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# Modeling expansion of individual leaves in the potato canopy

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## Abstract

A model to simulate expansion of individual leaves in potato (*Solanum tuberosum* cv. Kennebec) was developed by modifying a growth simulation routine from the model POTATO. Data for model development and testing were obtained from three soil–plant–atmosphere-research (SPAR) chamber experiments. The first experiment (D1) used six SPAR chambers with treatments of 14/10, 17/12, 20/15, 23/18, 28/23, or 34/29 °C day/night temperatures (16 h thermoperiod) at an elevated atmospheric carbon dioxide concentration ([$CO_2$]) of 740 $\mu$mol mol$^{-1}$. Experiment D2 used two SPAR chambers at 23/18 °C at 740 $\mu$mol mol$^{-1}$ [$CO_2$]. Experiment D3 duplicated the temperature treatments of D1 but at ambient [$CO_2$] (370 $\mu$mol mol$^{-1}$). Potato leaf area expansion was sensitive to air temperature and [$CO_2$]. Maximum individual leaf area values were highest at cooler temperatures and elevated [$CO_2$]. Growth duration, defined as the time interval between leaf appearance and when 99% of final area was attained, was negatively correlated with increasing temperature. Growth duration increased by about 4 days at 14/10 and 34/29 °C at ambient [$CO_2$]. Temperature response and leaf physiological aging functions were developed from D1 and used to modify the existing growth model. D2 and D3 data were used to evaluate the modified model simulations during conditions of non-limited and limited carbohydrate availability. By varying an input to the model that simulates the effect of plant carbohydrate status on leaf expansion, the model was shown to be capable of reproducing leaf growth curves within 8% of the measured final area. The modified leaf expansion model is suitable for integration with existing potato models that simulate canopy leaf appearance. The expansion model provides an approach for coupling plant assimilate, water, and nutrient status with canopy expansion and the new response functions in the model can potentially be modified for use in different crop models.

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## 1. Introduction

Appearance, expansion, and duration of individual leaves are critical determinants of potato canopy growth and development. Potato models typically simulate canopy development as an overall increase in leaf area index instead of focusing on individual leaves (e.g. IBSNAT, 1993; Kooman and Haverkort, 1995; Shaykewich et al., 1998). However, potato crop model predictions in response to environment, assimilate partitioning, and nitrogen can be improved by focusing at the individual leaf level (Vos, 1995). Little efforts have focused on modeling at the leaf level presumably due to lack of suitable modeling approaches and data sets. Several recent studies have been conducted to simulate individual leaf appearance rates in potato (e.g. Cao and Tibbitts, 1995; Fleisher et al., 2006). However, work is needed to develop a mechanistic approach to simulate the expansion of these leaves once they appear in the canopy.

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The expansion of the potato canopy for several days after emergence is highly correlated with air temperature (van Delden et al., 2000; Vos, 1995). Most potato models estimate leaf area expansion rate as an exponential function of cumulative thermal time. Once a pre-defined stage of potato development is reached, a linear relationship between leaf area growth and intercepted photosynthetically active radiation (PAR) is used to predict canopy expansion (e.g. IBSNAT, 1993; Kooman and Haverkort, 1995; Shaykewich et al., 1998). Conceptual carbohydrate pools for total canopy leaf and stem mass are computed by way of empirical partitioning coefficients. Leaf carbohydrate content is derived by using a fixed ratio between leaf area to dry mass, specific leaf area (SLA; $\mathrm{cm}^2$ leaf $\mathrm{g}^{-1}$ dry mass). Thus, in order to move to an individual leaf basis, leaf expansion responses to temperature and plant assimilate supply need to be obtained.

Empirical growth curves have been used by researchers (e.g. Jefferies, 1993; Kirk and Marshall, 1992) to indicate the sigmoidal growth pattern of individual leaf area expansion versus time (Dale and Milthorpe, 1983). The CERES-Sorghum model (Ritchie et al., 1998) calculates potential leaf blade area expansion as a function of leaf tip position on the main stem and a cultivar specific maximum expansion rate using a Gompertz relationship (Thornley and Johnson, 1990) similar to Eq. (1). The estimate for leaf area is modified by empirical factors for water and nitrogen deficiencies in the plant:

$$A = A_0 \exp\left[\ln\left(\frac{A_\mathrm{f}}{A_0}\right)(1 - \exp(-D \cdot \mathrm{DAA}))\right] \tag{1}$$

where $A_0$ is the initial leaf area at appearance (0.05 $\mathrm{cm}^2$), $A_\mathrm{f}$ the final leaf area achieved ($\mathrm{cm}^2$), $A$ the leaf area ($\mathrm{cm}^2$), $D$ the decay in specific leaf expansion rate ($\mathrm{day}^{-1}$), and DAA is the days after appearance of leaf (day).

POTATO (Ng and Loomis, 1984) is one of the few explanatory type potato models that simulates individual organ (i.e. leaves, stems, roots, stolons, and tubers) growth by distinguishing between organ relative growth rate and the duration of growth. In their model, organ growth rate proceeds at a maximum relative rate, $R_\mathrm{max}$ (Eq. (2)). $R_\mathrm{max}$ is modified by the fraction or percentage of the cells in the organ capable of additional growth or expansion, $f$(age). This fraction is a function of the physiological age of the organ. The influence of air temperature on cell expansion rate, $f(T)$, modifies the organ growth at each time-step. Eq. (2) is modified by empirical factors, ranging from 0 to 1, that simulate the influence of limiting plant water, nutrient and assimilate status:

$$R = WR_\mathrm{max}\, f(\mathrm{age})\, f(T) \tag{2}$$

where $R$ is the organ growth rate (g $\mathrm{day}^{-1}$), $R_\mathrm{max}$ the maximum relative rate of organ growth (g $\mathrm{g}^{-1}$ $\mathrm{day}^{-1}$), $W$ the organ weight (g), $f$(age) the physiological age dependent expansion rate (g $\mathrm{g}^{-1}$) and $f(T)$ is the air temperature affect on cell division and expansion (unit less, 0–1).

Ng and Loomis (1984) estimated leaf area expansion by multiplying leaf growth rate $R$ (g $\mathrm{day}^{-1}$) by SLA. Empirical factors for light intensity and leaf age were used to modify the relationship between leaf area and dry mass. Due to lack of data on individual leaf expansion, response functions for $f(T)$ and physiological leaf age were derived from potato internode elongation studies and temperature responses for leaf appearance rates (Ng and Loomis, 1984). A linear relationship was used to describe the relationship between leaf physiological age and the fraction of the leaf still capable of growth ($f$(age)). $R_\mathrm{max}$ was also assumed to be the same for tubers, stems, leaves, and stolons.

In validating the model, Ng and Loomis (1984) cited these temperature-based functions as a primary reason for discrepancies between simulated and predicted leaf area. In addition, leaf growth may be more appropriately modeled on a leaf area expansion basis. Tardieu et al. (1999) and Bertin and Gary (1998) concluded that increases in individual leaf expansion were not causally connected with increases in dry mass within certain limits of whole plant assimilate supply. However, young leaves, which are incapable of producing enough photosynthate to support their own growth demand, must import carbon from other sources in the plant. These results indicate that leaf expansion in younger leaves should be modeled as an incremental increase in area rather than accumulation of carbohydrate, particularly when the assimilate supply in the plant is limiting.

Information on potato leaf expansion under non-limiting growth conditions, such as elevated atmospheric carbon dioxide concentration [$\mathrm{CO_2}$], is also needed to improve individual leaf growth simulations. Potatoes generally show a large positive response with [$\mathrm{CO_2}$] enrichment with increased yield and total mass (Collins, 1976; Wheeler et al., 1991; Yandell et al., 1988). Potato leaf sizes and total leaf mass in the canopy were shown to also exhibit a positive response (Wheeler et al., 1991) but information on individual leaf expansion is not available.

Our objectives were to (1) obtain experimental data on the time course of potato main stem leaf expansion at

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