



Improving potato drought simulations: Assessing water stress factors using a coupled model



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ABSTRACT

Effective water management is important for drought sensitive crops like potato (*Solanum tuberosum* L.). Crop simulation models are well suited for evaluating water limited responses in order to provide management and phenotypic-trait recommendations for more efficient production practice. There is considerable variation in how water stress components are implemented with regards to simulating soil, plant, and atmospheric relationships, thereby influencing the utility of model recommendations. Four water-stress factors were developed and implemented in the potato model SPUDIM in order to assess the contribution each factor provided for improving modeling accuracy. Iterative comparisons versus experimental data consisting of six irrigation treatments were used. Factors included *F1*, shifts in carbon allocation among shoot and root organs based on soil moisture availability, *F2*, coupled response of leaf water potential on leaf expansion, *F3*, and on stomatal conductance, and *F4*, increased tuber sink strength. *F2* and *F3* accounted for up to 88% of the improvement in root mean square error for total biomass. However, *F1* and *F4* were necessary to accurately simulate yield. *F4* was also required to reproduce trends of increasing water-use efficiency and harvest index with declines in water availability. When the full 4-factor model was considered, simulated responses for total, leaf, stem, and tuber dry weights were within 11% of observed values. Daily comparisons for whole plant net photosynthesis and evapotranspiration indicated *F3* was required to accurately simulate water use, but was too sensitive to very low leaf water potentials. The calibration coefficients used in the model remained stable over all six irrigation treatments, suggesting the full model can be utilized to evaluate water management strategies for potato.

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1. Introduction

Potato (*Solanum tuberosum* L.) is considered drought sensitive, with yield reductions beginning at moderate levels of soil moisture deficit (Jefferies, 1987, 1993; Gregory and Simmonds, 1992;

van Loon, 1981). Methods to improve water management practice are thus critical for growers to more effectively manage their operation. Modeling approaches are well-suited to this need by providing computer-based simulation of alternate irrigation practices and schedules on crop production and water use efficiencies without requiring timely and resource intensive field experiments (e.g. Arora et al., 2013; Salazar et al., 2012; Mantovani et al., 1995). However, successful implementation of any model derived recommendation depends on how accurately the effects of drought are simulated.

Water stress begins when transpiration demand exceeds root water uptake, resulting in a loss of turgor (Saseendran et al., 2008). Subsequent short- and long-term responses include declines in cell enlargement and leaf expansion rate, reduced photosynthesis and transpiration, and alterations in phenology, senescence, carbon allocation, and ultimately yield and water use efficiency. These responses are typically modeled for potato as four distinct factors: (*F1*) a shift in carbon allocation priority from haulm (leaf

Abbreviations: A_{daily} , daily whole plant net photosynthetic rate ($\text{mol CO}_2 \text{ plant}^{-1} \text{ d}^{-1}$ or $\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$); A_{season} , whole plant net photosynthetic rate aggregated over the total experimental season ($\text{mol CO}_2 \text{ plant}^{-1} \text{ season}^{-1}$); CO_2 , atmospheric carbon dioxide concentration (Pa); ET_{daily} , daily evapotranspiration or water demand (mm d^{-1}); ET_{season} , evapotranspiration or water demand aggregated over the total experimental season (mm season^{-1}); HI, harvest index (g tuber g^{-1} total); WUE, water use efficiency on either total or tuber mass basis (g L^{-1}); ψ_L , bulk hourly leaf water potential (MPa); ψ_{Ld} , bulk bre-dawn leaf water potential (MPa).

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and stem) to root, (*F2*) a reduction in plant growth rate, usually handled as a limitation in canopy expansion, (*F3*) a reduction in daily carbon gain, simulated as either a decline in radiation use efficiency or photosynthetic rate, and (*F4*) an increase in the tuber induction potential or, should tubers already have been formed when the stress occurs, an increase in demand for carbon for tuber bulking. SIMPOTATO (Hodges, 1992), SUBSTOR (IBSNAT, 1993), and LINTUL (van Ittersum et al., 2003) potato crop models use 24-h time-steps and are radiation use efficiency based in which increases in dry matter are linearly related to intercepted solar radiation. More mechanistic approaches such as SPASS (Gayler et al., 2002), WOFOST (de Koning et al., 1995), and POTATO (Ng and Loomis, 1984) use a non-linear relationship between irradiance and canopy photosynthesis to estimate daily carbon gain.

Direct linkages between photosynthesis (or carbon gain) and transpiration are not incorporated in these models, and plant water demand and water status are estimated based on ratios between simulated root water uptake and evapotranspiration demand. Thus, these models generally use empirical factors based on this ratio to reduce *F1* and *F2*, and adjust *F3*. However, there is a growing body of literature suggesting that models can be improved by explicitly accounting for the coupling between leaf or canopy energy balance and associated gas exchange processes (Boote et al., 2013; Egea et al., 2011; Yang et al., 2009a,b). These coupled approaches can simulate interactions among atmospheric conditions, soil water status, and crop photosynthesis and transpiration rates on a more detailed process level, thereby providing more fundamental insights into simulation of drought effects on plant growth processes. Such linkages can provide the opportunity to simulate and test various concepts regarding effects of water stress at the process level, particularly for *F2* and *F3*. For example, Tuzet et al. (2003) demonstrated the use of bulk leaf water potential (ψ_L) of the plant canopy as a signaling mechanism between root and soil water status to reduce stomatal conductance in coupled energy balance models. In this context, instead of implementing factor *F3* as an empirically derived value that directly reduces daily carbon gain or photosynthetic rate, factor *F3* describes a physiologically based approach for reducing photosynthetic rate via regulation of stomatal conductance. Similar concepts were demonstrated for linking predawn leaf and soil water potentials as a hydraulic signal for water stress and leaf expansion rate (Chenu et al., 2008; Tardieu et al., 2000). Both approaches were successfully implemented in the corn model MAIZSIM, which employs a gas exchange coupling (Yang et al., 2009a,b). Similar approaches for linking photosynthesis, transpiration, stomatal conductance, leaf turgor pressure and dawn values for soil matric potential were successfully implemented in the soybean model GLYCIM (Acock et al., 1985), suggesting there is potential for their adoption for mechanistic modeling of other crops.

Modeling shifts in carbon allocation in response to water stress is most frequently handled via simple changes in partitioning coefficients in which root growth is increased by a specified amount, usually proportional to the meteorological factor (e.g. IBSNAT, 1993; van Ittersum et al., 2003; Hodges, 1992). An alternative approach (Acock et al., 1985) is to allow root carbon demand to adjust dynamically based on the hourly transpiration demand of the plant as well as the potential ability of increments of growth of new roots to extract enough water from the soil to meet that current demand. Under cases where soil matric potential becomes restrictive enough to reduce transpiration, carbon originally intended for new haulm growth is partitioned to roots. The result is a more dynamic shift in the carbon allocation strategy employed by the plant; however, implementation of the routine requires the ability to simulate effects of soil moisture status on stomatal closure, and transpiration rate, something that can be more realistically modeled using gas exchange-energy balance approaches. It

is noticeable that few models include an explicit increase in tuber demand during periods of water scarcity (e.g. IBSNAT, 1993; Ng and Loomis, 1984). Recent work suggests that the presence of a strong tuber sink at the time of a water stress event can help mediate photosynthetic feedback inhibition (Fleisher et al., 2008b; Basu et al., 1999). Such an approach could be incorporated in the models by linking tuber carbon demand to unallocated assimilate supply.

SPUDSIM (Dathe et al., 2014; Fleisher et al., 2010) utilizes the aforementioned coupled approach to simulate potato growth and development, but has not been fully tested for simulation of water stress. The overall goal of this research was to modify the model utilizing these more fundamental mechanisms for water stress components and indicate, via comparison against experimental data, the relative importance of including particular water stress factors on simulation accuracy. Specific objectives were to (a) describe the approaches for water stress including *F1*, dynamic allocation to the roots as in Acock et al., *F2*, the ψ_L approach for mediating leaf expansion rate based on Chenu et al. (2008) and Tardieu et al. (2000), *F3*, the ψ_L approach for regulating stomatal conductance based on Tuzet et al. (2003), and *F4*, increased allocation from the plant assimilate pool to tubers, (b) evaluate the relative performance of these stress components iteratively against experimental data, (c) conduct an in-depth comparison for selected model versions, and (d) assess the degree to which the genetic component of the model was separated from the management and environmental aspects. Findings of which water stress factor has the most impact, and alternatively, which has the least, on improving accuracy in the model can help direct further research in terms of improving water stress modeling approaches.

2. Materials and methods

2.1. Spudsim

SPUDSIM is an explanatory crop model for simulation of potato growth, development, and yield as influenced by soil, environment, management, and genetic inputs (Fleisher et al., 2010). The model was integrated with 2DSOIL (Timlin et al., 1996) to simulate root distribution and architecture, and water, solute, heat, and gas movement in a two-dimensional soil profile accounting for variations in soil properties in vertical and horizontal directions. Soil inputs include parameters for physical properties, water retention and hydraulic conductivity, volumetric water contents, and mineral ammonium and nitrate concentrations of each defined soil horizon. Environmental data include hourly air temperature, solar radiation, wind speed, CO₂, relative humidity, and precipitation. Management inputs include latitude, longitude, elevation, planting and emergence date, planting density and depth, initial seed mass, row spacing, cultivar, and in-season fertilization and irrigation. Genetic components account for sensitivities to photoperiod, temperature, determinacy, and nitrogen content.

2.1.1. Growth and transpiration

An hourly time-step is used, although soil calculations can proceed at finer time-scales based on numerical convergence requirements. Photosynthetically active radiation (PAR) fluxes are partitioned for sunlit and shaded leaf classes within the canopy following de Pury and Farquhar (1997) and Campbell and Norman (1998). Diurnal variations of beam and diffuse PAR and near-infrared radiation (NIR) fractions are estimated using inputs for latitude, longitude, elevation, and time of day as in Campbell and Norman (1998), Spitters et al. (1986), and Weiss and Norman (1985). Values for CO₂, air temperature, used to simulate photosynthesis and transpiration rates diurnal variations (proceed at finer time-scales based on numerical relative humidity, windspeed, and

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