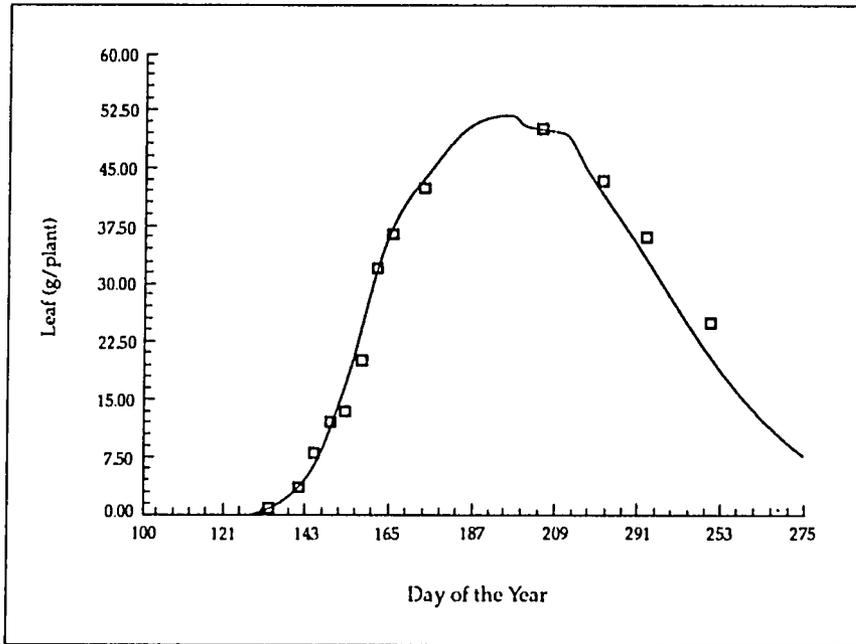
Figure 6A. Simulated (line) versus observed (symbols) seasonal leaf growth for Russet Burbank, Oregon 1988.

simulated growth continued to more than 50 g plant^{-1}. As mentioned previously, the model may continue to simulate leaf growth because there is no simulation of disease or
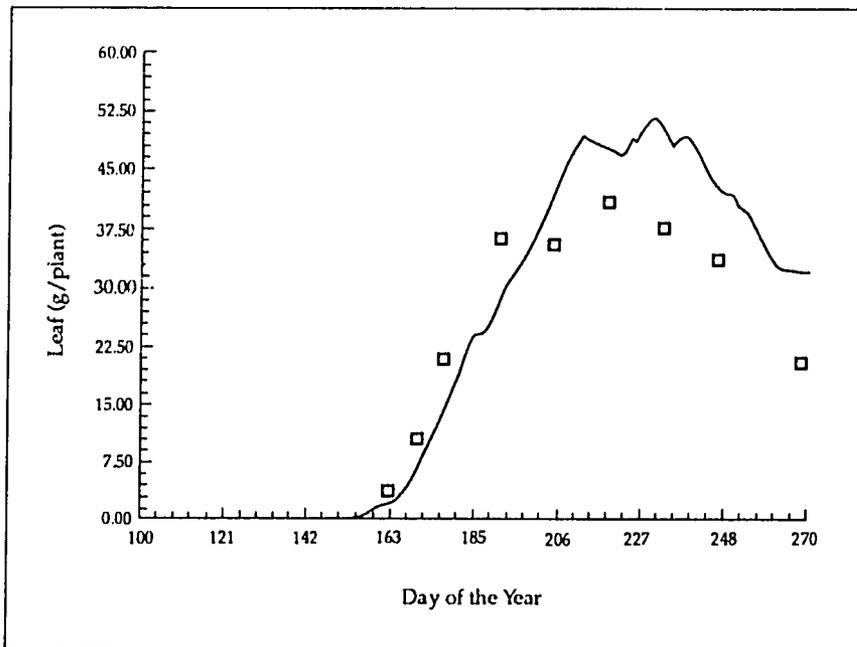

Figure 6B. Simulated (line) versus observed (symbols) seasonal leaf growth for Maris Piper, Scotland 1984.
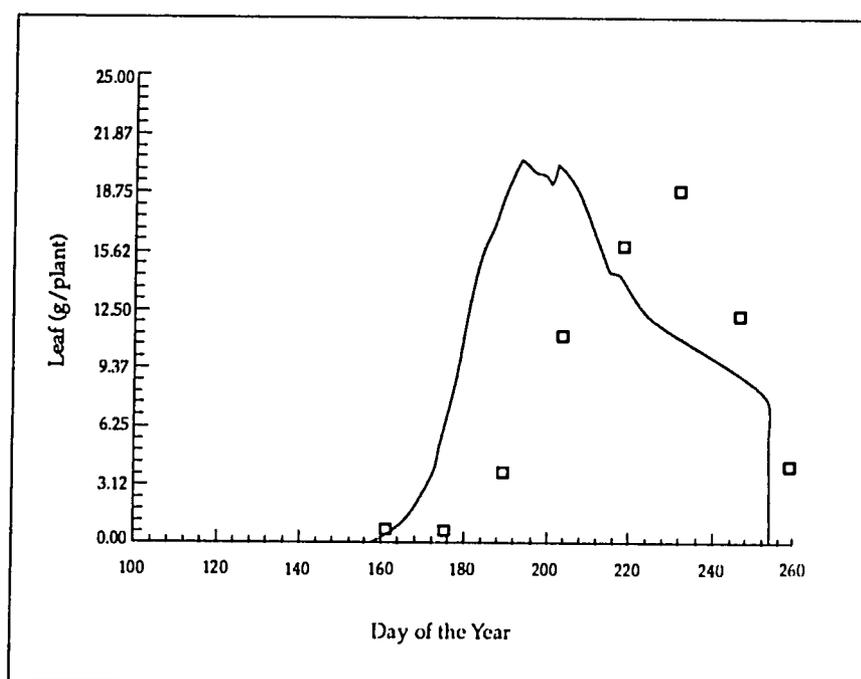
Figure 6C. Simulated (line) versus observed (symbols) seasonal leaf growth for Russet Burbank, North Dakota 1985.

insect effects in the model. Much smaller plants were observed in North Dakota (Figure 6C) due to the lack of irrigation. The model was successful in estimating the maximum canopy size (about 20 g plant^{-1}), but the time that maximum canopy size occurred was approximately 50 D prior to that observed in the field. The cessation of simulated leaf growth at Julian date 190 corresponds exactly to when tuber initiation occurred, providing evidence that the priority for assimilated C may be too rigid.

Simulation of Tuber Yield

Kiniry and Jones (1986) discuss the integration of numerous model processes in simulating maize grain yield within the CERES-Maize model. They noted that simulated grain yield was "affected by virtually every process simulated by the model." The same can be said of tuber yield simulation by SUBSTOR-Potato. Tuber yield is influenced by rate of development, intercepted radiation and use efficiency, biomass partitioning, fertility and soil water status, and other factors. Tuber yield also represents the variable of economic importance. Thus, accurate simulation of tuber yield is essential. We found that the simulation of tuber yield by our model was quite accurate (Figure 7), over a range of two or more than 20 Mg DM ha^{-1}. The intercept (0.40) and slope (0.958) and r value (0.897) of the predicted versus observed regression indicates that the model was not biased across this ten-fold range in
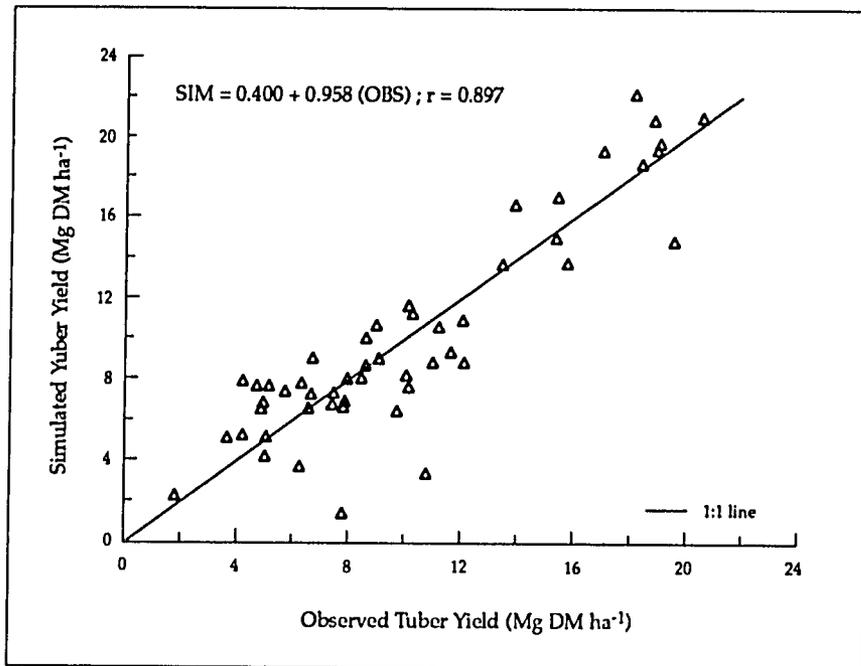
Figure 7.
Simulated
versus
observed
tuber yield.
n = 54.

tuber yield. Except for two outlying data points where yield was greatly underestimated, there was no systematic under- or overestimation of tuber yield. Seasonal tuber growth, for
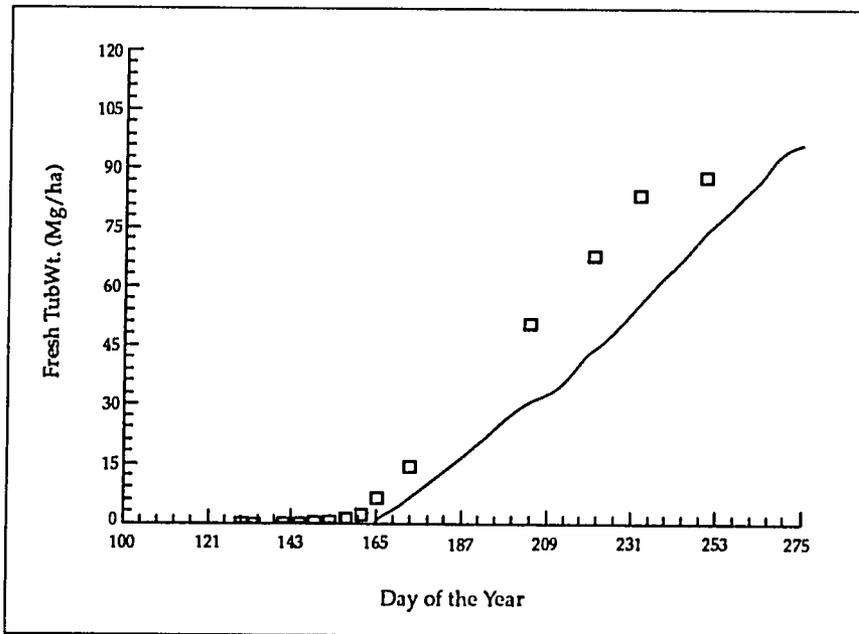

Figure 8A.
Simulated
(line) versus
observed
(symbols)
seasonal
tuber growth
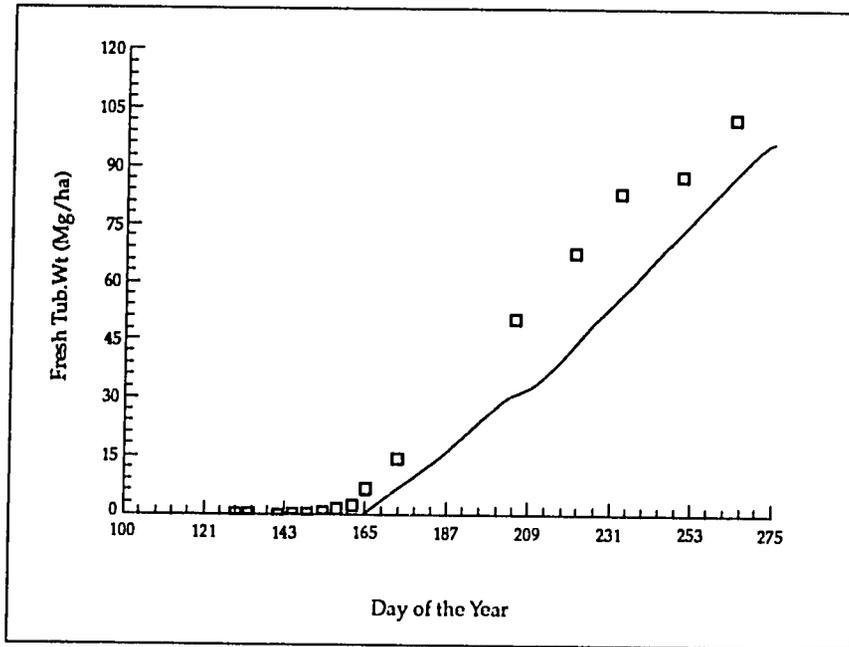*for Russet*
Burbank,
Oregon 1988.

Figure 8B. Simulated (line) versus observed (symbols) seasonal tuber growth for Maris Piper, Scotland 1984.

the same locations described previously for leaf growth, also indicates that the rate of tuber growth was accurately simulated by SUBSTOR-Potato (Figure 8A,B,C). This is true even where the simulation of leaf growth was not successful (e.g., North Dakota data set).
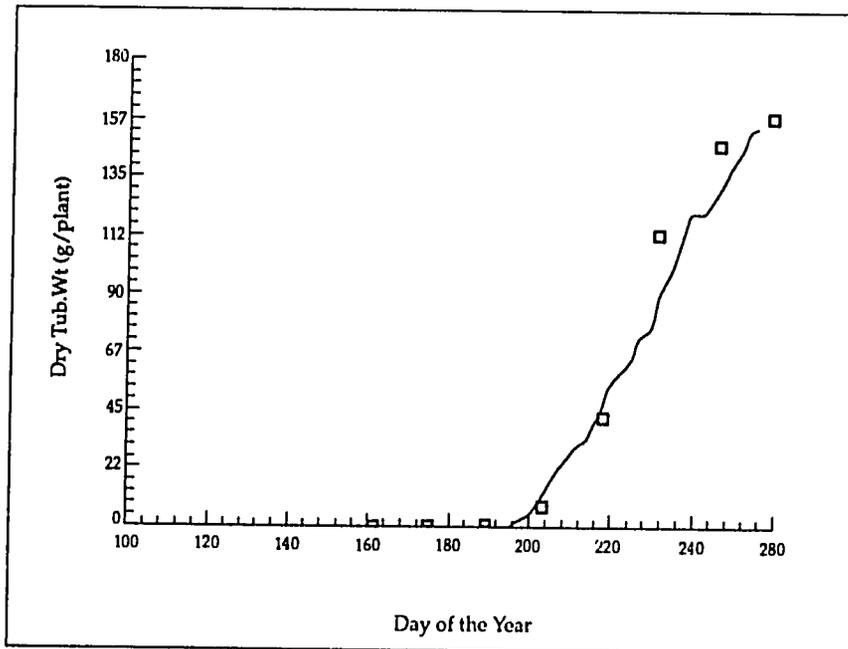

Figure 8C. Simulated (line) versus observed (symbols) seasonal tuber growth for Russet Burbank, North Dakota 1985.

Comparing the performance of our model with previous models for predicting tuber yield is difficult. Validation of many of the previous potato models consisted of seasonal growth within a single growing season or several growing seasons (e.g., Fishman et al., 1984; Ingram and McCloud, 1984; Ng and Loomis, 1984; Ewing et al., 1990). These models validate different approaches to modeling potato growth and development at the empirical or physiological levels, but give little indication of the response of cultivars to changing climate or management. Other models (Ng and Loomis, 1984; MacKerron, 1985; Greenwood et al., 1985a, b) conduct formal sensitivity analyses, making independent changes in key input variables to identify factors controlling growth and development. As discussed at the beginning of this section, we did not conduct a sensitivity analysis because of the diverse validation data set.

Jeffries et al. (1991), in their validation of a model originally developed by MacKerron and Waister (1985), compared simulated versus observed yield for three growing seasons with different levels of soil water stress. Their model accurately ($r^2 = 0.88$) simulated yield response to soil water stress, but was limited to a single cultivar (Maris Piper) at one location. Greenwood et al. (1985b) evaluated the performance of a model of potato growth and N status and found very good agreement between simulated and observed tuber yields. However, their validation data set included yield measurements from serial harvests, which may result in auto correlation from one harvest to the next. All experiments included were conducted on three different soils but under similar climatic conditions. Yield simulation by other CERES-type crop models, like CERES-Maize and SOYGRO, include validation data from different climates and cultivars. The validation of these models was similar to ours for SUBSTOR-Potato.

Simulation of End-of-season Biomass

End-of-season biomass (consisting of tubers, remaining vine biomass, and roots) is the summation of biomass accumulation and biomass loss due to senescence or root turnover. In our model, it is essentially a measurement at any time, which may be after desiccation of vine material. Accurate simulation of this variable is important for biomass and N cycling within the potato crop. We found that our model simulated end-of-season biomass about as well as tuber yield (Figure 9). This is not surprising because most of the biomass remaining at the end of the growing season is in the tubers. Except for two outlying, underestimated biomass yields, total end-of-season biomass tended to be slightly overestimated by the model. The overestimation of haulm biomass discussed earlier, due to the lack of pathogen- or pest-induced defoliation in the model, probably contributes to this overestimation.
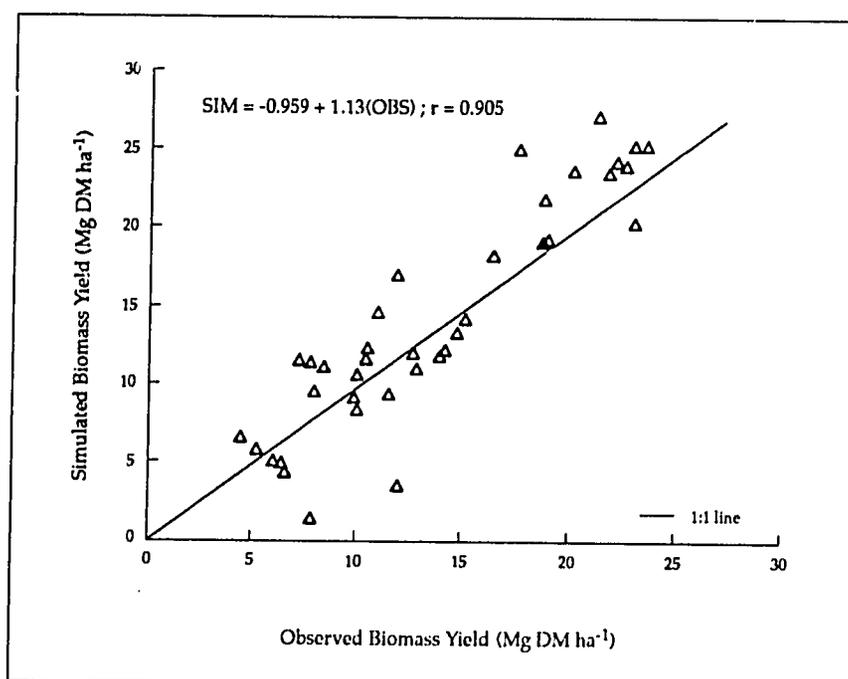
Figure 9.
Simulated
versus
observed
end-of-
season
biomass
yield. n = 40.

Conclusions

In this paper, we have discussed the development and initial validation of a new simulation model for potato growth and development. This model simulates the phenological development of the potato crop, including a new approach to incorporating temperature and photoperiod effects on tuber initiation. It also simulates growth using a capacity model for carbon fixation constrained by radiation, high temperatures, nitrogen deficit, and soil water stress.

The performance of this model for numerous cultivars grown in diverse climates was similar to that of other CERES-type crop models, but comparison to previous potato models is difficult. Previous models of potato growth are generally specific to cultivar, environment, or both, and validation in some cases consists of only seasonal growth patterns. The SUBSTOR-Potato model validation presented may be considered preliminary, but the model has great potential for simulating potato growth and evaluating potential changes in management in many regions.

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