

# ADAPTATION OF SUBSTOR FOR CONTROLLED-ENVIRONMENT POTATO PRODUCTION WITH ELEVATED CARBON DIOXIDE

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**ABSTRACT.** *The SUBSTOR crop growth model was adapted for controlled-environment hydroponic production of potato (*Solanum tuberosum* L. cv. Norland) under elevated atmospheric carbon dioxide concentration. Adaptations included adjustment of input files to account for cultural differences between the field and controlled environments, calibration of genetic coefficients, and adjustment of crop parameters including radiation use efficiency. Source code modifications were also performed to account for the absorption of light reflected from the surface below the crop canopy, an increased leaf senescence rate, a carbon (mass) balance to the model, and to modify the response of crop growth rate to elevated atmospheric carbon dioxide concentration. Adaptations were primarily based on growth and phenological data obtained from growth chamber experiments at Rutgers University (New Brunswick, N.J.) and from the modeling literature. Modified-SUBSTOR predictions were compared with data from Kennedy Space Center's Biomass Production Chamber for verification. Results show that, with further development, modified-SUBSTOR will be a useful tool for analysis and optimization of potato growth in controlled environments.*

**Keywords.** *Advanced life support, Controlled environment, Crop models, Hydroponics, White potato.*

**T**he SUBSTOR (Simulation of Underground Bulking Storage Organs) potato model integrates empirical and mechanistic sub-models to predict potato (*Solanum tuberosum* L.) growth, development, and yield as a function of climate, field, management, and genetic factors (Ritchie et al., 1995). This article discusses adaptations made to SUBSTOR for hydroponic controlled-environment white potato production under elevated atmospheric carbon dioxide concentration (1000  $\mu\text{mol mol}^{-1}$ ). The resulting modified-SUBSTOR model is expected to aid in analysis and optimization of potato growth in controlled environments to support NASA's Advanced Life Support Systems (ALSS) research program (Henninger, 1989) and may be of interest to commercial seed growers.

The approach was derived from similar modification efforts with the CROPGRO model for soybean described in Cavazzoni et al. (1997) and CERES-wheat described in

Tubiello (1995). Model inputs were adjusted, genetic coefficients and crop parameters were calibrated, and source code was modified where needed and justifiable from the literature. Time-series data for this effort was produced by potato experiments conducted at Rutgers University (New Brunswick, New Jersey). Published data from other sources were also utilized. Modified-SUBSTOR predictions were compared with data from Rutgers and Kennedy Space Center (KSC) for validation.

The goals of this research were:

- Generate time-series growth analysis data for hydroponic potato production with elevated atmospheric carbon dioxide concentration.
- Utilize experimental data and the modeling literature as a basis for adapting the field model SUBSTOR for hydroponic growth chamber production of white potato.
- Validate the modified-SUBSTOR model for a range of environmental conditions using data from Kennedy Space Center.

## MATERIALS AND METHODS

### MODEL BACKGROUND AND EQUATIONS

SUBSTOR is one of sixteen FORTRAN-based field crop models included in the DSSAT (Decision Support System for Agrotechnology Transfer) software (version 3.5) developed by the IBSNAT (International Benchmark Sites Network for Agrotechnology Transfer) project. SUBSTOR may be executed via the DSSAT interface, or as a standalone program given input files for experimental details, weather and soil data, and genetic coefficients.

SUBSTOR simulates growth and development of an individual potato plant and extends the result to the entire

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**Table 1. Definition of variables, symbols, and abbreviations used.**

Symbol	Description
$A_{init}$	Quantity of incident PPF absorbed by the canopy ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$A_{net}$	Net photosynthetic rate ( $\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )
$A_{ref}$	Quantity of transmitted PPF reflected from the substrate and absorbed ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$C_g$	Crop growth rate ( $\text{g biomass plant}^{-1} \text{d}^{-1}$ )
CTII	Cumulative tuber induction index (unitless)
DAT	Days after transplanting
$d_r$	Reflection coefficient of incident PPF from canopy leaves (unitless, 0 to 1)
$d_{tr}$	Substrate PAR albedo (unitless, 0 to 1)
G2	SUBSTOR genetic coefficient for leaf expansion rate ( $\text{cm}^2 \text{m}^{-2} \text{d}^{-1}$ )
G3	SUBSTOR genetic coefficient for maximum tuber–bulking growth rate ( $\text{g plant}^{-1} \text{d}^{-1}$ )
$k$	Canopy light extinction coefficient (0 to 1)
LAI	Canopy leaf area index ( $\text{m}^2 \text{leaf m}^{-2} \text{surface}$ )
LALWR	Leaf area to leaf weight ratio ( $\text{cm}^2 \text{g}^{-1}$ )
PAR	Photosynthetically active radiation between 400 and 700 nm
$PPF_{tr}$	Quantity of incident PAR transmitted through the canopy ( $\text{mol m}^{-2} \text{d}^{-1}$ )
P	Planting density ( $\text{plants m}^{-2}$ )
PD	SUBSTOR genetic coefficient for determinacy (unitless, 0 to 1)
PP	Photoperiod ( $\text{h d}^{-1}$ )
PPF	Photosynthetic photon flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
P2	SUBSTOR genetic coefficient for cultivar sensitivity to of photoperiod (unitless, 0 to 1)
$R_{max}$	Maximum increase/decrease in $A_{net}$ due to carbon dioxide concentration (unitless, 0 to 1)
$R_m$	Predicted increase/decrease in $A_{net}$ due to carbon dioxide concentration (unitless, 0 to 1)
RUE	Radiation use efficiency ( $\text{g MJ}^{-1} \text{PAR}$ intercepted or absorbed by canopy)
SRAD	Daily light integral ( $\text{MJ m}^{-2} \text{d}^{-1}$ )
TC	SUBSTOR genetic coefficient for vegetative growth sensitivity to air temperature (unitless, 0 to 1)
TII	Tuber induction index, a measure of daily relative strength of induction to tuberize (unitless, 0 to 1)
$\alpha$	Initial slope of $A_{net}$ response curve to carbon dioxide concentration
$\sigma$	Leaf scattering coefficient (unitless, 0 to 1)
$\theta$	Non–rectangular hyperbola coefficient (unitless, 0 to 1)

**Table 2. Summary of parameter and coefficient changes for modified–SUBSTOR.**

Parameter or Coefficient	Symbol	Field Value <sup>[a]</sup>	Calibrated Value
Cultivar sensitivity to temperature	TC	—	18
Cultivar sensitivity to photoperiod	P2	—	0.2
Determinacy	PD	—	0.8
Maximum tuber growth rate <sup>[b]</sup> ( $\text{g m}^{-2} \text{d}^{-1}$ )	G3	—	2.5
Maximum leaf area expansion ( $\text{cm}^{-2} \text{m}^{-2} \text{d}^{-1}$ )	G2	—	3000
Leaf area to leaf weight ratio ( $\text{cm}^2 \text{g}^{-1}$ leaf dry weight)	LALWR	270	322
Light extinction coefficient	K	0.55	0.63
Radiation use efficiency	RUE	3.5 / 4.0 ( $\text{g MJ}^{-1} \text{PAR}$ )	2.2 / 4.6 ( $\text{g MJ}^{-1} \text{PAR}$ absorbed)

<sup>[a]</sup> Coefficient values were not provided for the Norland cultivar.

<sup>[b]</sup> Value was parameterized as a function of photoperiod, light intensity, and daily light integral (eq. 2).

production area. Development is simulated as five distinct phenological stages, of which only the final two, vegetative and tuber growth, are required for growth chamber simulations with hydroponic nutrient delivery systems. The vegetative development stage begins with sprout emergence through the growth substrate and ends with tuber initiation. The tuber–bulking stage lasts from tuber initiation to plant maturity, the latter occurring when canopy leaf area index (LAI,  $\text{m}^2 \text{leaf m}^{-2} \text{ground}$ ) falls to 10% of the maximum achieved during the growth season.

Five cultivar–specific genetic coefficients affect development rates, organ growth, and plant ontology: TC, P2, PD, G3, and G2. These coefficients are constants in the model and are used to quantify differences in growth and development responses between potato cultivars (tables 1 and 2). One tuber initiation date is simulated for the entire plant because SUBSTOR does not simulate initiation or bulking of individual tubers. The tuber induction index (TII) is a

non–linear function of TC, P2, air temperature, and photoperiod. The TII variable is used in SUBSTOR to measure the daily relative strength (between 0 and 1) of the induction to tuberize, as described in Ewing et al. (1990). Tuber initiation date occurs when the cumulative value for TII exceeds 20. A single tuber growth rate, G3, stipulates the maximum daily tuber–bulking rate for the plant.

Daily biomass gain,  $C_g$  ( $\text{g plant}^{-1} \text{d}^{-1}$ ), during vegetative and tuber growth stages is calculated as:

$$C_g = \frac{\text{SRAD} \cdot \text{RUE} \cdot (1 - e^{-k \cdot \text{LAI}})}{P} \quad (1)$$

where

SRAD = daily light integral in MJ PAR (photosynthetically active radiation between 400–700 nm)  $\text{m}^{-2} \text{d}^{-1}$

RUE = radiation use efficiency ( $\text{g MJ}^{-1} \text{PAR}$ )

$k$  = canopy light extinction coefficient

P = planting density (plants m<sup>-2</sup>).

C<sub>g</sub> is modified by factors for air temperature, carbohydrate mobilization from senesced leaves, and nutrient availability. A carbon dioxide response function, identical to one used in the CERES–Maize model, generates a multiplier value, based on a non-linear function of the ambient carbon dioxide concentration, to further adjust equation 1. Canopy leaf senescence is modeled as a function of the plant age, canopy leaf area, LAI, and PD. Half of the senesced leaf carbohydrate is mobilized each day and immediately available for growth by the plant.

Carbohydrate partitioning to vegetative organs is based on a potential leaf growth rate for the entire plant that is modified by nutrient status, development stage, and air and soil temperature. Stem and root/stolon growth are fixed percentages of the potential leaf growth rate. Tubers have 100% priority for available assimilate, but actual tuber growth rate is restricted by air temperature, PD, and G3. Remaining assimilate is partitioned among leaves, stems, and root/stolons.

If C<sub>g</sub> exceeds predicted growth of vegetative organs and tubers, then the surplus is placed in a soluble reserve pool. Plant organs mobilize carbohydrate from this reserve pool when dictated by growth demand. There is no time limit on the “life” of carbohydrate placed into the reserve. If the daily reserve pool increases beyond 10% of the plant’s current leaf and stem dry mass, then the excess carbohydrate is dumped from the reserve pool and eliminated from the crop model. This can create a mass-balance problem because the mass of the reserve pool is not included in the plant mass.

#### EXPERIMENT DATA FOR SUBSTOR MODIFICATION

Four experiments were conducted within a retrofitted walk-in EGC environmental growth chamber (EGC, Environmental Growth Chambers, Inc., Chagrin Falls, Ohio) located in the New Jersey Agricultural Experiment Station Greenhouse at Rutgers University. Lighting was provided by 72 cool white fluorescent lamps (GE Cool White, 120V) evenly spaced among three drop-down panels spanning the chamber ceiling. The growth chamber was retrofitted with a re-circulating ebb and flood hydroponic nutrient delivery system and a Campbell 21X datalogger for automating data recording of canopy microclimate.

Disease-free potato plantlets were obtained using an in-vitro tissue culture propagation technique (Hussey and Stacey, 1981) from NatureMark, Inc. (Boise, Idaho). Twenty-four white potato plantlets (cv. Norland) were selected for uniformity and transplanted into one of four production trays at a planting density of 4.6 plants m<sup>-2</sup> at the start of each experiment. Each production tray was filled with gravel media (well-gravel, 2 mm diameter) to a 4 cm depth that served as growth substrate. Peter’s Professional Hydro-sol Formula (The Scotts Company, 5–11–26) and solution-grade calcium nitrate (Hydro-Gardens, Inc., 15.5–0–0) mixed with filtered tap water were used to create the nutrient solution at an electroconductivity of 1.7 ± 0.2 ms cm<sup>-1</sup>. Production trays were irrigated eight times per day (every three hours) for five minutes. The entire nutrient tank was emptied, cleaned, and replenished with new nutrient solution once per week. Opaque PE (polyethylene) film (white top, black bottom) was placed on top of the gravel in each production tray to separate root from shoot zones. Small slits

were cut in the plastic to allow for growth of the potato plantlets through the plastic film.

Silver-gray fiberglass window screening was used to define the growing area and to simulate the effects of guard row plants by attenuating the amount of side lighting received by the potato plants (Bugbee, 1994). After approximately three weeks following plantlet transfer to the growth chamber, the screen was erected around each plant to maintain a 0.22 m<sup>2</sup> rectangular production area per plant. The height of the screen was raised twice per week to match canopy height. Averaged environmental conditions for all four experiments were 20.0 °C ± 0.2 °C light-cycle temperature, 15.9 °C ± 0.2 °C dark-cycle temperature, 1020.2 ± 108.6 μmol mol<sup>-1</sup> CO<sub>2</sub>, 407.3 ± 20.8 μmol m<sup>-2</sup> s<sup>-1</sup> PPF (photosynthetic photon flux) (17.6 mol d<sup>-1</sup>), 71.6% ± 3.3% relative humidity, and 12-hour light period. Additional experimental information may be found in Fleisher (2001).

Non-destructive measurements included phenological observations and canopy light attenuation (incident PPF, reflected PPF, and transmitted PPF), which were used to calculate canopy light interception and absorption. PPF measurements were made with a Li-Cor line quantum sensor (LI-191SA) and point quantum sensor (LI-190SA). Growth analysis measurements of canopy leaf area, and stem, leaf, root/stolon, tuber, and senesced leaf dry masses were collected at 28, 42, and 56 days after transplanting (DAT) for three replicated experiments, and at DAT 105 for the fourth experiment.

#### SUBSTOR ADAPTATION PROCEDURE

Calibration of coefficients and parameters was based on experimental data from Rutgers and the literature. Changes to SUBSTOR source code, which were based on the modeling literature, were implemented as needed using the experimental data for model evaluation. Modifications to SUBSTOR were completed when additional changes could not be justified with data or existing literature. Model modifications are grouped below according to area of focus. Note that radiation units were converted from quantum flux density to radiometric units using a factor of 4.59 μmol m<sup>-2</sup> s<sup>-1</sup> / W m<sup>-2</sup> (Thimijan and Heins, 1983).

#### CULTURAL DIFFERENCES

Options within SUBSTOR’s input file were set to simulate non-limiting nutrient and water conditions, as assumed for potato production with hydroponics systems. Changes were implemented to the model source code to allow input of constant daily values for photoperiod, soil/root-zone temperature, substrate PAR albedo, SRAD, and carbon dioxide concentration within the input file. Sprout emergence date was fixed to day zero, forcing the model to begin with the vegetative growth development stage, which is consistent with culture practices used in hydroponic experiments.

#### CULTIVAR CALIBRATION

The calibrated values for the five genetic coefficients for cv. Norland are shown in table 2. Values for G2 and PD were determined from experimental data (Tibbitts et al., 1994) while P2 was estimated from a least squares error minimization program, included with DSSAT, using the data from the Rutgers experiments. Cumulative tuber initiation index (CTII) was increased from 20 to 30 in the code so as to

accurately simulate later dates of tuber initiation observed in the white potato experiments and literature (Wan et al., 1994; Wheeler et al., 1990).

Research conducted by Ng and Loomis (1984), whose POTATO model simulates initiation and growth rate of individual tuber organs, was used to justify modification to G3, the maximum tuber growth rate. In POTATO, tuber induction is strictly a function of photoperiod. Following the tuber initiation date, individual tubers in the POTATO model were assigned the same coefficient for maximum growth rate that was subsequently modified by assimilate status, tuber age, temperature, and plant water status. Once the plant is induced, a higher carbohydrate concentration within the plant will increase both growth rate and initiation of individual tubers. Thus, a higher daily light integral, which tended to increase the plant's carbohydrate pool, resulted in a larger overall tuber growth rate in the plant.

In order to simulate this effect in SUBSTOR, G3 was parameterized as a non-linear function of average daily photoperiod (PP) and daily light integral (SRAD) as in equation 2 ( $r^2 = 0.99$ ) using data from the Rutgers experiments conducted by Wheeler et al. (1996) and Tibbitts et al. (1994). This change allowed the maximum tuber growth rate to vary daily as a function of irradiance and photoperiod:

$$G3 = -11.6 + 0.0607 \cdot PP^2 + 0.0509 \cdot SRAD^2 + 6.56 \cdot \left( \frac{SRAD}{PP} \right)^2 \quad (2)$$

#### LIGHT ABSORPTION AND SUBSTRATE PAR ALBEDO

The substrate PAR albedo for the white plastic surface used as cover for the plant production trays in the Rutgers' growth chamber was measured to be 0.49. Previous work (Cavazzoni et al., 1997) has shown that a significant fraction of transmitted light can therefore be reflected back into the crop canopy, where it may be absorbed for photosynthesis. Prior to canopy closure (about DAT 42), integrated values from DAT 1 to DAT 42 for the intercepted and absorbed PAR values for the Rutgers experiments were measured as 148 mol m<sup>-2</sup> and 182 mol m<sup>-2</sup>, respectively (data not shown). In order to include the surface PAR albedo in equation 1, the use of intercepted light was replaced with that for absorbed light using the work of Boote and Pickering (1994), as shown in equations 3–6.

The quantity of incident PAR absorbed by the canopy ( $A_{init}$ ) is computed as:

$$A_{init} = (1 - d_r) \cdot \left( 1 - e^{-k \sqrt{1-\sigma} \cdot LAI} \right) \cdot PPF \quad (3)$$

where

- $d_r$  = reflection coefficient, from 0 to 1, of incident PAR from canopy leaves (equal to 0.06)
- $\sigma$  = leaf scattering coefficient, from 0 to 1 (equal to 0.2)
- $k$  = canopy light extinction coefficient previously defined (table 1).

The light transmitted through the canopy ( $PPF_{tr}$ ) is computed as:

$$PPF_{tr} = PPF - (A_{init} + d_r \cdot PPF) \quad (4)$$

The amount of  $PPF_{tr}$  subsequently absorbed by the canopy ( $A_{ref}$ ) is:

$$A_{ref} = (1 - d_r) \cdot d_{tr} \cdot \left( 1 - e^{-k \sqrt{1-\sigma} \cdot LAI} \right) \cdot PPF_{tr} \quad (5)$$

where  $d_{tr}$  is the substrate PAR albedo (measured as 0.49).

With these modifications, equation 1 becomes:

$$Cg = \frac{SRAD \cdot RUE \cdot (A_{init} + A_{ref})}{P} \quad (6)$$

where RUE is now based on absorbed light.

RUE was re-calculated from Rutgers experimental data based on the ratio between plant growth and daily absorbed PAR (table 2). Because of the higher measured quantity of absorbed PAR (182 mol m<sup>-2</sup>) versus intercepted PAR (142 mol m<sup>-2</sup>) prior to canopy closure, RUE on an absorbed light basis was 37% less than RUE on an intercepted light basis during the vegetative growth stage (table 2). However, absorbed RUE was significantly larger than intercepted RUE for the tuber-bulking stage (table 2). It has been suggested that RUE values tend to be higher in growth chambers than in field studies due to a larger diffuse light fraction, since diffuse light results in a more uniform distribution of light energy for lower, shaded canopy leaves (Tubiello, 1995).

#### LEAF AREA GROWTH AND CANOPY ARCHITECTURE

Leaf area to leaf weight ratio (LALWR) is a parameter used in SUBSTOR to estimate canopy leaf area. The measured value obtained from our experimental data was 19% higher than in the original model (table 2). This result was consistent with previous potato models, which reported higher values than in SUBSTOR (Ng and Loomis, 1984).

A spherical leaf distribution, an indication of canopy architecture, was estimated for the potato canopy based on visual observation. The canopy light extinction coefficient ( $k$ ) was changed to a value of 0.71, which assumes an average beam direction of 45° to the horizontal (Goudriaan, 1988). This was the value used in equations 1 and 6.

#### RADIATION USE EFFICIENCY AND AMBIENT CARBON DIOXIDE CONCENTRATION

An interactive effect of irradiance and carbon dioxide on net photosynthetic rates of white potato was demonstrated in controlled-environment experiments (Mackowiak and Wheeler, 1996; Stutte et al., 1996; Wheeler et al., 1991). A non-rectangular hyperbola (Thornley and Johnson, 1990) was used to fit data from Stutte et al. (1996), where short-term net photosynthetic rates ( $A_{net}$ ) were measured from mature canopy leaves at different atmospheric carbon dioxide levels at varying treatments of photoperiod and light intensity. Note that variables  $\alpha$  and  $R_{max}$  in equation 7 were parameterized as functions of light intensity and photoperiod, as shown in equation 8. Regression equations for  $\alpha$  ( $r^2 = 1.0$ ) and  $R_{max}$  ( $r^2 = 0.98$ ) were developed using Microsoft Excel. In replacing the original carbon dioxide function used in SUBSTOR with equations 7 and 8, it was assumed that the

carbon dioxide effect on  $A_{net}$  was transferable to daily carbohydrate gain.

$$R_m = \frac{1}{2\theta} \left\{ \alpha_{(PPF,PP)} C + R_{max(PPF,PP)} - \left[ \alpha_{(PPF,PP)} C + R_{max(PPF,PP)} \right]^2 - 4\theta \alpha_{(PPF,PP)} C R_{max(PPF,PP)} \right\}^{1/2} \quad (7)$$

$$\alpha = -0.00874 + 0.0000275 \cdot PPF + 0.000732 \cdot PP - 0.00000145 \cdot PPF \cdot PP - 0.00000833 \cdot PP^2 \quad (8a)$$

$$R_{max} = -2.80 + 0.00822 \cdot PPF + 0.284 \cdot PP - 0.000431 \cdot PPF \cdot PP - 0.00354 \cdot PP^2 \quad (8b)$$

where

- $R_m$  = normalized  $CO_2$  effect on  $A_{net}$
- $\theta$  = constant (0.98)
- $\alpha$  = initial slope of response curve, parameterized as a function of PP and PPF
- $C$  = atmospheric carbon dioxide concentration, in  $\mu\text{mol mol}^{-1}$  from 50 to 9999
- $R_{max}$  = maximum normalized  $A_{net}$  response.

#### CARBON PARTITIONING, BALANCING, AND SENESCENCE

Assimilate partitioning coefficients were modified so that stem growth was 40% of leaf, and root/stolons were approximately 45% of stem and leaf during vegetative growth. Following tuber initiation, stem growth rate increased to 60% of leaf growth and root to 40% of stem and leaf. These changes were based on observed leaf, stem, root, and senesced dry masses from the Rutgers white potato experiments.

A carbon mass-balance problem may result in the original SUBSTOR model when daily carbon gain exceeds potential organ growth rates. This problem was observed when simulations were conducted with daily light integrals larger than  $34.6 \text{ mol m}^{-2} \text{ d}^{-1}$  PPF. Reserve carbohydrate greater than

10% of leaf and stem is dumped in the original model. In addition, the mass of the carbon reserve pool is not accounted for in the plant dry mass. To address this, the soluble carbon reserve pool was included in the mass of the canopy, and carbohydrate in the reserve that exceeded 10% of leaf and stem dry masses was permanently added to stem mass.

Following tuber initiation, the leaf senescence rate in SUBSTOR is based on plant leaf area and plant age. The function was modified to use the maximum plant leaf area instead of current leaf area. This increased the rate of senescence throughout the plant lifecycle, in accordance with experimental data measurements (not shown). It has also been reported that leaf photosynthesis declines with age for white potato (Ng and Loomis, 1984). Once the maximum canopy area has been achieved, this effect was indirectly simulated by linearly decreasing RUE to a minimum value of 1.0.

## RESULTS AND DISCUSSION

Three different stages of modifications to SUBSTOR, represented by curves *a*, *b*, and *c* in figures 1–4, were simulated and compared with data from Rutgers University for LAI (fig. 1), tuber dry mass (fig. 2), stem dry mass (fig. 3), and total dry mass (fig. 4). Stage modifications were organized in the order in which they were implemented to the original SUBSTOR model. Modifications of SUBSTOR for culture differences and genetic coefficients are represented by curve *a*. Curve *b* includes modifications for curve *a* plus additions for RUE and absorbed light. Curve *c* includes curve *b* modifications plus the changes to LALWR, carbon dioxide response, leaf senescence, and carbon mass balancing.

Results from curve *a* show that nearly all carbohydrate was partitioned to tuber growth following tuber initiation (figs. 1–4). Vegetative growth and canopy development was prevented (fig. 1). This occurred because SUBSTOR gives tubers 100% priority for assimilates. This priority can be lowered by off-nominal environment and nutrient status, but the assumption of non-limiting conditions in hydroponics systems keeps the value at 100%. The increase in RUE in

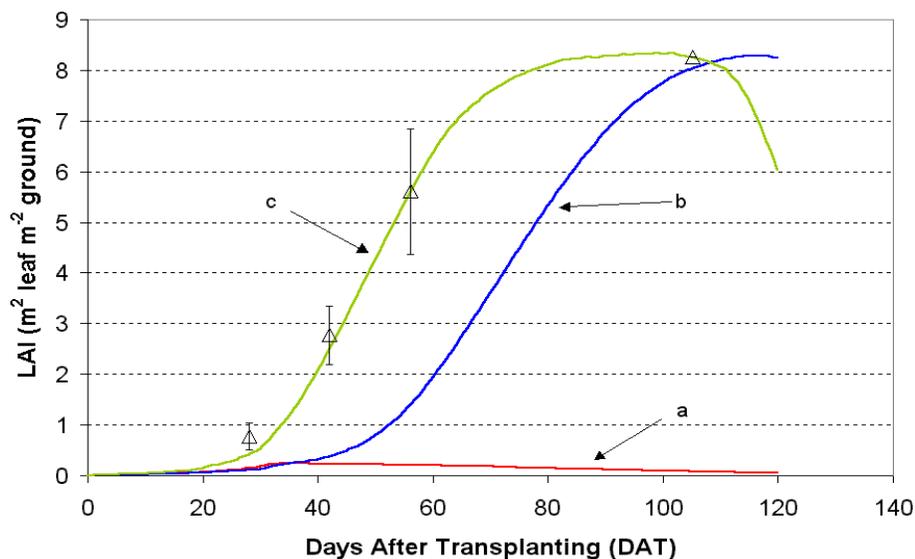


Figure 1. Modified-SUBSTOR predictions for leaf area index: *a* = initial and calibration modifications, *b* = absorbed light and substrate PAR albedo, and *c* = leaf area to leaf weight ratio, canopy extinction coefficient, carbon balancing, partitioning, carbon dioxide response, and senescence. Observed values ( $\Delta$ ) are from the Rutgers experiments and consist of averaged results of the three replicated experiments except for DAT 105.

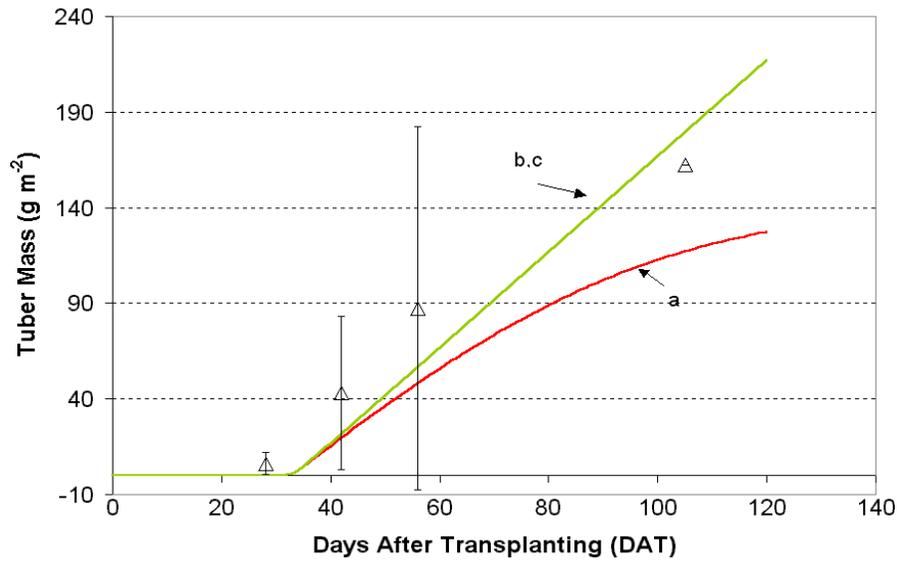


Figure 2. Modified-SUBSTOR predictions for tuber dry mass. Symbols are as described in figure 1.

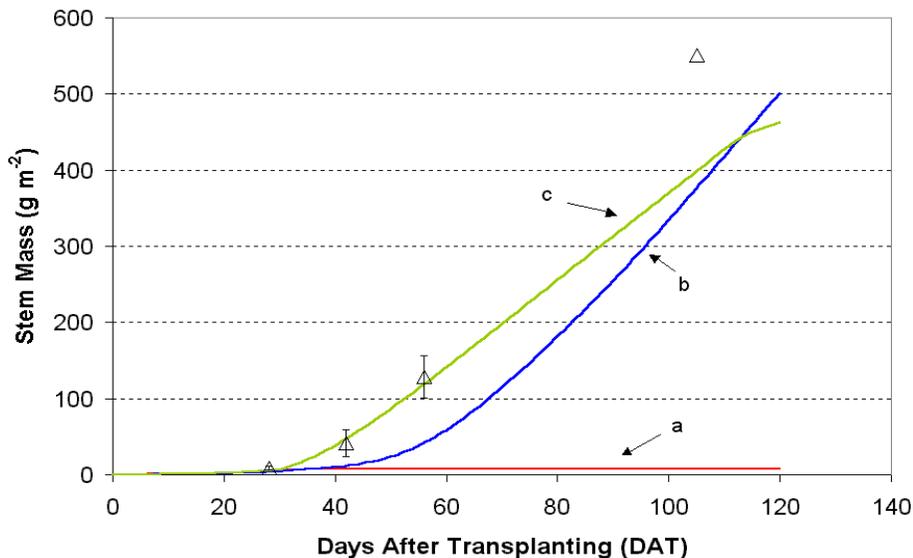


Figure 3. Modified-SUBSTOR predictions for stem dry mass. Symbols are as described in figure 1.

curve *b* largely addresses this problem; the higher daily carbohydrate fixation satisfies both tuber (fig. 2) and canopy growth (fig. 1) demand. However, there is a significant time-lag in canopy development until DAT 105 (figs. 1, 3, and 4). The increase in LALWR in curve *c* largely addresses this problem. Comparisons between simulated and experimental data over time were favorable for curve *c*: at harvest (DAT 105), deviation from the observed leaf, stem, senesced leaf, and tuber dry masses were less than 1%, -28%, -5%, and 11%, respectively. The higher deviation for stem mass (-28%) was most likely due to the model partitioning more carbohydrate to the root zone. Another explanation may be that higher nitrogen levels, such as those used in controlled-environment experiments, favor vegetative growth (such as shoot growth) over tuber growth (see, for example, Krauss, 1978). There is no provision in SUBSTOR to account for this phenomenon because only nutrient deficiencies are reflected in the tuber demand for assimilates. More data would need to

be collected on nitrogen nutrition, and root, stem, and tuber mass partitioning to confirm these observations.

Modified-SUBSTOR simulations (using curve *c* modifications) were compared with growth analysis data for three Kennedy Space Center (KSC) experiments (Wheeler et al., 1996) for validation purposes (table 3). The study reported total and yield dry mass at a harvest day of 105 DAT. Each experiment used a 12-hour photoperiod, except for experiment 3, which switched from 12 to 16 hours at DAT 65. Additional experimental conditions are summarized in table 3. The results show that modified-SUBSTOR was able to simulate total dry mass and tuber dry mass at harvest (DAT 105) within 5% of observed values for experiments 1 and 2. However, total dry mass was over-predicted by 32% in the third experiment. This indicates that modified-SUBSTOR was unable to realistically simulate the growth of potato vegetative organs under the higher daily light integral (>37 mol m<sup>-2</sup> d<sup>-1</sup> PPF) provided by the increase in photoperiod in experiment 3.

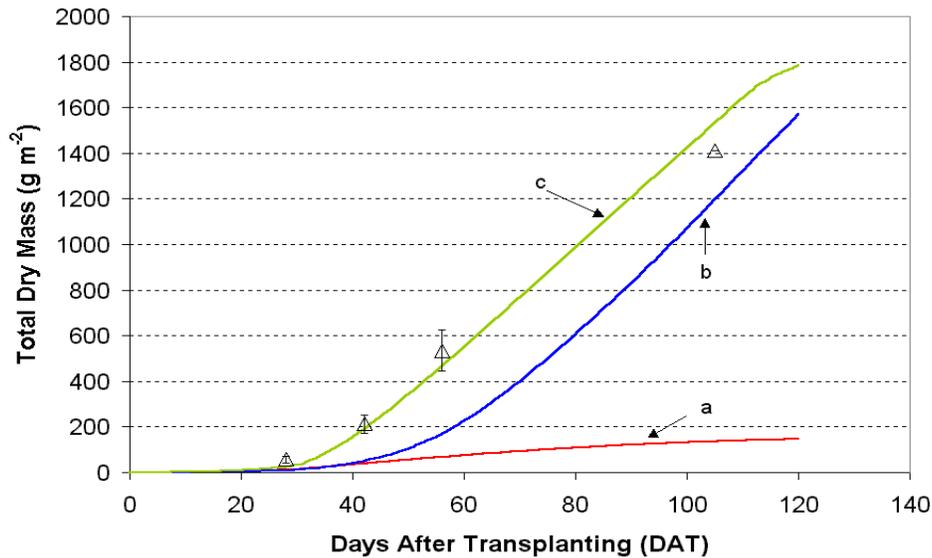


Figure 4. Modified–SUBSTOR predictions for total dry mass. Symbols are as described in figure 1.

Table 3. Verification of modified–SUBSTOR using Kennedy Space Center data (Wheeler et al., 1996).<sup>[a]</sup> A substrate PAR albedo of 0.6 was used for the white production trays used at KSC (Cavazzoni et al., 1997).

Experiment	Total Dry Mass at DAT 105 (g m <sup>-2</sup> )			Tuber Dry Mass at DAT 105 (g m <sup>-2</sup> )		
	Observed	Predicted	%	Observed	Predicted	%
1	2354	2410	+2.4	767	737	-3.9
2	2619	2612	-0.3	1134	1131	-0.3
3	2877	3795	+31.9	1754	1774	+1.2

[a] Experimental conditions were 20°C/16°C day/night temperature cycle for the first 28 DAT and then switched to 16°C. Light intensities were 655, 866, and 849  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPF for experiments 1, 2, and 3, respectively. Atmospheric carbon dioxide concentration was maintained at approximately 1000  $\mu\text{mol mol}^{-1}$ . Twelve-hour photoperiods were used except in experiment 3, where the photoperiod increased to 16 hours after DAT 65.

Existence of a feedback mechanism for controlling leaf carbon assimilation under higher daily light integrals was suggested by Stutte et al. (1996). Their work showed that photosynthetic rates under conditions of high irradiance, elevated carbon dioxide, and high photoperiod (>12 h) decreased below those measured at shorter photoperiods. Since light response curves for  $A_{net}$  for white potato were linear for the irradiance range used in their experiment, the cause for this phenomenon was believed to relate to the limiting rate of carbon unloading in the leaves. Another possibility may be related to observations of leaf damage and decline in  $A_{net}$  when the photoperiod was switched from short to long photoperiods (Wheeler et al., 1996; Stutte et al., 1996). Such injuries may be related to photo-inhibitory damage from exposure to high daily integrals. Further improvement of the SUBSTOR model should focus on evaluating and modeling effects of carbohydrate partitioning under high daily light integrals as this may relate to the inability of the products of photosynthesis to be transported out of the leaf. Any such mechanisms will be important to elucidate and quantify for future modeling work on potato, and its absence from modified–SUBSTOR may explain the over–prediction of plant dry mass at the higher daily light integrals of experiment 3.

## CONCLUSIONS

Modifications implemented to the DSSAT crop model SUBSTOR allowed simulation of white potato growth in hydroponic systems in controlled environments with elevated carbon dioxide concentration. Modifications were based on experimental growth and development data and modeling literature and included coefficient and parameter calibration and the adaptation of various subroutines. The most significant model changes included altering the daily growth routine from an intercepted to absorbed light basis, modifying the radiation use efficiency value, and calibrating the leaf area to leaf weight ratio. Modified–SUBSTOR outputs for total biomass and yield were compared with data from Kennedy Space Center. Results showed the model accurately predicted total biomass and yield at harvest for the following range of inputs: 400 to 900  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPF, 16° to 18° C air temperature, 12–hour photoperiod, 1000  $\mu\text{mol mol}^{-1}$  carbon dioxide concentration, and a planting density of 4.6 to 5 plants  $\text{m}^{-2}$ .

Modified–SUBSTOR may be used to aid analysis and optimization of potato growth in controlled environments for use in NASA’s Advanced Life Support Systems research program and commercial seed growers. Future efforts should focus on quantifying effects of photoperiod on long–term photosynthetic rates, carbohydrate partitioning from the leaves, and crop development. Such changes will extend the useful range of model predictions and more accurately simulate effects of carbon dioxide concentration and light intensity on potato plant growth.

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## REFERENCES

- Boote, K. J., and N. B. Pickering. 1994. Modeling photosynthesis of row crop canopies. *HortScience* 29(12): 1423–1434.
- Bugbee, B. 1994. Effects of radiation quality, intensity, and duration on photosynthesis and growth. In *International Lighting in Controlled Environments Workshop*, 39–50. T. W. Tibbitts, ed. NASA CP-95-3309. Kennedy Space Center.
- Cavazzoni, J., T. Volk, and G. Stutte. 1997. A Modified CROPGRO model for simulating soybean growth in controlled environments. *Life Support and Biosphere Sci.* 4: 43–48.
- Ewing, E. E., W. D. Heym, E. J. Batutis, R. G. Snyder, M. Ben Khedher, K. P. Sandlan, and A. D. Turner. 1990. Modifications to the simulation model POTATO for use in New York. *Agric. Syst.* 33(2): 173–192.
- Fleisher, D. H. 2001. Crop modeling for multiple crop production and control for advanced life support systems. PhD diss. New Brunswick, N.J.: Rutgers University.
- Goudriaan, J. 1988. The bare bones of leaf–angle distribution in radiation models for canopy photosynthesis and energy exchange. *Agric. and Forest Meteorology* 43(3): 155–169.
- Henninger, D. L. 1989. Life support systems research at the Johnson Space Center. In *Lunar Base Agriculture: Soils for Plant Growth*, 173–191. D. W. Ming and D. L. Henninger, eds. Madison, Wisc.: ASA.
- Hussey, G., and N. J. Stacey. 1981. In vitro propagation of potato. *Annals of Botany* 48(6): 787–796.
- Krauss, A. 1978. Tubercization and abscisic acid content in *Solanum tuberosum* as affected by nitrogen nutrition. *Potato Res.* 21(3): 183–193.
- Mackowiak, C. L., and R. M. Wheeler. 1996. Growth and stomatal behavior of hydroponically cultured potato (*Solanum tuberosum* L.) at elevated and super-elevated CO<sub>2</sub>. *J. Plant Physiology* 149(3): 205–210.
- Ng, N., and R. S. Loomis. 1984. Simulation of growth and yield of the potato crop. Simulation Monographs. Wageningen, The Netherlands: Pudoc.
- Ritchie, J. T., T. S. Griffin, and B. S. Johnson. 1995. SUBSTOR: Functional model of potato growth, development, and yield. In *Modelling and Parameterization of the Soil–Plant–Atmosphere System: A Comparison of Potato Growth Models*, 401–434. P. Kabat, B. Marshall, B. J. van den Broek, J. Vos, and H. van Keulen, eds. Wageningen, The Netherlands: Wageningen Press.
- Stutte, G. W., N. C. Yorio, and R. M. Wheeler. 1996. Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *J. American Society of Horticultural Science* 121(2): 264–268.
- Thimijan, R. W., and R. D. Heins. 1983. Photometric, radiometric, and quantum light units of measure: A review of procedures for interconversion. *HortScience* 18(6): 818–822.
- Thornley, J. H. M., and I. R. Johnson. 1990. *Plant and Crop Modelling: A Mathematical Approach to Plant and Crop Physiology*. Oxford, U.K.: Clarendon Press.
- Tibbitts, T. W., W. Cao, and R. M. Wheeler. 1994. Growth of Potatoes for CELSS. NASA Contractor Report 177646, Contract NCC2-301. Moffett Field, Cal.: Ames Research Center.
- Tubiello, F. 1995. Simulation of the effects of carbon dioxide, climate change, and controlled environments on wheat growth and development. PhD diss. New York, N.Y.: New York University.
- Wan, W. Y., W. Cao, and T. W. Tibbitts. 1994. Tuber initiation in hydroponically grown potatoes by alteration of solution pH. *HortScience* 29(6): 621–623.
- Wheeler, R. M., C. L. Mackowiak, J. C. Sager, W. M. Knott, and C. R. Hinkle. 1990. Potato growth and yield using nutrient film technique (NFT). *American Potato J.* 67(3): 177–187.
- Wheeler, R. M., T. W. Tibbitts, and A. H. Fitzpatrick. 1991. Carbon dioxide effects on potato growth under different photoperiods and irradiance. *Crop Science* 31(5): 1209–1213.
- Wheeler, R. M., C. L. Mackowiak, G. W. Stutte, J. C. Sager, N. C. Yorio, L. M. Ruffe, R. E. Fortson, T. W. Dreschel, W. M. Knott, and K. A. Corey. 1996. NASA's biomass production chamber: A testbed for bioregenerative life support studies. *Advances in Space Research* 18(4/5): 215–224.