

# Seasonal Variability of Leaf Appearance Rate of Proleptic and Epicormic Shoots of Peach (*Prunus persica*) Grown in Normal and Deficit Irrigation Treatments

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## Abstract

Much attention is devoted to understanding whole plant physiology and the architectural manipulation of peach tree canopies to optimize yield, minimize losses and to understand developmental responses to the environment. One method to visualize and understand plant physiological responses is to synthesize field data sets into mechanistically-based computer simulation models. The L-PEACH model is a functional-structural interactive plant model that simulates 3D peach tree architecture and carbohydrate flow and distribution. The construction of this virtual tree is based on metamers, repetitive subunits defined as node+leaf+axillary meristem+internodal segments. The rate at which metamers are added over the course of a field season is very important for modeling shoot growth rates but not well established experimentally. Additionally, the canopy is composed of several shoot types that behave differently. In this 2010 California field study, we investigated seasonal patterns of leaf appearance rates (LAR), the time interval between successive leaves, in normal and deficit irrigated treatments on both proleptic and epicormic shoots of mature de-fruited trees. Leaf appearance and leaf growth rate measurements were recorded three times per week from the beginning of the season in April to the end of the growing season in late September. LAR fluctuated over the course of the season and generally slowed as the season progressed. Epicormic shoots added leaves at a significantly faster rate than proleptic shoots in both water deficit and normally irrigated treatments. Although there was a difference in stem water potential between irrigation treatments, there were no significant differences in the LAR between water treatments.

## INTRODUCTION

Peach and other stone fruits are of great economic value to the state of California, as well as many other parts of the world. Much attention is devoted to understanding whole tree physiology and the architectural manipulation of the canopy to optimize yield, minimize losses and to understand responses to our changing environment. One method to visualize and understand plant physiological responses is to synthesize field data sets into mechanistically based computer simulation models. The L-PEACH model is a 3D functional-structural interactive model of tree growth based on carbon partitioning among individual organs (Allen et al., 2005; Lopez et al., 2008; Da Silva et al., 2011).

The L-PEACH and most functional-structural plant models are constructed from metamers, repetitive sub-units defined as node+leaf+axillary meristem+internodal segments (White, 1979). When constructing a model of a growing plant from metamers, it is necessary to accurately time the appearance rate of each metamer, which is likely dependent upon a combination of genetics, environmental influences and cultural practices. The appearance rate of metamers can be represented by the leaf appearance rate (LAR) which we define here as the time elapsing between the visual appearances of two successive leaf tips. The LAR is generally thought to be constant in constant conditions (Villalobos and Ritchie, 1992), and changes with fluctuating conditions (Bertero, 2001). Previous experiments in peach show that metamer emergence (Pagès et al., 1996) and leaf emergence rate (Kervella et al., 1995) slows with thermal time over the course of the season whatever

the branching order. Having LAR values based on field data of the different shoot types that constitute the canopy of the tree is necessary for accurate growth predictions generated by the L-PEACH model.

The canopy of a peach tree is made up of three unique shoot types. Proleptic shoots are the main fruiting shoots that grow from overwintered buds (Wilson, 2000; Costes, et al., 2006). Epicormic shoots commonly called water sprouts or suckers, grow vigorously from preventitious buds, often in response to pruning or limb damage (Fink, 1983; Wilson and Kelty, 1994). These shoots are less productive in terms of fruiting and often shade out the important fruit-bearing proleptic shoots. Syleptic shoots are secondary shoots that branch from axillary meristems of current season's proleptic or epicormic shoots (Costes et al., 2006).

Environmental factors have a large influence on vegetative vigor. Plant growth is strongly influenced by temperature (Ong and Baker, 1985) and fruit tree vegetative growth is enhanced by increased irrigation (Behboudian and Mills, 1997). Seasonal effects of temperature and water relations on vegetative growth are the integrated results of many daily growth events (Berman and DeJong, 1996; Basile et al., 2003; Solari et al., 2006). These short-term interactions, when scaled over weeks to months, are important determinants of seasonal carbon partitioning trends in the L-PEACH model. Solari et al. (2006) investigated daily responses of vegetative growth to manipulation of water status of peach trees grown on different rootstocks in the field and found that relative shoot extension growth rate was linearly correlated with midday stem water potential. Solari and DeJong (2006) later confirmed that root pneumatic pressurization increased leaf water potential and relative shoot extension of peach trees on both vigorous and dwarfing rootstocks. Water stress is also an important factor controlling fruit growth (Berman and DeJong, 1996; Génard and Huguet, 1996). Thus, while it is clear that even mild plant water stress can limit expansive fruit and shoot growth in peach, less is known about its effects on rate of the addition of new plant parts, specifically shoot metamers.

As fundamental as this question is, there have been few field-based studies in woody perennials that have monitored shoot metamer appearance rate or LAR over an entire growing season and none of these integrate water relations. For modeling purposes we wish to know how LAR in peach trees varies over the course of the season and how it differs between shoot types that constitute the canopy. Because water has been previously shown to affect shoot growth we were also interested in observing water's effect at a metamer scale. In this field study, we tracked the LAR and growth rate of each leaf on selected proleptic and epicormic shoots on trees grown in normally irrigated and water deficit treatments over the entire growing season.

## **MATERIALS AND METHODS**

This research was conducted during the 2010 season at the UC Davis Wolfskill experimental orchards in Winters, CA. Four-year old peach trees of the 'Laurie May' variety (unreleased) grafted on Nemaguard rootstock growing in a sandy clay loam were used in this study. Trees were spaced 1.83 meters (m) apart in the row, with 5.18 m between rows and trained to the Kearney Agricultural Center perpendicular-V system (KACV) (DeJong et al., 1994). Nitrogen was applied twice per year, 112 kg/ha in February and 56 kg/ha in September.

### **Experimental Design**

A randomized complete block design (RCBD) with three blocks, one experimental unit per treatment block combination (normal and deficit irrigation) was set up. There were three replications of each treatment. Within each treatment were three subsamples (trees) with four shoots per tree (two proleptic and two epicormic) that were randomly selected from both the west and the east-facing sides of the tree (18 shoots per shoot type per treatment). Shoots were replaced if they became damaged or ended growth early.

### **Irrigation Regime**

Following the depletion of winter rains, normally irrigated trees were watered an average of 5.84 cm approximately every two weeks using micro sprinklers. Water deficit was attempted by entirely plugging the micro sprinklers of selected blocks. Plant water status was regularly monitored by taking stem water potential ( $\Psi_{ST}$ ) readings from each tree using a pressure chamber as described by (Mccutchan and Shackel, 1992).

### **Leaf Appearance Rate Measurements**

In order to assess the leaf growth rate and the LAR, incremental measurements of every leaf grown on selected shoots were taken using a metric ruler. These repeated measurements were collected three times a week from April 5<sup>th</sup> to September 29<sup>th</sup>. Hourly temperatures were recorded by two HOBO data loggers (Onset Computer Corporation, Bourne, MA) located in the orchard and confirmed by the local California Irrigation Management Information System (CIMIS) weather station located on site.

### **Data Analysis**

Leaf lengths recorded in the field were imported into a database, post-processed and analyzed using Python 2.7 (<http://www.python.org/>) and matplotlib library (<http://matplotlib.org/>). When taking field measurements of very small leaves it was impossible to capture the exact initiation point of the leaf without imposing damage. Additionally, the appearance of the leaf sometimes happened between days of data collection. Therefore, we normalized the leaf appearance to the time when a new leaf was 0.5 cm long. This initiation time was estimated by fitting the incremental leaf lengths, to a classical growth curve using the Gompertz model:  $y(t) = a e^{b e^{-ct}}$ , where  $a$  is defined as the upper asymptote,  $b$  is related to the speed of growth,  $c$  the lower asymptote, and  $t$  the time in hours. Once the initiation point of each leaf was established, we estimated the time interval between two successive leaves in hours. The LAR values were gathered per ten-day time interval and averaged per shoot and averaged again across shoots for any leaves initiated during each ten-day time interval. These means were then plotted to compare the LAR for different water treatments and shoot types. Analysis of variance was calculated using the means of LAR per shoot using SAS statistical software (SAS Institute Inc., Cary, NC).

## **RESULTS AND DISCUSSION**

Most studies find that the LAR is constant under a constant temperature as observed in potato (Tibbitts and Cao, 1995) and sunflower (Villalobos and Ritchie, 1992). However, in the field, there are varying environmental conditions to which the LAR will respond. In this study, LAR for both proleptic and epicormic shoots varied throughout the season (Fig. 1), indicating that LAR was not constant in field conditions and probably fluctuated due to multiple fluctuating environmental parameters. Temperature has been reported to play an important role in leaf appearance (Tibbitts and Cao, 1995; Villalobos and Ritchie, 1992) as has photoperiod and radiation (Rawson, 1993; Bertero, 2001; Pieters, 1985). However no clear relationships between temperature or radiation were apparent in our field data. Which environmental parameters play the most significant role in LAR is still unclear as there is discrepancy in the literature. Additionally, it is difficult to isolate environmental factors in field studies.

In both irrigation treatments epicormic shoots added leaves at a faster rate than proleptic shoots (Figs. 2 and 3). This is not surprising, as epicormic shoots are known to be more vigorous. Their vigorous nature allowed epicormic shoots to grow all season, while proleptic shoots stopped their growth by mid to late June.

Due to heavy rains during the previous winter (58.9 cm from September 2009-May 2010) and the efficient water holding capacity of the soil, it was difficult to achieve a large water deficit until late in the growing season after the soil water was depleted (Fig. 4). By this time in late July and early August, proleptic shoots stopped their growth and epicormic shoots were slowing down. Thus, only epicormic shoots were moderately water stressed.

Generally, epicormic and proleptic shoots grew slower (Figs. 2 and 3) in deficit irrigation treatments but these differences were not significant.

While the LAR of both shoot types fluctuated a lot over the season, there was a general tendency for LAR of both shoot types to slow down near the end of the season. These findings were confirmed by other potted tree studies on young peach trees that also reported a decrease in LAR (Kervella et al., 1995) and metamer emergence rate (Pagès et al., 1996) over the course of the season but much less variation within the season.

## CONCLUSIONS

The LAR for both proleptic and epicormic shoots fluctuated over the course of the season. This indicates that the rate of leaf appearance was not constant and reacted to the environment. More research is needed to determine which environmental parameters are most important to the LAR in peach. Due to their increased vigor, epicormic shoots had faster rates of leaf appearance than proleptic shoots. Additionally epicormic growth extended late into the season, long after proleptic shoots stopped their growth. While there were differences in stem water potential, no significant differences were observed for LAR in between irrigation treatments.

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## Figures

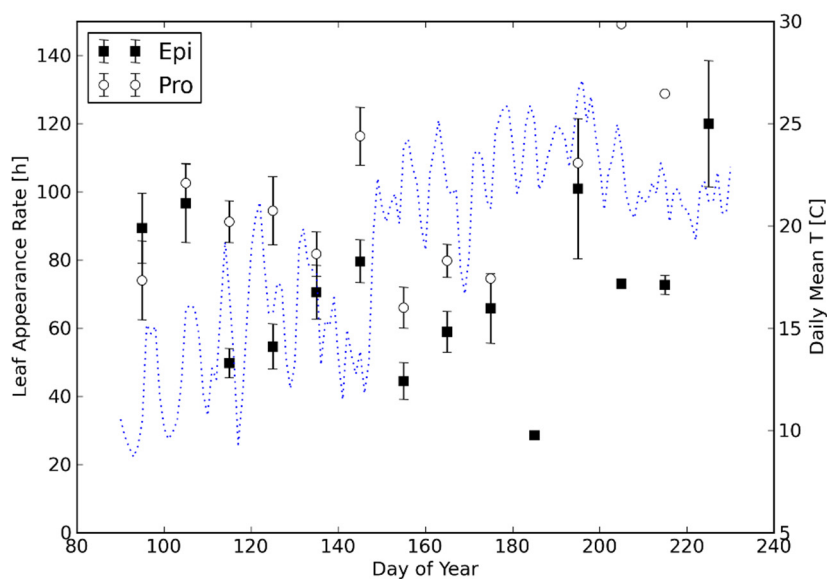


Fig. 1. Estimated mean leaf appearance rate plotted in ten-day periods for epicormic and proleptic shoots over the course of the season. Daily mean temperature is plotted as a dotted line.

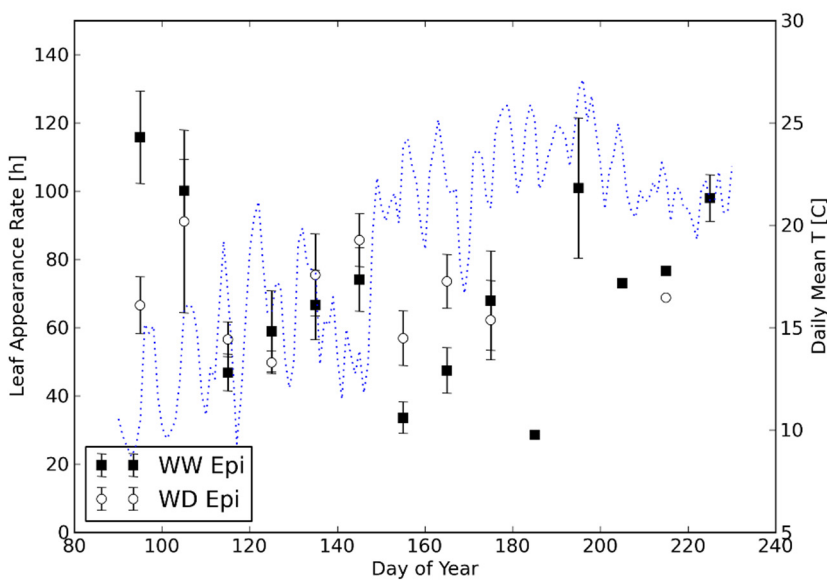


Fig. 2. Estimated mean leaf appearance rate plotted in ten-day periods for epicormic shoots over the course of the season in normal and water deficit treatments. Daily mean temperature is plotted as a dotted line.

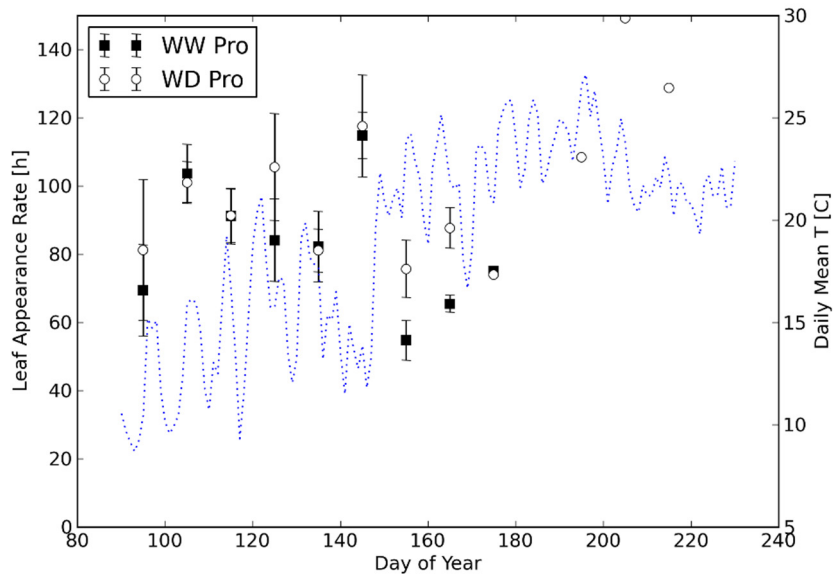


Fig. 3. Estimated mean leaf appearance rate plotted in ten-day periods for proleptic shoots over the course of the season in normal and water deficit treatments. Daily mean temperature is plotted as a dotted line.

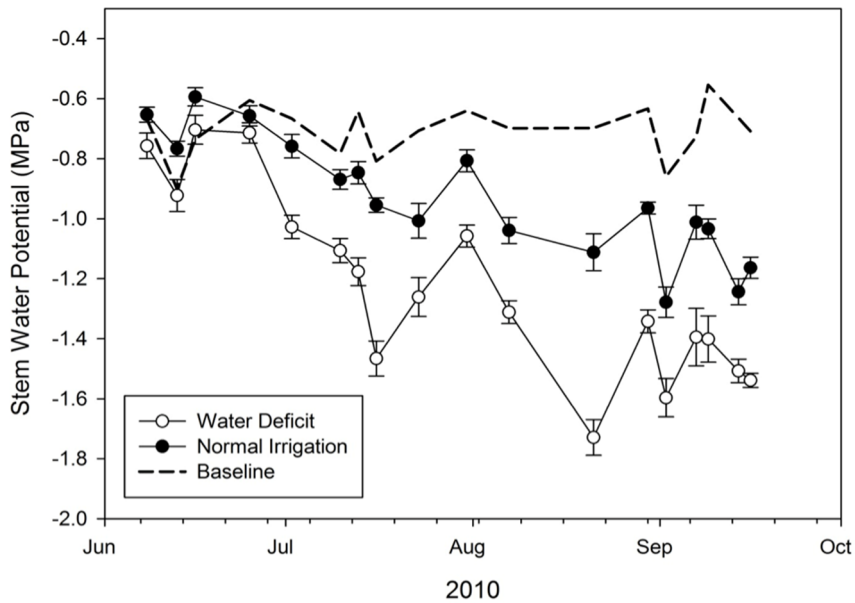


Fig. 4. Stem water potential readings for the 2010 season in normal and water deficit irrigation treatments compared with estimated baseline values that would represent no water stress.

