Modeling final leaf length as a function of carbon availability during the elongation period

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Abstract

   Each leaf is both a sink and a source of carbon that determines the growth of plant structure. Therefore, simulation of individual leaf expansion is essential in modeling plant structural growth. Leaf expansion has been often fitted to logistic sigmoidal functions that require initial and final leaf length, and duration of elongation to be known. A different method, based on the compound interest law, determines leaf length using initial length, relative elongation rate and duration of elongation. We aimed to evaluate which factors are most important in explaining final leaf length variability. Elongation of individual leaves on peach shoots was monitored over 21 days. Individual leaf lengths were fitted to logistic functions to determine their initial and final lengths, and durations of elongation in growing degree hours. Parameters that could affect final leaf length were evaluated: shoot characteristics below the leaf, initial length, duration of elongation, and temperature during the initial days after leaf appearance. Final leaf length had significant relationships with leaf area and length of the shoot axis excluding sylleptic branches, but it was not significantly related to initial length or duration of elongation. Total shoot leaf area and temperature during the initial days after leaf appearance also affected final leaf length. Our results showed that final leaf length is mainly determined by factors acting during leaf elongation. Based on these data, we used compound interest law and carbon availability concepts to develop a mechanistic model of final lengths of individual leaves.

Keywords: leaf expansion, leaf area, temperature, growing degree days, relative growth rate, *Prunus persica*

INTRODUCTION

   Modeling the source of carbon is an important aspect for simulating plant structural growth. Carbon assimilation depends on canopy leaf area, which in turn is composed of individual leaf areas. In some cases, e.g., peach trees growing in an orchard, canopy leaf area continues expanding during most of the growing season. Thus, growing leaves can be carbon sinks competing with leaf, stem, fruit and root growth as well as with carbon storage. Leaf expansion has often been fitted to logistic sigmoidal functions that require determination of initial and final leaf length, and duration of elongation. A different option is to use the compound interest law (Blackman, 1919): leaf length is determined by initial length, relative elongation rate (RER) and duration of elongation. This approach works as follows: for each time interval in growing degree days, there is a potential RER (RER_{pot}); the potential growth at a given time interval is a function of RER and current length. If this potential growth is not achieved, e.g., due to insufficient carbon, the actual length is less than the potential and the leaf will not be able to reach the final potential length for any subsequent point in time. This approach has been used to study and model fruit growth in peach (DeJong and Goudriaan, 1989) and it has been shown that limited carbon availability reduced fruit relative growth rate (Grossman and DeJong, 1995; Pavel and DeJong, 1993).

   Work on leaf size has shown that lower amounts of light produced smaller leaves (Fournier and Andrieu, 2000), fruiting plants had smaller leaves than non-fruiting plants (Greer and Weston, 2010), and larger leaves were found on longer shoots (Barlow, 1980).

These studies suggest an effect of carbohydrate availability on final leaf length. Another study found that light affects leaf expansion during the initial phase instead of during the whole leaf expansion period (Granier and Tardieu, 1999). This compares with work that predicted final fruit size using temperatures during 30 days after bloom (Lopez and DeJong, 2007), suggesting that conditions during the initial stages of organ elongation may have an important effect on organ length. However, leaves of different sizes did not show differences in initial size (Gonzalez et al., 2010) or duration of elongation expressed in growing degree days (Demotes-Mainard et al., 2013). We hypothesized that final leaf length is determined during leaf elongation following the compound interest law constrained by carbon availability.

The aim of this study was (i) to analyze if the final leaf length is determined by several characteristics of the shoot, initial length, duration of elongation, and temperature over different periods during leaf elongation, and (ii) to develop a mechanistic model to simulate final leaf length as a function of carbon availability during the elongation period following the compound interest law.

MATERIALS AND METHODS

The study was conducted in an experimental orchard at the University of California in Davis, CA (38°32'29" N, 121°47'46" W, elevation 20 m a.s.l.). Peach (*Prunus persica* L. Batsch 'Redhaven') trees were planted in 2006 at inter-plant distances of 3.5 m between N-S oriented rows and 1.8 m along rows. They were trained to an open vase system. Irrigation and fertilization were applied to avoid water and nutrient deficiency.

In each of five trees, two actively elongating shoots without fruit were selected and labelled. On each shoot two leaves were monitored every day from 30 June 2009 to 11 July 2009, and every two days from 11 July to 20 July. Leaf length was measured between 09:00 and 10:00 a.m. each day from leaf appearance (approximately 2 cm length) to the end of elongation. At the end of the experimental period, labeled shoots were cut and the following data below the monitored leaves were recorded: node number, length of each shoot, length of each leaf on the shoot (including sylleptic branches) and on the axis of the shoot (excluding sylleptic branches). A sample of leaves was used to establish relationships between leaf length, area and dry weight.

Hourly data of air temperature and solar radiation were obtained from the CIMIS (California Irrigation Management Information System). Air temperature data were obtained from the weather station of Davis (station nº. 6), located about 1 km from the experimental orchard. Solar radiation data were obtained from the weather station of Winters (station n°. 139), located about 15 km from the experimental orchard.

Growing degree hours (GDH, °Ch) were calculated as the accumulation of the temperature above 7°C h^{-1} (DeJong and Goudriaan, 1989). Elongation was characterized for each leaf using a logistic sigmoid function:

$$L_i = (L_{max} - L_{min})/(1 + \exp((t_{mid} - t_i)/k)) + L_{min} \qquad (1)$$

where L_i is leaf length at time t_i in growing degree hours, L_{min} is initial leaf length, L_{max} is final leaf length, t_{mid} is the inflexion point of the function and defines the middle of the elongation period, and k is a scaling factor. Duration of elongation was defined as the GDH required by the leaf to extend from 5 to 95% of its final elongation ($L_{max} - L_{min}$).

Using this logistic sigmoid function, we estimated the day when each leaf reached a length of 2 cm (leaf appearance). The relationship between mean temperature of a range of days starting from this time (1-20 days) and L_{max} was estimated. A coefficient of determination was calculated for each range, in order to find the number of initial days whose mean temperature had the highest correlation with L_{max}. Regression analysis was used to study the effect of different variables on L_{max}: leaf area of the shoot, leaf area of the shoot axis (excluding sylleptic branches), length of the shoot axis, temperature, initial length and duration of elongation. R statistical software (R Foundation for Statistical Computing, Vienna, Austria) was used for the analysis.

MODEL

We developed a mechanistic model of elongation of leaves competing for carbon resources at the shoot level. The model was written using L+C language and L-studio software based on the compound interest law and carbon availability for each step.

We used as inputs data of daily temperature and solar radiation corresponding to our period of measurements and data of shoot axis leaf area below the monitored/modeled leaves. A logistic sigmoid function common for all the leaves represented the potential length (see below). Initial length (L_{min}) and a scaling factor (k) were obtained from the logistic sigmoid functions adjusted to our individual leaf length measurements. Potential final leaf length (L_{max}) was determined as the maximum leaf length measured in our shoots. Using the potential length function, we calculated the potential relative elongation rate (RER_{pot}) for each leaf and time step (day) as proposed by Blackman (1919):

$$RER_{pot} = (\ln(L_{pot,2}) - \ln(L_{pot,1}))/(t_2 - t_1) \tag{2}$$

where t_1 and t_2 are times in growing degree hours at the beginning and end of the time step, $L_{pot,1}$ and $L_{pot,2}$ are potential leaf lengths at times t_1 and t_2.

Daily intercepted solar radiation was obtained from daily solar radiation data multiplied by a light interception coefficient that was considered constant for all the shoots. Individual leaf area and dry weight were calculated from leaf length. Daily net assimilation for each shoot was calculated using the method proposed by Rosati et al. (2002). We calculated a source to sink (SS) coefficient for each shoot by dividing the carbon assimilated during one time step by the carbon required for the potential increase in dry weight of leaves in that time step ($0 \leq SS \leq 1$). SS and RER_{pot} were used to calculate the elongation for each leaf and step according to the following formula (modified from Blackman, 1919):

$$L_2 = SS(L_1 \exp((t_2 - t_1) RER_{pot}) - L_1) + L_1 \tag{3}$$

where t_1 and t_2 are times in growing degree hours at the beginning and end of the time step, L_1 and L_2 are leaf lengths at times t_1 and t_2, RER_{pot} is potential relative elongation rate for that time step, and SS is the source to sink coefficient for that time step. The phyllochron was calculated from our data as the GDH between the inflexion points (t_{mid}) of two consecutive leaves in one shoot. After each phyllochron, a new elongating leaf was started with a length of 2 cm, assuming potential growth before leaf appearance.

We calculated the coefficient of determination of the 1:1 line and the percentage root mean square error (%RMSE) to compare measured final lengths of our monitored leaves with simulated final lengths of leaves growing under the same conditions of light and temperature.

RESULTS

Patterns of daily solar radiation and temperature during the leaf monitoring period are shown in Figure 1. Measurements of leaf length were significantly ($R^2>0.99$) related to time in growing degree days using logistic sigmoid functions (Figure 2). The fitted functions allowed us to determine initial leaf length and duration of elongation.

Shoots in this study had between 33 and 56 nodes below the monitored leaves, shoot length ranged between 0.61 and 1.93 m and total leaf area ranged between 1746 and 9145 cm² per shoot. Final leaf length was significantly related to leaf area of the shoot axis excluding sylleptic branches, length of the shoot axis, total leaf area of the shoot and temperature during the initial 4 days (Table 1). It was also significantly related to mean temperature during the period of 4 to 9 days after leaf appearance, but the highest coefficient of determination corresponded to the initial 4 days (data not shown). The combination of shoot characteristics and mean temperature during the initial 4 days increased the correlation with final leaf length. Shoot axis leaf area and temperature during the initial 4 days together explained 72% of the variance in final leaf length (Table 1). Final leaf length was not correlated with initial leaf length or duration of elongation (Table 1).
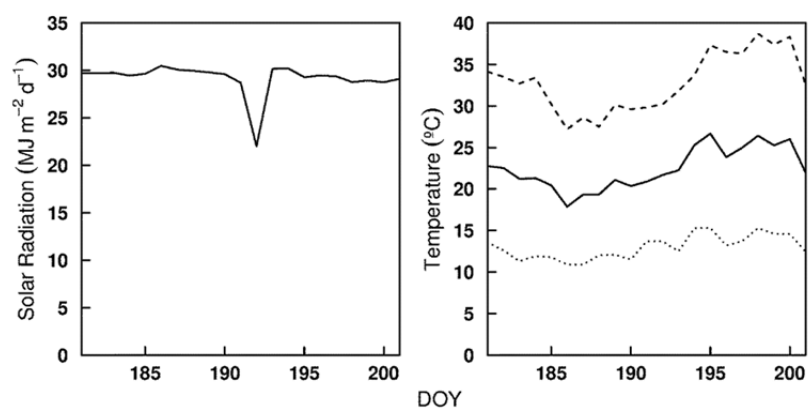
Figure 1. Patterns of daily solar radiation and daily mean (continuous line), maximum (long dashed line) and minimum (short dashed line) temperature during the leaf monitoring period.
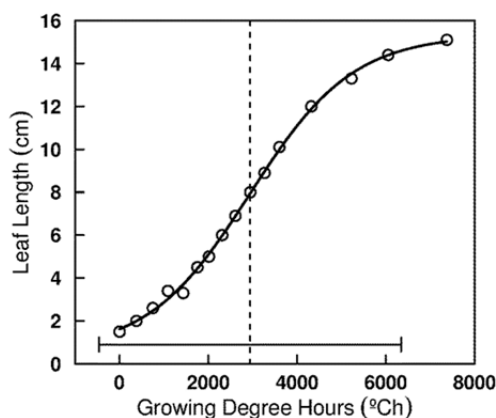

Figure 2. Individual leaf elongation in growing degree hours. Each observation (open circle) represents a length measurement of the leaf. A logistic sigmoid function was fitted to the data (continuous line). Inflexion point (t_{mid}) is indicated by a vertical dashed line. Duration of elongation is indicated by a horizontal line.

Table 1. Coefficients of determination of the regressions between the independent variables and final leaf length.

Independent variables (x)	Coefficient of determination (R^2)
Shoot axis leaf area (excluding sylleptic branches)	0.58***
Shoot axis length	0.57***
Shoot total leaf area	0.43**
Temperature initial 4 days	0.25*
Initial length	NS
Duration of elongation	NS
Shoot axis leaf area + Temperature initial 4 days	0.72***
Shoot axis length + Temperature initial 4 days	0.71***
Shoot total leaf area + Temperature initial 4 days	0.61***

Statistical significance of the regression analysis is indicated by *($P<0.05$), **($P<0.01$), ***($P<0.001$) and NS, not significant ($P≥0.05$).

Potential length and relative elongation rate (RER_{pot}) functions used in our model are shown in Figure 3. Values of leaf length simulated by our mechanistic model were significantly correlated with leaf length values measured in the field (Figure 4).
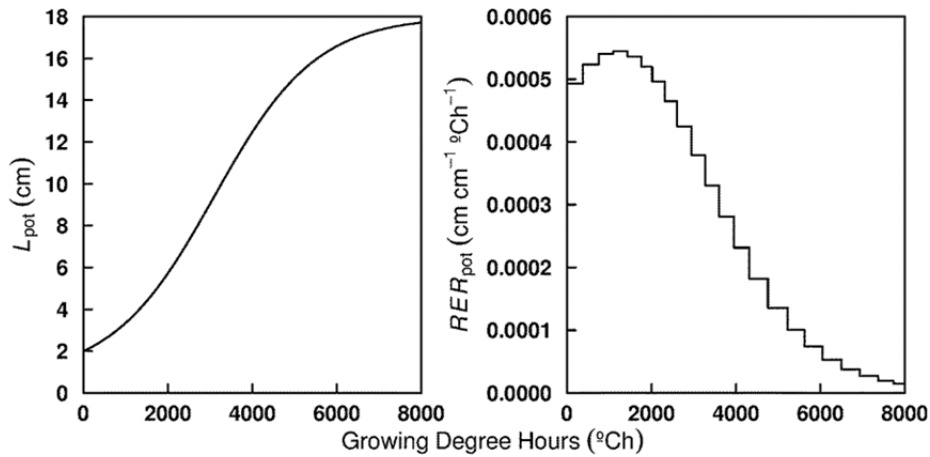
Figure 3. Potential leaf length (L_{pot}) common for all the leaves employed in our model and potential relative elongation rate (RER_{pot}) of one leaf for each time step (day).
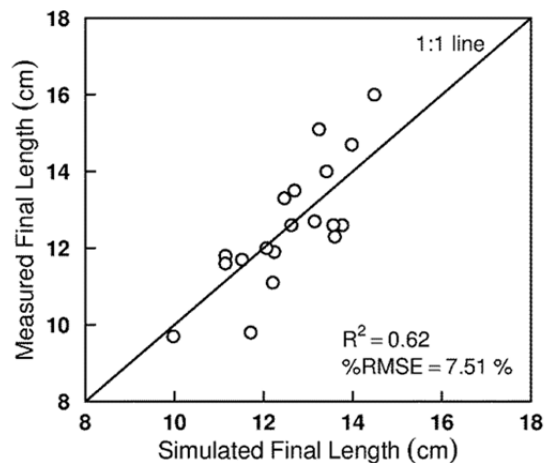

Figure 4. Relationship between simulated and measured final leaf lengths. Each observation (open circle) represents one individual leaf.

DISCUSSION

This study showed that final individual leaf length was correlated with characteristics of the shoots on which they developed. Leaf area of the shoot axis explained a high percentage of final leaf length variance (0.58), followed closely by shoot length (0.57), and with a lower percentage total leaf area of the shoot (0.43). The effect of shoot leaf area on final individual leaf length could be related to carbohydrate availability since high shoot leaf areas could photosynthesize more carbohydrates for the growth of leaves. This would agree with experiments that showed that shading and fruiting reduced final leaf area (Fournier and Andrieu, 2000; Greer and Weston, 2010). The effect of shoot length on final leaf size has been suggested previously (Barlow, 1980). In our case, shoot length was correlated with the leaf area of the shoot axis (R^2=0.80). Therefore, it appears that it is the supporting leaf area and not shoot length by itself that is the cause of variation in individual leaf size. Leaf area of the axis excluding sylleptic branches explained more variance in final leaf length than total shoot leaf area did. This could indicate branch autonomy in terms of carbohydrates in the shoot axis with respect to sylleptic branches. High branch autonomy has been previously shown at the level of scaffolds and small fruiting branches (Marsal et al., 2003) and at the fruiting-shoot level (Volpe et al., 2008).

Mean temperature during the initial 4 to 9 days of elongation was significantly related

with final leaf length. The idea that final leaf length was affected by temperatures during the initial phase of growth rather than the whole elongation period can be explained considering that RER_{pot} is highest at early stages of leaf elongation (Figure 3). Hence, conditions at that time, e.g., insufficient carbon, would have an important effect on growth, as suggested by Blackman (1919) and observed in fruit (Lopez and DeJong, 2007) and leaves (Granier and Tardieu, 1999). Final leaf length was not correlated with initial leaf length or duration of elongation in growing degree hours, in coincidence with previous studies (Demotes-Mainard et al., 2013; Gonzalez et al., 2010).

We developed a mechanistic model for simulating final lengths of individual leaves using compound interest law and carbon availability. The model explained 62% of the variance in measured final leaf lengths. This model simulated competition between elongating leaves in autonomous shoots. Incorporating competition with other organs (internodes, fruits and maybe roots), storage and respiration may improve the accuracy of the model. Also we used data from a weather station nearby, but there could be differences in local temperatures among shoots. An empirical relationship with shoot axis leaf area and temperature after 4 days predicted the final leaf length better than the mechanistic model. We think that this could be due to the fact that our model did not incorporate some effects of temperature on carbon source (photosynthesis) and sink (respiration). Water stress and nutrition could also affect leaf growth, but our peach trees were well-irrigated and fertilized. In general, our experimental results and the mechanistic model agreed and complemented each other. This combination was useful for improving our understanding of leaf and plant organ growth.

CONCLUSIONS

Final individual leaf length was correlated with leaf area and length of the supporting shoot axis excluding sylleptic branches, and, to a lesser extent, with total leaf area of the shoot and temperature during the initial 4 days after leaf appearance. The combination of leaf area of the shoot and temperature of the initial 4 days explained most of the variance in final leaf length. This agrees with effects of carbon availability on elongation following the compound interest law.

We used the compound interest law and carbon availability concepts to develop a mechanistic model of final lengths of individual leaves. Modeled leaf lengths were correlated with measured final lengths but the model did not account for all of the variation in leaf lengths measured in the field. This approach can be used for modeling individual leaf expansion, especially under circumstances that affect carbon availability, e.g., different plant spacing, light interception, vegetative vigor, crop load or training systems.

ACKNOWLEDGEMENTS

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