



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 use 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} season^{−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

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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 for total 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 mechanistically 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, root, 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-specified 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

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