Simulation of potato gas exchange rates using SPUDSIM

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ABSTRACT
SPUDSIM was developed from the model SIMPOTATO to incorporate mechanistic approaches for simulating photosynthesis and canopy growth and development needed to improve modeling accuracy for studies involving nutrient/water stress and climate change. Modifications included routines for simulating individual leaf appearance rates and leaf expansion as a function of leaf physiological age and plant assimilate status. Coupled sub-models for leaf-level photosynthesis, transpiration, and stomatal conductance were used to replace the older radiation efficiency approach. A radiation transfer routine that estimated diffuse and direct-beam photosynthetically active radiation for sunlit and shaded leaves was also added. During each time increment, net photosynthetic rate was estimated for sunlit and shaded leaf area. Photosynthate was partitioned among leaves in the canopy according to leaf age, potential expansion, and plant assimilate status. Assimilate allocation to branches, roots, and tubers proceeded according to partitioning coefficients defined in the original model, SIMPOTATO. Remaining photosynthate was stored in the canopy and, when accumulated over a threshold amount, reduced leaf-level photosynthetic rate via feedback inhibition. Whole plant gas exchange and harvest data from SPAR (soil–plant–atmosphere research) chamber experiments conducted at USDA-ARS, Beltsville, MD were used to evaluate SPUDSIM predictions over a broad range of temperatures from 12.6 to 32.3 °C (24-h average basis). An additional independent SPAR chamber dataset was used to parameterize SPUDSIM crop coefficients. Root mean square error (RMSE) was less than 0.29 mol CO2 m-2 s-1 for seasonal daily net assimilation rates and indices of agreement (IA) were 0.80 and higher except at the 32.3 °C study (0.62). Comparison of canopy photosynthetic rates at four different days indicated the model slightly under-predicted leaf area early in the season and over-predicted later in the season. IA and RMSE for leaf-level photosynthetic rates were above 0.88 and less than 1.6 μmol CO2 m-2 s-1 respectively for all studies except the 32.3 °C (0.61 and 3.8 μmol CO2 m-2 s-1). Dry matter predictions fell within two standard deviations of measured values for most plant organs at harvest. Overall, these results indicated that SPUDSIM accurately captured potato growth and development responses over a wide-range of temperatures and will be suitable for a variety of applications involving complex soil–plant–atmosphere relationships.

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1. Introduction

The United States is the 5th largest potato growing country in the world, producing 19.7 million metric tons on 453,000 ha in 2006 (USDA, 2007). As with other agricultural crops, there are significant risks and challenges involved in potato production due to uncertainties with climate, pests, and other pressures. As operations increase in size and complexity, farmers are required to manage, interpret, and make decisions upon large amounts of information. Fluctuating market prices, costs of fertilizers, pesticides and irrigation, environmental impact concerns from agricultural practices, land-use pressures, and projected climate change factors create additional demands on farmers, crop consultants, policy planners and scientists. Over the past 40 years, computer models have been developed that attempt to mimic crop responses to climatic and management factors. Mechanistic process-level crop models are needed to encapsulate knowledge on the soil–plant–atmosphere system, test hypotheses, evaluate the behavior of complex agricultural systems, and study alternative production scenarios under different climatic, management, and geographic locations (Reddy and Reddy, 1998). These models, frequently referred to as 'explanatory', are integrated with computerized decision support systems to help manage and interpret large amounts of complex information in order to help farmers reduce risk (Uehara and Tsuji, 1998; Timlin et al., 2002; Wang et al., 2002). Many explanatory crop models are still at an
early stage of development and do not necessarily include state-of-the-art science due to (a) lack of perceived need to incorporate this new information, (b) lack of resources, or (c) other knowledge gaps that prevent adoption of new research in the models (Anbumozhi et al., 2003). By including this new information into the models, more reliable predictions of growth and development in response to climatic and nutritional stresses can be obtained.

Potato models generally simulate crop growth and development by using a ‘big-leaf’ approach. Rather than accounting for individual leaves and branches, the canopy is modeled as a single stem and leaf. Simulated canopy leaf area growth is based on environment and plant nutritional status calculated by the model (e.g. International Benchmark Sites Network for Agrotechnology Transfer, 1993; Kooman and Haverkort, 1995; Hodges, 1992; Shaykewich et al., 1998). Potential daily gains in plant dry weight are obtained by multiplying an estimate for canopy light interception by a conversion factor known as radiation use efficiency (RUE, g carbohydrate (CHO) MJ⁻¹ daily intercepted radiation). Canopy leaf area is estimated from leaf dry weight using a parameter that describes the relationship between leaf dry matter and area. Other empirical factors that approximate limiting effects of plant nutritional status, water content, and temperature modify this potential growth rate. Conceptual carbon (C) pools are used to plant leaf and stem dry mass are then computed through the use of empirical partitioning coefficients as opposed to predicting individual leaf appearance, expansion, and duration.

RUE-based models have been successfully applied to a variety of studies for many crops and are popular due to their relative simplicity. However, such models can over-estimate daily growth rate due to the non-linearity of leaf response to light (Thornley, 2002). Factors such as leaf nitrogen content, water stress, senescence, elevated atmospheric carbon dioxide concentration (CO₂) and rising air temperatures play significant roles in influencing plant photosynthetic and respiration rates that cannot be mechanically accounted for with an RUE approach (Demetriades-Shah et al., 1992, 1994). Modeling the diurnal interplay among light, temperature and leaf nutrition and water status on leaf and canopy photosynthetic rates also requires a process-level approach (Lizaso et al., 2005). Replacing RUE with a more direct simulation of leaf and canopy level gas exchange responses may help overcome such limitations (Loomis and Amthor, 1999) and improve simulation of stress and climate change.

SPUDSIM is a new explanatory-type crop model that was developed as part of a series of crop models by the United States Department of Agriculture - Agricultural Research Service (USDA-ARS) that are available under the GUICS computer software package (Timlin et al., 2002). The primary goals of these models are to evaluate production scenarios (dry matter production, nutrient and water use, soil conservation, etc.) under different management options and potential climate change effects, provide decision support for farmers and agricultural policy planners, and address additional scientific questions related to breeding, hypothesis testing, yield-gap analysis, etc. The models operate on an hourly time-step and are thus sensitive to diurnal variations in above and below ground environments.

SPUDSIM is based in large part on a series of modifications to the older potato model SIMPOTATO (Hodges, 1992). Modifications focused primarily on replacing the original ‘big-leaf’ approach to simulating the whole canopy with methods to predict the appearance and expansion of individual leaves and branches in the canopy. The RUE approach was replaced with a leaf-level coupled model for photosynthesis, transpiration, and stomatal conductance that operates on an hourly time-step. Such modifications should help improve accuracy to response and climate change scenarios but need to be validated before the model can be used in these applications.

The objective of the current work was to briefly describe these SPUDSIM modifications and validate the model’s ability to accurately simulate potato gas exchange, including seasonal canopy level photosynthetic rates, and diurnal leaf and canopy level photosynthesis and transpiration, under non-water and nutrient stress conditions. Comparisons of end-of-season simulated versus measured dry matter results from the same validation dataset were also included to further evaluate potential limitations and knowledge gaps in the model.

2. Materials and methods

2.1. Model implementation

SPUDSIM was coded using C++. Phenological components and carbon allocation routines were similar to those of SIMPOTATO (Hodges, 1992). Developmental progress of the plant (i.e., emergence, vegetative growth, tuber initiation, tuber bulking, and maturity) was based on thermal-time indices. Tuber initiation was simulated as a single date based on solar radiation, canopy leaf area index, nitrogen status, air and soil thermal time. Tubers and roots were simulated as a single large organ. In both models, carbon allocation to stem, roots and tubers was based on leaf growth, developmental stage, and plant carbon/nutrient/water status. Crop coefficients (Table 1) accounted for differences in potato cultivar sensitivity to environmental and nutritional factors. They primarily affected tuber initiation and allocation of carbon among vegetative and tuber organs.

SPUDSIM was integrated with 2DSOIL, a modular comprehensive soil model that simulates water, heat, and gas movement as well as plant root activity in a two-dimensional profile (Timlin et al., 1996). The basic weather data needed to run SPUDSIM included hourly values of solar radiation, air temperature, relative humidity, rainfall, and CO₂. For this study, measured hourly environment data recorded in the growth chambers were used. Management inputs included planting and emergence date, planting density and depth, seed reserve at planting, row spacing, cultivar, amount, type and incorporation depth of crop residue, and in-season fertilization and irrigation information. Soil inputs included parameters for the soil water retention and hydraulic conductivity (van Genuchten, 1980), initial volumetric water contents, mineral ammonium and nitrate concentrations, and soil pH of each user defined soil horizon.

At each hourly time-step, appropriate input data were transferred from 2DSOIL to SPUDSIM from which water and nutrient uptake, plant development, gas exchange, carbon allocation, and organ initiation were simulated (Fig. 1). Model iterations continued until either harvest date, maturity date, or other user-specific end point was reached. Model outputs include dry weights of all organs, transpiration and photosynthetic rate, assimilate status, leaf and lateral branch numbers, and leaf area index. Major differences between SPUDSIM and SIMPOTATO for describing canopy architecture and light interception and gas exchange were detailed below.

2.1.1. Canopy architecture

SPUDSIM simulated the appearance of individual leaves (Fleisher et al., 2006a) and their expansion rates (Fleisher and Timlin, 2006) on potato mainstems and lateral branches. Leaf appearance rate followed a non-linear response with temperature (Eq. (1)) with rates accumulated at an hourly basis using the previous 24-h average air temperature. As implemented in the model, leaves could appear on any lateral or mainstem branch i.e., each branch accumulated leaf appearance rate separately, as long as sufficient plant assimilate supply was available to support the
The appearance of lateral branches was assumed to have the same temperature response.

\[
r = R_{\text{max}} \left( \frac{T_{\text{max}} - T}{T_{\text{opt}} - T_{\text{opt}}} \right)
\]

where \( r \) – leaf appearance rate (leaves branch\(^{-1}\) d\(^{-1}\)); \( R_{\text{max}} \) – maximum leaf appearance rate (leaves branch\(^{-1}\) d\(^{-1}\)), 0.96; \( T_{\text{max}} \) – ceiling temperature where \( r = 0 \), 39.5 °C; \( T_{\text{opt}} \) – optimum temperature where \( r = R_{\text{max}} \), 27.2 °C; \( T \) – average daily temperature from previous 24 h (°C).

Individual leaf expansion rate was modeled using a modification of an organ expansion routine introduced by Ng and Loomis (1984) and adapted by Fleisher and Timlin (2006). The routine simulated individual leaf expansion primarily as a function of genetic potential and temperature, with external factors for nutrient, water, and plant assimilate supplies limiting the

![Diagram](image-url)

Fig. 1. General time-step implementation of the SPUDSIM potato model. Shaded boxes indicate routines that were substantially modified from the older SIMPOTATO model.
expansion (Eq. (2)). All leaves were assumed to have the same potential to expand to the same maximum size and at the same potential rate, but actual expansion was limited during each time-step by temperature and plant assimilate supply. The expansion of each leaf was tied to carbon demand through the use of specific leaf area (SLA) fixed at 270 cm² leaf g⁻¹ dry weight for new leaf growth.

\[ R_A = A \cdot R_{\text{max}} \cdot f(\text{age}) \cdot f(T) \cdot f(C) \]  

(2)

where \( R_A \) – rate of leaf expansion [cm² d⁻¹]; \( R_{\text{max}} \) – maximum relative rate of area expansion [cm² cm⁻² d⁻¹]; \( A \) – leaf area [cm²]; \( f(\text{age}) \) – physiological age dependent expansion rate [cm² cm⁻² d⁻¹]; 0–1; \( f(T) \) – air temperature effect on cell division and expansion [unit less, 0–1]; \( f(C) \) – affect of assimilate supply on potential leaf expansion [unit less, 0–1].

2.1.2. Light interception and gas exchange

In SIMPOTATO, interception of daily photosynthetically active radiation (PAR) was estimated using the Monsi and Saeki (Hirose, 2005) approach for exponential attenuation of light in the canopy. Intercepted PAR was multiplied by RUE to estimate daily growth rate. SPUDSIM replaced this approach with a leaf-level gas exchange routine that simulated photosynthetic and transpiration rate per unit leaf area. The routine (Kim and Lieth, 2003) consisted of a coupled biochemical model of photosynthesis for C3 leaves (de Pury and Farquhar, 1997; Harley et al., 1992; Farquhar et al., 1980) with a model for stomatal conductance (Ball et al., 1987) and an energy budget at the leaf surface (Campbell and Norman, 1998). Parameters for photosynthetic capacity (maximum carboxylation rate (Vcm), potential rate of electron transport (Jm), and rate of triose phosphate utilization (TPU), were obtained from experimental data (as described in the following section). The response of these values to leaf temperature used an Arrhenius function as described in Kim and Lieth (2003).

A canopy light attenuation routine based on Sinclair et al. (1976) and Campbell and Norman (1998) estimated the hourly fraction of PAR incident on sunlit and shaded leaves within the canopy. The routine also divided the canopy into corresponding fractions of sunlit and shaded leaf area index. The sunlit/shaded canopy components vary during the day with solar elevation. Estimates of photosynthetic and transpiration rate for a representative sunlit and shaded leaf were then scaled up to the whole canopy for the current time-step.

Total photosynthetic for the hourly time-step was temporarily placed in a short-term assimilate pool. Respiration losses due to growth and maintenance for each plant organ were subsequently subtracted from this assimilate pool prior to partitioning. Growth respiration costs were fixed at 30% for stems, roots, and tubers and 40% for leaves (Ng and Loomis, 1984). Maintenance respiration was a function of temperature (Q10 factor), organ type and mass, and metabolic activity. Allocation of remaining assimilate was distributed among leaves, stems, roots, and tubers as previously described. Residual assimilate was stored in a soluble carbon reserve pool temporarily located in the leaves. Leaf SLA was allowed to vary from a maximum of 270 to a minimum of 175 cm² g⁻¹ based on the size of this pool. The build-up of carbon reserve in the leaves has been negatively correlated with declining leaf photosynthetic rate (Basu et al., 1999; Morcuende et al., 1997; Chatterton, 1973), and was included in SPUDSIM as an end-product feedback inhibition of photosynthesis. Feedback inhibition was simulated as a decrease in Vcm, Jm, and TPU that was linearly proportional to the decrease in overall canopy SLA.

2.2. Datasets and model calibration

Data from three experiments were used for (i) parameterization of SPUDSIM, including parameter estimation for the C3 biochemical sub-model and calibration of crop coefficients, and (ii) evaluation of SPUDSIM gas exchange predictions. Photosynthetic parameters for the C3 biochemical sub-model were obtained from unpublished studies in 2002 in two EGC¹ growth chambers (Environmental Growth Chambers, Inc., Chagrin Falls, OH, USA). Potato (Solanum tuberosum cv. Kennebec) was grown in 20 L pots in a peatmoss–vermiculite mixture (Jiffy Mix, Jiffy Products of America, West Chicago, IL, USA). Air temperatures were maintained at 25°C with a 14-h thermoperiod, and a photosynthetic photon flux (PPF) of 1200 μmol m⁻² s⁻¹ was provided with 50% metal–halide/50% high pressure sodium lighting via dimmer control. Pots were watered once daily and supplemented with 5–10 N-P-K fertilizer (Miracle-Gro, The Scotts Company LLC, Marysville, OH, USA) every two weeks. Starting two weeks after emergence, a portable photosynthesis system (LI-6400; LI-COR, Lincoln, NE, USA) fitted with a red/blue LED light source (LI6400-02B) mounted onto a 6-cm² leaf chamber was used to determine leaf photosynthetic rate (A) at eight different substomatal CO₂ partial pressures (Ci) for fully expanded potato leaves on eight pots (four pots per chamber) at five weekly intervals. Site elevation was 41 m and atmospheric pressure was 101.5 kPa. Saturating irradiance of 1500 μmol PAR m⁻² s⁻¹ and leaf temperature of 25°C were used when measuring these A/Ci responses. Data were pooled together and the NLIN procedure in SAS (The SAS system for Windows, SAS Inst., Cary, NC, USA) was used to derive values for Vcm25 and Jm25 following Parsons et al. (1997).

Data for crop coefficient calibration and model validation came from studies conducted in 2007 and 2004 in soil–plant–atmosphere-research (SPAR) chambers located at USDA-ARS facilities in Beltsville, MD, USA. SPAR chambers, located outdoors and transparent to sunlight, provided precise control over air temperature, humidity, CO₂, and fertigation and automatic monitoring of PAR (above and below the canopy), temperature, relative humidity, and CO₂. SPAR chambers used in these experiments were designed for pot studies and consist of a rectangular 1.1 m × 1.1 m × 2.3 m (length × width × height) Plexiglas enclosure (1 m² horizontal production area) including air handling, cooling coils, and heating elements. Each SPAR chamber formed a semi-closed system for measurement of CO₂ flux. CO₂ leakage rates were estimated on a daily basis using an N₂O tracer gas system (Baker et al., 2004). Chamber CO₂ was maintained via injection of pure CO₂ from a compressed gas cylinder to a mass flow controller (Omega Engineering, Inc., Stanford, CT, USA) located in the chamber’s air duct using a feed-forward, feedback PID control. The CO₂ concentration was maintained at setpoint during daylight hours only. At night-time, the CO₂ concentration depended on whole plant respiration and ranged between 554 and 1000 ppm as the canopy increased over time. Each chamber has a dedicated infrared gas analyzer (LI-6262, Li-Cor Biosciences Inc., Lincoln, NE, USA) that monitored the sample line at 30 s intervals. Canopy transpiration rates were measured at 15-min intervals from the amount of water vapor condensed by the chamber cooling coils and collected into a pressure transducer located at the bottom of each chamber (Timlin et al., 2007; McKinion and Hodges, 1985). Detailed physical descriptions and operational methods have been described previously (Baker et al., 2004; Kim et al., 2004).

¹ Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA and does not imply the exclusion of other available products.
the carbon content of all recovered biomass in each chamber. Such carbon ‘recovery’ checks provided a measure for the accuracy of the season and consistently indicated recovery rates of 90% and higher (not shown).

Both SPAR experiments used the same cultivar, pot sizes, and growth medium as the 2002 study. Pots were fertilized with 1/2 L one-half strength Woody’s solution (Robinson, 1984) 5× per week until harvest. Since all chambers were physically located adjacent to one another, photoperiod and daily light integrals were identical. In the 2007 experiment, treatments consisted of three different stem densities grown at ambient or elevated CO₂ concentrations. Differences in dry weights among stem densities were not observed (unpublished data) and results from the three ambient CO₂ chambers were pooled to obtain crop coefficient values.

2.3. Model validation

Gas exchange data from a 2004 Daylit temperature study experiment were used to evaluate SPUDSIM. Temperature treatments consisted of a 14 h thermoperiod at 34/29, 28/23, 23/18, 20/15, 17/12, or 14/10 °C. Harvest dates were based on canopy maturity and were conducted at DAE 49, 54, 56, 62, 62, and 63 days after emergence (DAE) as ranked from warmest to coolest temperature study. Rooting medium in each pot was gently removed and washed through a 1-mm sieve using tapwater. Leaf area was recorded for each pot and all plant organs were separated and dried to constant weight at 75 °C. The experiment was described in further detail in Fleisher et al. (2006b).

SPUDSIM was used to simulate hourly and daily (24 h) photosynthesis and transpiration using measured hourly weather data (air temperature, solar radiation, relative humidity, wind-speed, and CO₂) for each study. All model parameters were identical for each simulation (Table 1). Comparisons of simulated versus measured (a) daily net CO₂ assimilation over the course of the season and (b) diurnal variations in canopy net photosynthetic transpiration rate for select days were conducted. Deviations between measured and simulated data were quantified using root mean square error (RMSE, Eq. (3)) and the index of agreement (IA, Eq. (4)) (Willmott, 1981), which varies between 0 (poor model) and 1 (perfect model). Comparisons among measured and simulated dry matter partitioning were also conducted.

\[
\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^{n} (\text{measured}_i - \text{simulated}_i)^2}
\]

\[
\text{IA} = 1.0 - \frac{\sum_{i=1}^{n} (\text{simulated}_i - \text{measured}_i)^2}{\sum_{i=1}^{n} (\text{measured}_i - \text{measured}_i)^2}
\]

3. Results

3.1. SPUDSIM parameterization

Parameterization included estimating Vcm, Jm, and TPU photosynthetic parameters for the C3 biochemical sub-model and calibrating SPUDSIM crop coefficients. Leaf-level data from the 2002 experiment were used for deriving photosynthetic parameter values as described in the previous section. Results from the non-linear regression for Vcm and Jm, at 25 °C, are indicated in Table 1, and the corresponding curve-fitting in Fig. 2. Since a TPU limitation was not observed, a value reported by Wullschleger (1993) for potato was used.
influence on tuber initiation, and high temperatures can delay, and even prevent, tuber initiation from occurring (IBSNAT, 1993). Tuber initiation was delayed at the warmer temperatures (and never occurred in the 34/39 °C study) in both the simulated and measured data. In SPUDSIM, this delay resulted in a build-up of the carbon reserve pool, which in turn resulted in increased feedback inhibition. After tubers initiated in the 28/23 °C study (DAE 31), the new sink helped reduce the carbon reserve pool and mediate the negative feedback on photosynthesis. In addition, simulated leaf appearance rate increased at higher temperatures, and leaves continued to emerge in the canopy as long as there was sufficient carbon reserve available to support the initial mass of a new leaf. For a short-period after its emergence, a newly emerged leaf also represented an initial sink for carbon and additional storage of carbon reserve. Thus, these spikes in the simulated net assimilation data at the 28/23 and 34/29 °C studies were associated with a sudden decrease in the carbon reserve pool either as a result of tuber initiation or new leaf appearance.

Fig. 3. Comparison of daily net CO₂ assimilation rates between measured and simulated gas exchange data for six temperature studies. The daily light integral for all six studies was shown for the 17/12 °C study.
Simulated total and tuber dry mass at harvest compared favorably (within two standard deviations) with measured biomass for most temperatures (Table 4). Carbon partitioning to stems and leaves was also accurate, although stem growth was over-predicted for cooler treatments. Tuber production at the 28/23°C study and net daily assimilation rates (Fig. 3) were over-estimated towards the end of the season. In the 14/10°C experiment, leaf addition in the canopy ceased once tubers initiated, the plant then apparently shifting nearly all new assimilate to tuber growth. However, as simulated, new leaves continued to form in the canopy after tuber initiation, resulting in additional leaf area development. Leaf dry weight at harvest was slightly over-predicted (14.5 versus 12.1 ± 2.5 g plant⁻¹, Table 4) and simulated leaf area was 3803 cm² plant⁻¹ versus a measured 2580 cm² plant⁻¹. This increased leaf area resulted in the higher assimilation rates and high dry mass predictions. As noted previously, the determinacy coefficient, G1 (Table 1), influenced the simulated demand for assimilate between tubers and vegetative organs. The over- and under-predictions at cool and warm temperatures indicate there was a temperature dependency not accounted for in the parameter.

3.3. Diurnal comparisons

Comparisons among measured and simulated hourly net photosynthetic rates were conducted on four representative dates. These included two partly cloudy and sunny days (where daily

### Table 2

Index of agreement results for seasonal daily assimilation and diurnally varying canopy and leaf-level gas exchange data. Diurnal comparisons for canopy net photosynthesis (Pnet) were conducted during the early and late portions of each experiment under sunny (S = 40 mol PAR m⁻² d⁻¹) or partly cloudy (PC = 22 mol PAR m⁻² d⁻¹) conditions. Diurnal leaf-level comparisons were conducted prior to harvest. Diurnal comparisons for canopy transpiration (Trans) were conducted during mid-season under sunny and partly cloudy conditions as defined above.

<table>
<thead>
<tr>
<th>Study</th>
<th>Seasonal</th>
<th>Diurnal canopy Pnet (µmol CO₂ m⁻² s⁻¹)</th>
<th>Diurnal leaf Pnet (µmol CO₂ m⁻² leaf⁻¹)</th>
<th>Diurnal canopy Trans (mmol H₂O m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Late</td>
<td>Mid</td>
<td></td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>PC</td>
<td>S</td>
<td>PC</td>
</tr>
<tr>
<td>14/10</td>
<td>0.89</td>
<td>0.93</td>
<td>0.79</td>
<td>0.81</td>
</tr>
<tr>
<td>17/12</td>
<td>0.80</td>
<td>0.95</td>
<td>0.69</td>
<td>0.94</td>
</tr>
<tr>
<td>20/15</td>
<td>0.90</td>
<td>0.67</td>
<td>0.89</td>
<td>0.80</td>
</tr>
<tr>
<td>23/18</td>
<td>0.86</td>
<td>0.89</td>
<td>0.88</td>
<td>0.66</td>
</tr>
<tr>
<td>28/23</td>
<td>0.80</td>
<td>0.97</td>
<td>0.76</td>
<td>0.52</td>
</tr>
<tr>
<td>34/29</td>
<td>0.62</td>
<td>0.71</td>
<td>0.56</td>
<td>0.36</td>
</tr>
</tbody>
</table>

* Transpiration measurements were unavailable for this treatment due to equipment malfunction.

### Table 3

Root mean square error (RMSE) results for seasonal daily assimilation and diurnally varying canopy and leaf-level gas exchange data. Symbols and information on diurnal data as in Table 2.

<table>
<thead>
<tr>
<th>Study</th>
<th>Seasonal (µCO₂ m⁻²)</th>
<th>Diurnal canopy Pnet (µmol CO₂ m⁻² s⁻¹)</th>
<th>Diurnal leaf Pnet (µmol CO₂ m⁻² leaf⁻¹)</th>
<th>Diurnal canopy Trans (mmol H₂O m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Late</td>
<td>Mid</td>
<td>S</td>
</tr>
<tr>
<td>14/10</td>
<td>0.226</td>
<td>2.41</td>
<td>6.49</td>
<td>11.1</td>
</tr>
<tr>
<td>17/12</td>
<td>0.287</td>
<td>2.85</td>
<td>7.20</td>
<td>5.43</td>
</tr>
<tr>
<td>20/15</td>
<td>0.202</td>
<td>9.55</td>
<td>5.01</td>
<td>11.42</td>
</tr>
<tr>
<td>23/18</td>
<td>0.226</td>
<td>4.71</td>
<td>5.31</td>
<td>17.0</td>
</tr>
<tr>
<td>28/23</td>
<td>0.200</td>
<td>2.31</td>
<td>7.04</td>
<td>19.5</td>
</tr>
<tr>
<td>34/29</td>
<td>0.144</td>
<td>3.47</td>
<td>4.92</td>
<td>24.3</td>
</tr>
</tbody>
</table>

* Transpiration measurements were unavailable for this treatment due to equipment malfunction.

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* Total mass includes senesced leaf weight and soluble carbon reserve pool not indicated in the data above.
light integral was less than 22 or greater than 40 mol PAR m\(^{-2}\) d\(^{-1}\) respectively) early (DAE 19 and 26) and late (DAE 49 and 50) in the growing season. IA and RMSE results for the comparisons were shown in Tables 2 and 3 and diurnal patterns were illustrated for the 20/15 °C study (Fig. 4). In general, both IA and RMSE showed slight differences between sunny and partly cloudy days depending on early or later dates. During the early date, plant canopies had not closed yet, and IA values were slightly higher and RMSE lower, for sunny days. At later dates, when the canopy had closed, the reverse was true, particularly for the warmer temperature chambers. Also, as plants aged, IA slightly declined and RMSE increased, particularly for the warmer treatments.

Since time-series measured leaf area data were not available as inputs to the model, gas exchange predictions were highly dependent on SPUDSIM’s ability to simulate leaf area patterns correctly. We suspected the early–late, sunny–partly cloudy results were primarily due to a combination of under- and over-prediction of leaf area early and late in the season and an over-prediction of leaf-level photosynthetic rates in response to higher PAR during sunny days. Model subroutines that might have contributed to the errors included those that affect leaf area simulation, prediction of hourly sunlit/shaded irradiance and leaf area fractions, and the photosynthesis sub-model. To determine how well the model worked against data without errors introduced by leaf area predictions, leaf-level photosynthetic rates were calculated for the day prior to harvest by dividing the measured canopy gas exchange rate by the leaf area obtained at harvest (Fig. 5). IA and RMSE (Tables 2 and 3) indicated accurate predictions by SPUDSIM with RMSE less than 1.6 μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\) and IA values 0.88 and above for all treatments except 34/29 °C (note that the offset response for the 34/29 °C treatment was a result of the simulated feedback inhibition – carbon reserve was depleted during the night-time hours but increased during the day). However, it was apparent from inspection of Fig. 5 that on a leaf-level basis, simulated values responded more strongly to high irradiance than the measured values. This indicated that the leaf-level photosynthesis routine did slightly exaggerate the leaf-level response to high irradiance.

For transpiration, two diurnal comparisons were made at partly cloudy (DAE 39) and sunny (DAE 40) dates, sunny and partly cloudy as defined previously, during mid-season. Transpiration was accurately simulated during both days, with IA ranging from 0.81 to 0.97 and RMSE from 0.57 up to 1.92 (Tables 2 and 3). Diurnal patterns are illustrated for the 23/18 °C study (Fig. 6). Although there were no apparent differences in the accuracy of the simulation for the sunny or partly cloudy dates, IA increased and RMSE decreased with warmer temperatures for the partly cloudy date, indicating a better fit to the measured data. This trend reflected an under-prediction of transpiration at the 14/10 and 17/12 °C studies for the partly cloudy date (not shown) and was likely a result of SPUDSIM simulation errors with respect to leaf area production at those temperatures. Unlike the results with leaf-level photosynthesis responses, transpiration rate was not consistently biased with high irradiance.

4. Discussion

Overall, the results indicated SPUDSIM simulations were accurate with respect to the measured data. In order to use the model for case-specific studies, model users need to collect the appropriate climate, management, and soils data described in
Section 2 and calibrate the crop coefficients $A_1$ through $A_8$ and $G_1$ and $G_3$ (Table 1) for the particular potato cultivar to be studied. Coefficients are typically obtained by minimizing differences in simulated versus measured agronomic data (e.g., leaf, stem, tuber dry mass) with an independent dataset as was done for the present study (note that parameter values for leaf-level gas exchange, $V_{cm25}$, $J_{m25}$ and $TPU_{25}$, are expected to be conserved for all cultivars (Wullschleger, 1993)). Crop coefficients in explanatory crop models were intended to be independent of environment, cultural, and management effects, encapsulating only genetic differences among cultivars or varieties. In practice however, calibration of crop coefficients tends to be site-specific for most models, limiting the ability to extrapolate model predictions to other climates and management practices without additional calibration (Sinclair and Seligman, 2000; Passioura, 1996). The validation data in the current study covered a wide-range of temperatures. Since the crop coefficient values (Table 1) used in the present simulations were obtained via calibration from a separate experiment conducted at only one of these temperature studies ($23/18 \, ^\circ C$), validation of the gas exchange simulations was particularly rigorous. Overall simulation results were accurate with high $IA$ and low $RMSE$ for all studies except $34/29 \, ^\circ C$. Although potatoes are primarily grown in cooler regions, there has been some interest in higher altitude tropical production (Manrique et al., 1989), and the present results suggested SPUDSIM would be applicable over most of this range, at least in the case of non-limiting nutrients and water.

Some of the under- and over-predictions of gas exchange, and ultimately dry weights, were strongly connected to the parameter for cultivar determinacy ($G_1$). Determinacy in a crop describes the extent to which reproductive growth (such as flowering, fruit and seed-set and their growth) overlaps vegetative growth (e.g., Loomis and Connor, 1992). In general, the more determinate the crop is, the shorter the duration of overlap. This concept has been used in several potato models in addition to SPUDSIM that have the ability to simulate different potato varieties (e.g., International Benchmark Sites Network for Agrotechnology Transfer, 1993; Hodges, 1992) to quantify shifts in tuber and vegetative organ sink strength.

Fig. 5. Simulated and calculated net photosynthetic rate converted to a leaf-level basis for each temperature study prior to chamber harvest. Data points are hourly averages of instantaneous rates.
following tuber initiation. This value ranges between 0 and 1 indicating a relative scale from indeterminate to determinate variety. A completely determinate variety with a G1 coefficient value of 1 gives tuber growth 100% priority for assimilate while an indeterminate variety with a value of 0 satisfies vegetation growth demand first before allocating remaining assimilate to the tubers. A separate calibration of crop coefficients using all of the temperature data from the validation set yielded a more determinate crop with a G1 value of 0.8, instead of 0.2 (Table 1). Using that value provided even more accurate simulation results (not shown), with improved dry matter and net assimilation rate predictions at the 14/10 and 34/29 °C treatments. Ewing (1981) indicated carbon partitioning in potato is sensitive to temperature. In SPUDSIM, the demand for carbon for above and below ground organs was influenced by temperature; however, the current results indicate an additional temperature dependency in the G1 parameter not currently addressed by the model.

Although leaf-level photosynthetic rates were accurately simulated (Fig. 5), there appeared to be over-predictions to high irradiance. In SPUDSIM, the same values for the leaf-level photosynthetic parameters were used for representative leaves from sunlit and shaded classes. Thus, photosynthetic capacities of sunlit or shaded leaves were not accounted for. However, photosynthetic capacity is expected to decline with canopy depth, in large part associated with exponentially decreasing leaf nitrogen content (e.g. Hikosaka and Hirose, 1998). Not accounting for the reduced capacity of shaded leaves during mid-day likely resulted in the over-estimate observed in Fig. 5.

Many potato models increase RUE following tuber initiation (e.g. IBSNAT, 1993; Hodges, 1992) based on observations that photosynthesis and net assimilation appeared higher following tuber initiation (Sale, 1973). In this case, it has generally been argued that the presence of tubers provided a type of positive feedback control on photosynthetic rate (Moorby, 1978). However, since RUE-based approaches do not couple daily assimilation rate with growth demand, mass balancing issues can occur. For example, in models such as SUBSTOR and SIMPOTATO, when extra assimilate exceeded 10% of the haulm weight, it was removed from the model. From our measurements of leaf-level photosynthesis, differences in photosynthetic parameter values prior- and post-tuber initiation have not been observed (not shown). However, various authors have reported evidence of end-product feedback inhibition on photosynthesis in plant leaves (Basu et al., 1999; Morcuende et al., 1997) which, in potato, was apparently mediated to some extent by appearance of tuber and fruiting sinks (Tekalign and Hammes, 2005; Basu et al., 1999). In SPUDSIM, we coupled this effect with changes in leaf SLA based on Bertin et al. (1999) in which structural leaf mass and mobile carbon assimilate pool vary in response to the sink-source balance in the plant. The use of this feedback approach helped mass balance the model and provided accurate simulation results without resorting to the need to inflate the photosynthetic parameters. However, based on the results at higher temperatures, particularly at 34/29 °C where the leaf-level photosynthetic response was strongly mediated by feedback (Fig. 5), the mechanism appeared to cover-up for over-predictions in leaf-level photosynthetic rate. Nonetheless, this approach may be a more robust method for simulating climate change effects on seasonal plant photosynthetic rates than RUE-based approaches as it accounts for possible inhibitory effects of excess plant carbon status on potential growth.

One of the main purposes for developing SPUDSIM was to provide a robust model capable of accurate climate change simulations that could be adapted to various regions and management routines with a minimum of calibration. The evaluation of seasonal assimilation and diurnal photosynthetic rates indicated the gas exchange component of SPUDSIM was accurate over a wide-range of temperatures, at least at ambient CO2. The incorporation of leaf-level canopy growth and development routines, and replacement of the RUE approach with a state-of-the-art leaf-level gas exchange/energy balance approach, provided a platform from which more recent knowledge on the response of various plant processes to nutrient and water stress can be included, and similar approaches have begun to appear in other models (e.g. Alagarswamy et al., 2006; Lizaso et al., 2005). The canopy simulation of transpiration rate (Tables 2 and 3 and Fig. 5) indicates SPUDSIM can accurately simulate water use, although further testing with field data is required. Additional steps for linking the photosynthetic routine with plant nitrogen and water status, and their uptake from the soil, are currently underway. The integration of SPUDSIM with the 2DSOIL two-dimensional soil simulator (Timlin et al., 1996) will permit evaluation of complex soil-plant-atmosphere system issues in an in-depth basis. These include the impact of climate change, cropping rotations, nutrient dynamics and movement in soil, water usage and drought responses, and assessment of conservation practices on soil health.

5. Conclusion

SPUDSIM is a new USDA-ARS potato model that incorporated recent advances in individual leaf appearance, growth, and gas exchange. These modifications essentially replaced the big-leaf, radiation use efficiency (RUE) approach used in older potato models with a more mechanistic depiction of canopy growth and development. Specifically, routines for individual leaf appearance rates and individual leaf expansion were developed using experimental data. A biochemical model of photosynthesis, stomatal conductance, and transpiration were coupled and
incorporated in SPUDSIM to predict photosynthetic rate and transpiration for both shaded and sunlit leaves in the potato canopy. Comparison of SPUDSIM predictions versus gas exchange and dry mass data indicated the model predicts plant growth accurately over a broad range of temperatures. Planned additions to the model include components for water and nitrogen stress on gas exchange, organ expansion, and initiation, and are expected to make the model suitable for simulating off-nominal conditions typically experienced by farmers. SPUDSIM has been integrated with a two-dimensional soil simulator in order to more effectively study impacts of climate change, crop rotations, nutrient dynamics, water use, and evaluation of conservation and other management practices on soil quality.

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