Simulating Leaf Expansion and Canopy Development in Potato as a Function of Nitrogen and CO_2.

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Introduction

Long term growth responses to N are mainly a function of increased leaf area and light interception. Therefore, the ability to simulate the effects of nitrogen on leaf growth and canopy development is important for potato simulation models that can be used to manage nitrogen applications. Most models simulate the effects of nitrogen on canopy growth at the whole plant level, i.e., the plant is viewed as a "big leaf". Recently, more mechanistic, leaf level models of photosynthesis have been developed to better estimate carbon assimilation and evapotranspiration rates as a function of environmental and basic physiological variables. In order to scale the simulations to the whole plant level, information on the growth of individual leaves is necessary. The relationship between carbon assimilation and N uptake is further complicated by atmospheric CO_2 concentrations and the effects on carbon assimilation rate, carbon partitioning and N content in the plant. Recently, Fleisher and Timlin (2006) presented a method to simulate growth of individual leaves in a potato canopy as a function of temperature and carbon availability. The objective of this study was to quantify leaf expansion rates in potato as a function of nitrogen application rate and CO_2 level and further extend the model.

Nitrogen Uptake Measurements and Data

Data on leaf growth rates were obtained from an experiment with potato carried out in pots in outdoor daylit growth chambers. Six N levels (2 to 14 mM N) were applied with irrigation. A day/night temperature regime of 23/18 °C was maintained. We measured daily canopy level carbon assimilation, N uptake, and transpiration rates. Two CO_2 levels were used to provide differences in carbon availability, 370 and 700 umol l[-1]. Because there were only six chambers the experiments were carried out in two consecutive periods in the summer of 2005.

Figure 1. View of three of the six SPAR (Soil Plant Atmosphere Research) Units.

Mainstem leaves were selected and tagged at three to four insertion points, 6,9, 15 and if available, 18 on five plants in each chamber. Length and width were measured two times a week. Leaf addition rates were also measured. Leaves on three insertion points on the apical stem were also identified, tagged and measured.

Model Description

A Gompertz equation was fit to the leaf expansion data to smooth the data and obtain growth duration and maximum growth rate.

$$A = A_0 Exp\left[ln\left(\frac{A_f}{A_0}\right)\left(1 - exp(-D \times DAA)\right)\right] - - - - -1$$

A is area of a single leaf (cm²), A_0 is initial leaf area (0.05 cm²), A_f is final leaf area, D is decay in specific leaf expansion rate (day⁻¹) and DAA is the days after appearance of the leaf (day). The first derivative of this equation was used to describe the daily rate of canopy growth (R_{Di}) at day i. Growth duration (the time it takes the leaf to reach 95% of it's final size) and average growth rate over that period were also calculated from this equation.
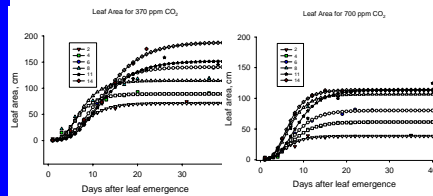

Figure 1. Measured and predicted leaf areas for leaf at insertion point 12 on the mainstem. Leaves were slightly larger for ambient CO_2 treatment (function of light?). Response to N treatments was similar for both CO_2 levels. Similar fits were obtained for the other leaves.

Relative growth rate R_R was calculated from the smoothed data as

$$L_{Ri} = \frac{1}{A_{i-1}}\left(\frac{A_i - A_{i-1}}{1}\right) - - - - - -2$$

L_{Ri} is the relative growth rate at time i. A_i and A_{i-1} are leaf areas at time i and time i-1. Relative growth rate L_{Ri} was normalized by dividing L_{Ri} by its maximum rate (L_{Ri} at time i =1). The resultant function is essentially an age correction factor that determines the proportion of the leaf that is actually growing at a time step.
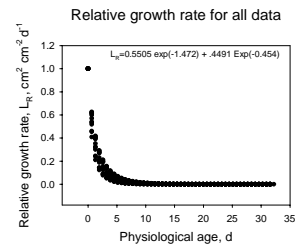

Figure 2. Relationship between leaf physiological age (scaled by temperature so that expansion is complete at 15 days after the leaf first emerges, (Fleisher and Timlin, 2006)). All data fit to one line. The coefficients of the line for these data are not significantly different from those in Fleisher and Timlin (2006) for other data sets. This relationship acts as an age factor where relative growth rate decreases as the leaf ages.

The equation to calculate leaf expansion rate at time *i* is:

$$L_i = (L_{Ri})L_{MAX}f(T)f(N) - - - - - -3$$

L_{MAX} is the maximum growth rate at the optimal temperature cm² d⁻¹, f(t) is a temperature factor (Fleisher and Timlin, 2006), and f(N) adjusts for N availability. L_{Ri} comes from Eq. 2 (Figure 2). The relationship for relative growth rate and L_{Max} were taken from Fleisher and Timlin (2006). The value for L_{Max} in Fleisher and Timlin was 10 cm². We used 8.6 cm² here.

Results from Experiments

The results are from leaf expansion data per treatment where expansion rates of leaves at insertion points 6, 9, 12 and 15 were averaged.
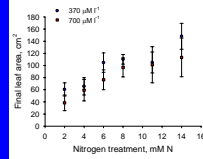

Figure 3. Mean final leaf area (WF from Eq. 1). As a function of N treatment and CO2 level. There is a threshold N rate where final leaf size is not strongly affected. The light interception data (not shown) showed a similar relationship.
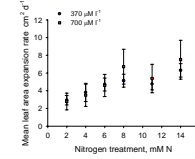
Figure 4. Mean rate of leaf expansion. This is the slope of the linear increase shown in Figure 1. There is a nitrogen effect as in final leaf size and the relationship is similar. The effect of N on leaf expansion is less at the higher N levels.

Only final leaf area and the mean expansion rated were significant functions of nitrogen treatment. The N treatment effect was larger than the CO_2 effect. The time to reach 95% of final size was highly variable and not related to N treatment.
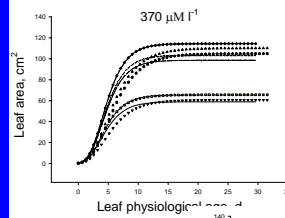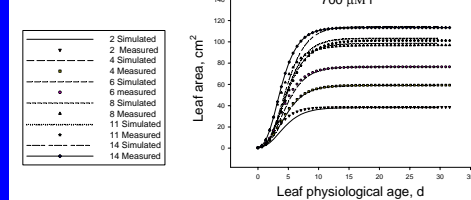
Simulations

Figure 5. Simulated and measured leaf areas. The measured data are smoothed data from the Gompertz equation (Eq. 1) averaged over several leaf insertion classes.

Values for the nitrogen function in Eq. 3 were fitted by eye for each curve. The resultant function is given in the next figure and has a similar form to the relationship between expansion rate and nitrogen treatment shown in Figure 3. The function shows slight differences in the effects of N stress between elevated and ambient CO_2 levels. However, as Figures 3 and 4 suggest, the differences may not be significant. There was also not a significant CO_2 effect on total leaf area. The leaves from the elevated CO2 treatment, although not larger, where denser, i.e., more mass per unit volume.
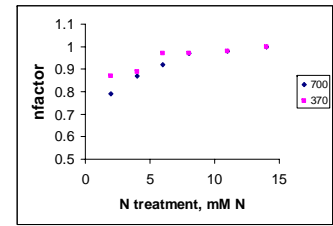

Figure 6. Fitted function to adjust expansion rate for nitrogen

The N function is purely empirical at this time and is only related to nitrogen treatment in the experiment. Further work needs to establish relationships with nitrogen uptake from the soil and nitrogen status in the plant. It does demonstrate that we can adjust the daily increment of leaf expansion for nitrogen stress. Since the age function decreases with time, the effects of N stress will also based on Eq. 3.

Summary and Conclusions

- The rate of expansion of a leaf and it's final area are functions of nitrogen availability but the growth duration is not.

- A function for leaf expansion rate that accounts for leaf age effects on growth rate with temperature and nitrogen adjustments appears to be a promising method to simulate leaf expansion in potato.

- These results were achieved by using mean expansion data from several mainstem leaves. We need to see if this can be extended to single leaves, and to apical and branch leaves.

- Carbon limitations also affect leaf expansion rates, especially for higher order leaves in potato. This also will be addressed in the model.

References

Fleisher, D.H. and Timlin, D.J. Modeling Expansion of Individual Leaves in the Potato. Canopy Agric. Forest Meteor. 139(84:93). 2006.