



Rate of shoot development (phyllochron) is dependent of carbon availability, shoot type, and rank in peach trees

Anna Davidson¹ · David Da Silva¹ · Theodore M. DeJong¹

Received: 23 October 2018 / Accepted: 12 June 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Key message Crop load or carbohydrate availability, affects the phyllochron, leaf length, and leaf area of proleptic and epicormic shoots on mature, field-grown *Prunus persica* trees.

Abstract It is well known that shoot growth rates can be strongly influenced by availability of carbohydrates to support growth. Additionally, carbohydrate availability for vegetative growth is influenced by crop load, since fruits are strong sinks for photosynthates. Thus, while crop load is known to have significant effects on shoot growth rates it is not clear whether this effect is limited to extension growth rates of internodes or whether it also affects shoot development such as the rate at which nodes are added to shoots, i.e., the phyllochron. In this study, we investigated the effect of the presence and absence of the crop on the phyllochron of proleptic and epicormic shoots on mature, field-grown peach trees. Leaf growth measurements were recorded three times per week from the beginning to the end of the growing season and used to calculate the phyllochron on trees from two treatments; one with 100% of the crop left on it (unthinned or fully cropped) and a treatment of trees where the crop was completely removed (non-cropped). The phyllochron fluctuated but generally increased over the season due to a rank effect. The phyllochron was longer on trees with heavy crop loads. Although there were large differences in phyllochrons between treatments in both shoot types, only differences observed in epicormic shoots were statistically significant. Additionally, leaf length and leaf area were also significantly reduced by crop load in both shoot types. These findings indicate that the phyllochron of field-grown peach trees is apparently sensitive to carbohydrate availability in the tree and should be considered when trying to accurately predict the timing of the addition of new phytomers along a shoot.

Keywords Proleptic · Epicormic · Cropload · Carbohydrate partitioning · *Prunus persica* · Water sprout

Introduction

Functional–structural plant models (FSPMs) can be used to integrate anatomical structure with carbon dynamics (Cieslak et al. 2011). FSPMs are computational models that simulate 3D plant architecture, as governed by physiological processes and their interactions with the environment. The L-PEACH model, a FSPM, is a virtual plant simulation model of the carbon supply and demand for reproductive and vegetative growth in peach trees (Allen et al. 2005; Lopez et al. 2008; Da Silva et al. 2011). It is based on

the hypothesis that carbohydrate partitioning is driven by competition among individual plant organs, based on each organ's growth potential (Grossman and DeJong 1994). Carbon balance models have been used to identify and understand environmental factors (Loomis et al. 1979; Penning de Vries and Van Laar 1982) and cultural practices limiting growth (Cieslak et al. 2011) of crop plants.

Development, growth and carbon allocation processes can be analyzed using FSPMs at the organ level (Cieslak et al. 2011). The L-PEACH and most functional–structural virtual plant growth simulation models (Vivin et al. 2002; Allen et al. 2005; Cieslak et al. 2011) are constructed from phytomers, also called metamers. The phytomer is comprised of the node and the tissues and organs derived from it including the leaf, axillary bud and internode (Gray 1879; White 1979). The time elapsing between the additions of phytomers can be represented and easily measured by the time of appearance of leaves at each node. The number of

Communicated by Knoche.

✉ Anna Davidson
adavidson@ucdavis.edu

¹ Department of Plant Sciences, University of California Davis, One Shields Avenue, Davis, CA 95616, USA

leaves emerged per unit of time along a shoot is termed leaf appearance rate (LAR). The inverse of LAR is termed the phyllochron, the time elapsing between the successive leaves on a stem (Wilhelm and McMaster 1995).

The phyllochron is based on growth and development, which are interactive processes resulting from interactions between genotype and environment (Lambers et al. 2008), and influenced by cultural practices. Many studies show that under constant environmental conditions, the phyllochron is constant, or linear (Fleisher et al. 2006; Raper and Thomas 1975; Cao and Tibbits 1995; Villalobos and Ritchie 1992). However, when environmental factors change, phenotypic plasticity is observed in the phyllochron and other morphological features such as leaf length or area. Temperature is considered to be the main environmental factor influencing the phyllochron in annual plants (Dennett et al. 1978; Rawson and Hindmarsh 1982) followed by photoperiod (Rawson and Hindmarsh 1992; Rawson 1993), day-length (Cousens et al. 1992; Kirby 1995), and water status (Silk 1980; Mathews et al. 1987).

Even though knowing what controls the rate of the addition of new phytomers is fundamental to understanding shoot growth, very few phyllochron studies have been conducted in woody perennials and even fewer in deciduous fruit trees. Modeling the phyllochron of trees as opposed to herbaceous annuals or monocots poses unique challenges because trees are inherently more complex. In addition to their larger size, a tree is a collection of hundreds of shoots, each with an apical meristem that generates new phytomers. A tree also initiates vegetative buds in the late summer followed by a period of winter dormancy. Gordon et al. (2006) found that in peach buds approximately the first ten leaf primordial nodes are preformed between leaf drop in the fall and bud break in the spring. Subsequent nodes are formed after bud break (neofomed), meaning their abundance is dictated by current season's conditions.

In addition, a peach tree is made up of three unique types of shoots, each behaving differently within the canopy. 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). Their growth is completely neofomed, and determined by current season's conditions. These shoots bear few fruit and often shade out the fruit-bearing proleptic shoots on a mature bearing peach tree. The third type of shoots, sylleptics, are secondary shoots that branch from axillary meristems from current season's proleptic or epicormic shoots (Costes et al. 2006).

A previous field study in peach showed that phyllochron for epicormic shoots was significantly less (leaves appeared at a faster rate) than that for proleptic shoots

(Davidson et al. 2015). This was apparently related to the more vigorous nature of the epicormic shoots. Additionally, the phyllochron for both shoot types was nonlinear when plotted against both time and thermal time (growing degree-days or growing degree-hours) and generally increased over the course of the season. Kervella et al. (1995) and Pagès et al. (1996) also reported a nonlinear gradual decrease in leaf and phytomer emergence rates, respectively (plotted in growing degree-days), as the number of leaves increased over the course of the season. They also reported significant differences between main and first order shoots of young potted peach trees. Similar patterns have been reported for leaf emergence in grapevine (Schultz 1992).

Carbohydrate availability for vegetative growth is strongly influenced by crop load (Maggs 1963; Grossman and DeJong 1995). Fruits act as strong sinks for photosynthate, particularly during the last stage of fruit growth (DeJong and Grossman 1995) and heavy unthinned cropping has been shown to reduce vegetative growth (DeJong et al. 1987; Berman and DeJong 2003). Previous studies on the effects of crop load manipulation on carbohydrate availability for epicormic shoot initiation with 13-year-old peach trees (Gordon et al. 2006; Gordon and DeJong 2007) showed significantly less total-canopy shoot dry weight was produced by fully cropped trees than by fruit thinned or defruited trees.

Earlier, Grossman and DeJong (1995) studied the presence of crop on the seasonal patterns of above-ground vegetative growth in terms of current year stem length, current year stem and leaf dry weight, and trunk radial increment and found that the presence of fruit reduced final stem length and dry weight by 43 and 56%, respectively, on a late maturing peach cultivar. However, the presence of fruit did not have detectable effects on final stem length; stem dry weight or leaf dry weight on an early maturing cultivar.

While it is evident that crop load affects the total biomass of vegetative growth (Berman and DeJong 2003; Grossman and DeJong 1995) and shoot extension growth rate (Berman and DeJong 1996; Grossman and DeJong 1995) in peach, it is not clear if crop load affects the phyllochron.

The literature of the effects crop and thus carbon availability, on the phyllochron of deciduous tree species is scarce. Therefore, this experiment was conducted to determine if the presence of crop affects the phyllochron of two different shoot types in mature peach trees; epicormic and proleptic, grown in field conditions during the 2011 growing season. The overall objective of this study was to further-clarify factors that influence shoot growth in peach trees and determine if defruiting (carbohydrate availability) needs to be incorporated into phytomer-based functional-structural models of tree growth and development such as the L-PEACH model.

Materials and methods

This research was conducted during the 2011 season at the UC Davis Wolfskill experimental orchards in Winters, CA (38°32'N, 121°58'W). Five-year-old peach trees of the Laurie May variety (unreleased) grafted on the low vigor-Controller 9 rootstock growing in a sandy clay loam soil 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. Irrigation using micro-sprinklers commenced on May 2 and continued approximately every week until September 19th. Irrigation was scheduled by employing the soil water balance method where the input was calculated through evapotranspiration and the output was the estimated water requirement through irrigation. Drainage and runoff were assumed to be negligible. Crop evapotranspiration was determined by multiplying reference ET [obtained by the on-site CIMIS weather station (California Irrigation Management Information System, <http://www.cimis.water.ca.gov/>)] by a crop coefficient given in FAO 56 (Allen et al. 1998). Plant water status was monitored by taking mid-day stem water potential (Ψ_{ST}) readings on each experimental tree weekly from May 4th until August 18th using a pressure chamber as described by McCutchan and Shackel (1992).

Two north–south oriented rows of trees (in the middle of a total of eleven rows) were organized into a randomized block design with two treatments: (1) fully cropped trees that set a heavy crop of fruit that were not thinned, and (2), non-cropped trees that had the entire crop removed by hand on April 22 (approximately 1 month after fruit set) and two shoot type, epicormic and proleptic shoots. There were a total of 24 trees in the experiment, 4 shoots per tree (2 shoot types) for a total of 48 proleptic shoots and 48 epicormic shoots. A random sample of 10 fruits per tree were collected from each tree and weighed to obtain the weight of the fruits at the time of removal to create a growth potential curve of fruit from this particular variety.

After bloom on March 9, when the vegetative buds began to burst, two epicormic and two proleptic shoots located at approximately breast height were randomly tagged from both the east and west-facing scaffolds of each tree and followed over the growing season. Shoots were considered proleptic if they grew from an overwintered bud on last year's wood. Shoots were classified as epicormic if they were vigorous neoformed shoots growing from branches older than 1-year-old. If shoots became damaged or ended growth uncharacteristically early, then a shoot in a similar location was selected and followed for the duration of the experiment.

Fruit from fruited trees were harvested, counted and weighed on July 1 to estimate the relative decrease in carbohydrate availability for vegetative growth in the fruited compared to the non-fruited treatment. From a separate sample of ten heavily hand-thinned trees (one fruit per small shoot (< 25 cm) two per large shoot (> 25 cm) in the same orchard, a sample of 50 fruit (five per tree) were removed every 7–10 days for the entirety of the fruit growth period from April 9th to July 1st. These fruit were weighed, dried at 50 °C for 5 days, and weighed again. The mean fresh weights were used to generate a potential fruit growth curve for the Laurie May variety in the 2011 season. These data along with the weights and counts of the harvested unthinned trees allowed us to estimate the relative carbon deficit in the fruited, unthinned treatment trees by subtracting the actual mean total fruit weight from the unthinned trees from a calculated total mean potential fruit weight based on the size of the fruit on the heavily thinned trees. This represented the carbon deficit relative to the potential total carbon demand for fruit growth in the heavy cropped trees.

Phyllochron measurements

To assess leaf growth rate and the phyllochron, incremental measurements of every leaf appearing on the tagged shoots were made using a metric ruler three times per week from April 13th to August 17th. Hourly temperatures were recorded by two HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA) located in the orchard and checked against the local CIMIS weather station located on-site.

Data analysis

Leaf lengths measured 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 occurred between days of data collection. Therefore, leaf appearance was normalized to the time when a new leaf was estimated to be 2 cm long. This normalized leaf appearance time was estimated plotting the individual leaf lengths to create a leaf growth rate and fit to a classical growth curve using a Gompertz model (Gompertz 1825) as previously described by Davidson et al., (2015). With the normalized leaf appearance times we estimated the time interval between two successive leaves in thermal time using a modified growing degree-hours (GDH) scale that was developed and described in further detail by Davidson et al. (2015) but loosely based on Richardson et al. (1975).

The GDH model was developed as linear on both sides of a plateau-shaped optimum. The base temperature (tempB) was 4 °C, the critical or maximum temperature (tempC) was 40 °C and the optimal temperature spanned 18–32 °C (tempO1 and tempO2). Therefore, when the current temperature (tempH) was below tempB or above tempC, nothing was added to the GDH accumulation. When tempB < tempH < tempO1, tempH – tempB was added to GDH accumulation. When tempO2 < tempH < tempC, (tempC – tempH) × (tempO1 – tempB)/(tempC – tempO2) was added to the GDH accumulation. When tempO1 ≤ tempH ≤ tempO2, tempO1 – tempB was added to GDH.

A grand mean phyllochron for each treatment was calculated by taking the mean phyllochron for each tree (two shoots per tree) and calculating the mean of all the trees within a in a given 10-day time interval. Analysis of variance with one standard error from the mean was calculated using JMP version 10 (SAS Institute Inc., Cary, NC, USA, 1989–2010).

Table 1 Mean (\pm SE) number of fruit per tree on trees of the unthinned treatment

Fruit harvest 2011	
Mean number of fruit per tree on unthinned trees	633.9 \pm 124.9
Individual fresh fruit weight on non-cropped trees at time of removal (g)	2.19 \pm 0.413
Individual fresh fruit weight on unthinned trees at harvest (g)	58.9 \pm 8.79
Individual fresh fruit weight on heavily thinned trees at harvest (g)	140.5 \pm 18.04

Mean individual fresh fruit weight of non-cropped trees at the time of fruit removal; of unthinned trees at harvest and of heavily thinned trees at harvest

Fig. 1 The seasonal pattern of mean fruit fresh weight accumulation of Lorrie May peach on heavily pruned trees compared to the mean final fresh weight of fruit on unthinned trees. The error bars represent the standard error of ten replicates

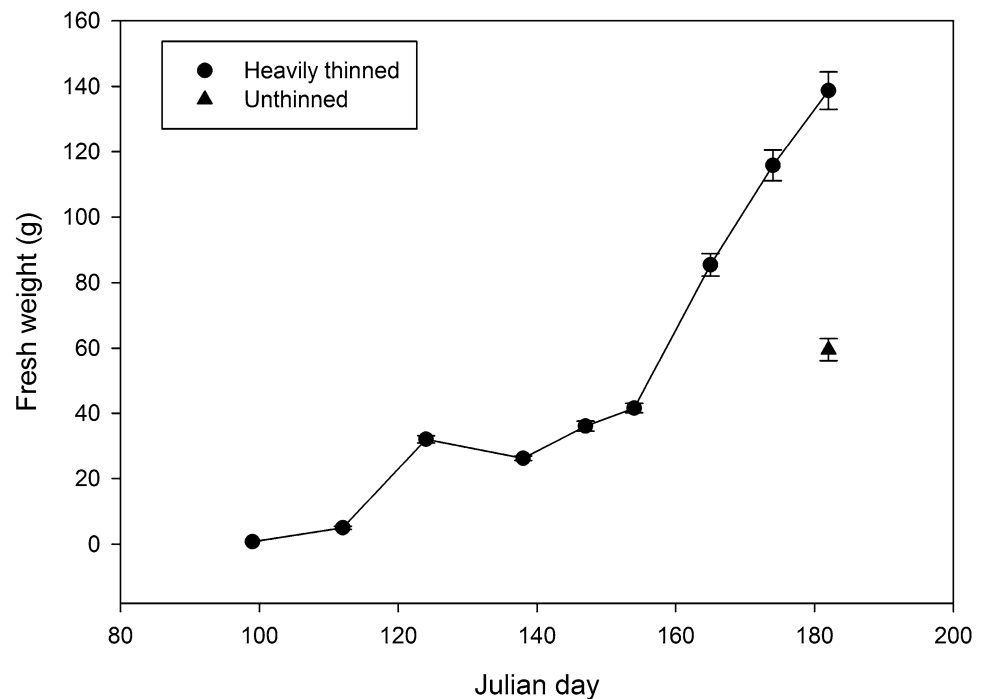


Table 2 Mean (\pm SE) seasonal phyllochron in GDH and hours, leaf length and leaf area for proleptic shoots in unthinned cropped and non-cropped trees ($N=197$)

Proleptic shoots	Full-crop	Non-cropped	<i>P</i> value
Phyllochron (GDH)	1095.0 \pm 39.65	988.5 \pm 39.89	0.0716
Phyllochron (h)	99.6 \pm 3.73	88.6 \pm 3.74	0.0505
Leaf length (cm)	13.2 \pm 0.42	15.6 \pm 0.44	<0.0006*
Leaf area (cm ²)	37.9 \pm 2.47	52.3 \pm 2.4	<0.0004*

*Statistically significance ($p = .05$)

Table 3 Mean (\pm SE) seasonal phyllochron in GDH and hours, leaf length and leaf area for epicormic shoots in unthinned cropped and non-cropped trees ($N=222$)

Epicormic shoots	Full-crop	Non-cropped	<i>P</i> value
Phyllochron in GDH	823.3 \pm 43.32	676.2 \pm 43.78	0.0285*
Phyllochron (h)	74.2 \pm 2.480	59.9 \pm 3.99	<0.0207*
Leaf length (cm)	15.6 \pm 0.33	18.3 \pm 0.34	<0.0001*
Leaf area (cm ²)	52.2 \pm 2.22	70.5 \pm 2.24	<0.0001*

*Statistically significance ($p = .05$)

for the non-cropped trees in both proleptic (Table 2) and epicormic shoots (Table 3), providing additional evidence that growth of the unthinned trees was carbon limited.

The mean phyllochron for proleptic shoots was less for cropped trees for the first data interval at the start of

data collection around day 95. By the second mean data interval near day 105, the phyllochron was the same in both cropping regimes, approximately 600 GDH (Fig. 2). From days 110–140 there were significant differences in phyllochron values between treatments ($p = .05$). At day 155 this difference disappeared and cropping no longer appeared to have an effect on the phyllochron. Interestingly, 30 days later the phyllochron of previously cropped trees tended to be less than the non-cropped trees.

At the start of the experiment the phyllochron for epicormic shoots in both cropping regimes had a mean phyllochron of about 275 GDH (Fig. 3). Significant differences between cropping treatments began to appear around day 120 and continued until day 185, which coincided with fruit harvest that occurred on day 180. Following day 180, there were no significant treatment differences in the phyllochron of epicormic shoots.

The phyllochron for both shoot types and both treatments fluctuated over the course of the season but generally increased as the season progressed apparently due to a rank or shoot aging effect. Generally, proleptic shoots on cropped trees had a longer phyllochron (slower LAR) than epicormic shoots.

When averaged over the course of the entire season, the overall mean phyllochron for proleptic shoots in the unthinned, fully cropped treatment did not differ significantly from the non-cropped treatment (Table 2). The mean phyllochron of epicormic shoots was significantly higher in the cropped treatment compared to the defruited treatment (Table 3).

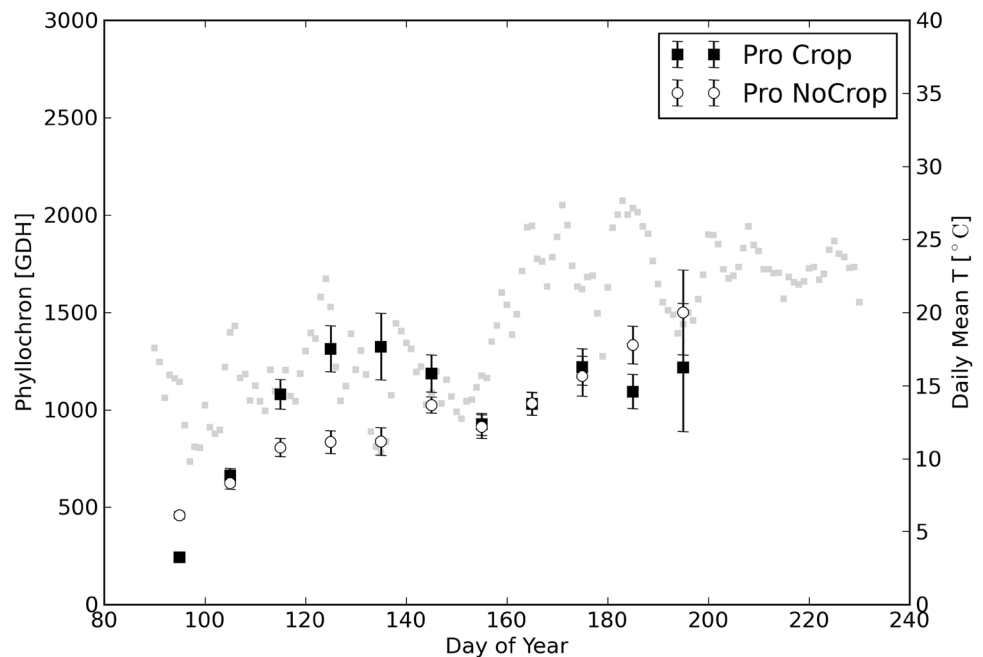
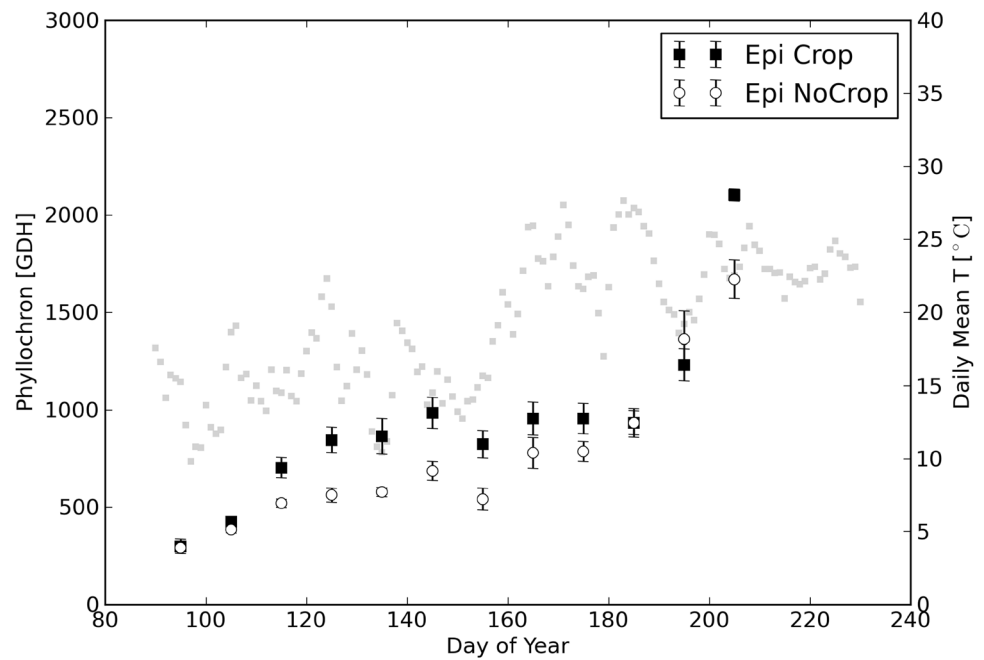
Fig. 2 The mean phyllochron plotted in 10-day intervals of proleptic shoots of heavily cropped (black squares) and non-cropped (white circles) peach trees. Error bars represent the standard errors of the means. Mean daily temperature is plotted in gray in the background

Fig. 3 The mean phyllochron plotted in 10-day intervals of epicormic shoots of heavily cropped (black squares) and non-cropped (white circles) peach trees. Error bars represent the standard errors of the means



Discussion

The potential sink demands of reproductive and vegetative organs are dependent upon their genetically determined maximum growth potentials and maintenance requirements, and the environmental factors affecting growth (DeJong and Grossman 1992; Grossman and DeJong 1995). Maximum growth potential is defined by the genetically determined maximum biomass increase of an organ when grown under optimal environmental conditions in the presence of a non-limiting supply of photosynthate (Grossman and DeJong 1995). Therefore, to achieve its maximum growth potential, an organ must grow at its potential relative growth rate, the rate of increase in dry weight per unit dry weight per unit time throughout development (Grossman and DeJong 1995). To determine the maximum growth potential of the fruit in this study a growth potential curve was determined (Fig. 1) from fruit harvested every 10 days from ten heavily thinned trees that we assume had a non-limiting supply of photosynthate. Likewise, in one treatment 100% of fruit were removed allowing for the evaluation of the potential vegetative growth and the potential of the phyllochron under the given environmental conditions in the orchard. The observed fruit growth of the unthinned trees was compared to the growth potential of the fully thinned trees to estimate a relative carbon deficit in unthinned trees (Table 1). This provided an indication of the carbon that was available for fruit growth relative to the total potential demand for fruit growth in the heavily cropped trees. Since fruit are considered to be the most efficient carbon sink in peach trees during much of the fruit growth period, it is safe to assume that dry matter

available for shoot growth in the unthinned trees was much less than in non-cropped trees. The fruit data indicates that the cropped trees were significantly carbon limited relative to supplying fruit demands and had substantially less carbon available to supply vegetative sink demands. Carbon limitations on vegetative growth were also evidenced by shorter and smaller leaves in the cropped trees compared to the uncropped trees (Tables 2 and 3). Grossman and DeJong (1995) reported that vegetative growth (current year stem length, current year stem and leaf dry weight, and trunk radial increment, stem relative extension rates (RER) and stem/leaf relative growth rates (RGR) on fruited compared to defruited trees were resource-limited shortly after vegetative bud break on fruited trees of both early and late maturing peach cultivars. They also reported that the resource limitation on vegetative growth was not constant over the growing season. On the late maturing cultivar, the resource limitation on stem growth occurred during 6–8 weeks after bloom when stem RGR and RER were less on fruited trees compared to defruited trees. Stem and leaf dry weights on fruited trees were also less than those on defruited trees during this period.

With the exception of studies in peach (Kervella et al. 1995; Pagès et al. 1996), grapevine (Schultz 1992) and kiwifruit (Cieslak et al. 2011) there are few studies that focus on the phyllochron of deciduous fruit tree species. Furthermore, all of these studies ignored the potential role of carbon availability on the phyllochron. This study tested whether defruiting, and hence, having more available carbohydrates for vegetative growth, would affect the phyllochron, which varies over time. Indeed, we observed the phyllochron was

significantly influenced by the fruiting condition of the tree, thus the phyllochron is not genetically fixed. We also observed significant effects on leaf growth.

These results can have significant consequences for modeling plant growth and development. Many plant growth models are based on the assumption that the phyllochron of shoots can be modeled effectively as a function of temperature and light exposure, perhaps with other minor environmental factors, while growth is highly dependent on carbon availability as well as environmental factors. This research indicates that previous methods of modeling the phyllochron are not valid for trees like peach, since in this study, both growth and the phyllochron were responsive to carbon availability. This information should be incorporated into plant growth and carbon balance models for accurate predictions of vegetative growth. Additionally, the phyllochron (as well as exhibiting differences between treatments) was not constant over the season and did not appear to be systematically related to temperature or light exposure since it tended to be longer as temperatures and day-length increased and then decreased. This was consistent with other phyllochron studies in peach (Kervella et al. 1995; Pagès et al. 1996) and in kiwifruit (Cieslak et al. 2011).

Because our GDH scale accounted for the influence of temperature, the fluctuations in the phyllochron throughout the season other than those attributable to the presence of fruit are likely due to rank effects (developmental aging of the apical meristem) or other environmental/physiological parameters that varied over the season. Kervella et al. (1995) and Pagès et al. (1996) also reported a gradual decrease in leaf and metamer emergence rates, as the number of leaves increased over the course of the season. As previously mentioned, following the harvest of the heavily fruited trees, the gap of the phyllochron between cropping treatments closed suggesting plasticity of the phyllochron subject to carbon availability.

Many previous phyllochron studies with both annual and perennial plants have been conducted under controlled environmental conditions and on young, potted plants and have tended to ignore the potential plasticity of the phyllochron, especially with regard to conditions leading to substantial deficits of carbon to support plant growth. This field study and previous research (Davidson et al. 2015) indicates that more attention needs to be given to the origin of shoots (proleptic vs. epicormic) as well as the potential effects of periods of carbon deficit on organ development, specifically the phyllochron when modeling shoot growth of plants.

Author contribution statement AD and TMD designed the experiment, AD conducted the field work, DDS did the modeling and produced the figures, all members analyzed the data, AD wrote the manuscript and TMD edited the manuscript.

Acknowledgements This research received no specific funding.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interests.

References

- Allen MT, Prusinkiewicz P, DeJong TM (2005) Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: the L-PEACH model. *New Phytol* 166:869–880
- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration. Guidelines for computing crop water requirements. FAO irrigation and drainage Paper no. 56. FAO, Rome, Italy, p 300
- Berman ME, DeJong TM (1996) Water stress and crop load effects on fruit fresh and dry weights in peach (*Prunus persica*). *Tree Physiol* 16:859–864
- Berman ME, DeJong TM (2003) Seasonal patterns of vegetative growth and competition with reproductive sinks in peach (*Prunus persica*). *J Horticult Sci Biotechnol* 78(3):303–309. <https://doi.org/10.1080/14620316.2003.11511622>
- Cao W, Tibbitts W (1995) Leaf emergence on potato stems in relation to thermal time. *Crop Sci* 87:474–477
- Cieslak M, Seleznyova AN, Hanan J (2011) A functional-structural kiwifruit vine model integrating architecture, carbon dynamics and effects of the environment. *Ann of Bot* 107:747–764
- Costes E, Lauri PE, Regnard JL (2006) Analyzing fruit tree architecture: implications for tree management and fruit production. *Hortic Rev* 32:1–61
- Cousens RD, Johnson MP, Weaver SE, Martin TD, Blair AM (1992) Comparative rates of emergence and leaf appearance in wild oats (*Avena fatua*), winter barley (*Hordeum sativum*) and winter wheat (*Triticum aestivum*). *J Agric Sci* 118:149–156
- Da Silva D, Favreau R, Auzmendi I, DeJong TM (2011) Linking water stress effects on carbon partitioning by introducing a xylem circuit into L-PEACH. *Ann Bot* 41:433–447
- Davidson A, Da Silva D, Quintana B, DeJong TM (2015) The phyllochron of *Prunus persica* shoots is relatively constant under controlled growth conditions but seasonally increases in the field in ways unrelated to temperature or radiation. *Sci Hortic* 184:106–113
- DeJong TM, Goudriaan J (1989a) Modeling peach fruit growth and carbohydrate requirements: reevaluation of the double-sigmoid growth pattern. *J Am Soc Hortic Sci* 114:800–804
- DeJong TM, Goudriaan J (1989b) Modeling the carbohydrate economy of the peach fruit growth and crop production. *Acta Hortic* 254:103–108
- DeJong TM, Grossman YL (1992) Modeling the seasonal carbon economy of deciduous tree crops. *Acta Hortic* 313:21–28
- DeJong TM, Grossman Y (1995) Quantifying sink and source limitations on dry matter partitioning to fruit growth in peach trees. *Physio Plantarum* 95(3):437–443
- DeJong TM, Doyle JF, Day KR (1987) Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (*Prunus persica*) cultivars. *Physiol Plant* 71: 83–88
- DeJong TM, Day KR, Doyle JF, Johnson RS (1994) The Kearney Agricultural Center Perpendicular “V” (KAC-V) orchard system for peaches and nectarines. *HortTech* 4:362–367
- Dennett MD, Auld BA, Elston J (1978) A description of leaf growth in *Vicia faba* L. *Ann Bot* 47:350–351
- Fink S (1983) The occurrence of adventitious and preventitious buds within the bark of some temperate and sub-tropical trees. *Am J Bot* 70:532–542

- Fleisher DH, Shillito RM, Timlin DJ, Kim SH, Reddy VR (2006) Approaches to modeling potato leaf appearance rate. *Agron J* 98:522–528
- Gompertz B (1825) On the nature of the function expressive of the law of human mortality, and on a new method of determining the value of life contingencies. *Philos Trans* 115:513–583
- Gordon D, DeJong TM (2007) Current-year and subsequent-year effects of crop-load manipulation and epicormic-shoot removal on distribution of long, short and epicormic shoot growth in *Prunus persica*. *Ann Bot* 99(2):323–332
- Gordon D, Damiano C, DeJong TM (2006) Preformation in vegetative buds of *Prunus persica*: factors influencing number of leaf primordia in overwintering buds. *Tree Phys* 26(53):7–544
- Gray A (1879) *Structural botany*. Ivsion, Blakeman, Taylor and Company, New York
- Grossman YL, DeJong TM (1994) PEACH: a simulation model of reproductive and vegetative growth in peach trees. *Tree Phys* 14:329–345
- Grossman YL, DeJong TM (1995) Maximum fruit growth potential following resource limitation during peach growth. *Ann Bot* 75:561–567
- Kervella J, Pagès L, Genard M (1995) Growth context and fate of axillary meristems of young peach trees. Influence of parent shoot growth characteristics and of emergence date. *Ann Bot* 76:559–567
- Kirby EJM (1995) Factors affecting rate of leaf emergence in barley and wheat. *Crop Sci* 35:11–19
- Lambers H, Chapin SF III, Pons TL (2008) *Plant physiological ecology*, 2nd edn. Springer, New York, p 321
- Loomis RS, Rabbinge R, Ng E (1979) Explanatory models in crop physiology. *Annu Rev Plant Physiol* 30:339–367
- Lopez G, Favreau RR, Smith C, Costes E, Prusinkiewicz P, DeJong TM (2008) Integrating simulation of architectural development and source–sink behaviour of peach trees by incorporating Markov chains and physiological organ function submodels into L-PEACH. *Funct Plant Biol* 35:761–771
- Maggs DH (1963) The reduction in growth of apple trees brought about by fruiting. *J Hortic Sci* 38:119–128
- Mathews M, Anderson M, Schultz H (1987) Phenologic and growth responses to early and late season water deficits in Cabernet franc. *VITIS* 26:147–160
- McCutchan H, Shackel KA (1992) Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L cv French). *J Am Soc Hortic Sci* 117:607–611
- Pagès L, Kervella J, Genard M (1996) Modelling variations of metamer emergence rate in peach trees. *Acta Hortic* 416:29–38
- Pavel EW, DeJong TM (1993) Relative growth rate and its relationship to compositional changes of nonstructural carbohydrates in the mesocarp of developing peach fruits. *J Am Soc Hortic Sci* 118:503–508
- Penning de Vries FWT, Van Laar HH (1982) *Simulation of plant growth and crop production*. Center for Agricultural Publishing and Documentation, Wageningen, p 320
- Raper CD, Thomas JF (1975) Temperatures in early post-transplant growth: influence on leaf and floral initiation in tobacco. *Crop Sci* 15:732–733
- Rawson H (1993) Radiation effects on rate of development in wheat grown under different photoperiods and high and low temperatures. *Aust J Plant Physiol* 20:719–727
- Rawson H, Hindmarsh J (1982) Effects of temperature on leaf expansion in sunflower. *Aust J Plant Physiol* 9:209–219
- Rawson H, Hindmarsh J (1992) Effects of temperature on leaf expansion in sunflower. *Aust J Plant Physiol* 9:209–219
- Richardson EA, Seely SD, Walker DR, Anderson JL, Ashcroft GL (1975) Pheno-climatography of spring peach bud development. *Hort Sci* 10:236–237
- Schultz HR (1992) An empirical model for the simulation of leaf appearance and leaf area development of primary shoots of several grapevine (*Vitis vinifera* L.). *Sci Hortic* 52:179–200
- Silk WK (1980) Plastochron indices in cantaloupe grown on an irrigation line source. *Bot Gaz* 141:73–78
- Villalobos FJ, Ritchie JT (1992) The effect of temperature on leaf emergence rates of sunflower genotypes. *Field Crops Res* 29:37–46
- Vivin P, Castelan M, Gaudillère JP (2002) A source/sink model to simulate seasonal allocation of carbon in grapevine. *Acta Hortic* 584:43–56
- White J (1979) The plant as a metapopulation. *Annu Rev Ecol Evol Syst* 10:109–145
- Wilhelm WW, McMaster GS (1995) Importance of the phyllochron in studying the development and growth of grasses. *Crop Sci* 35:1–3
- Wilson BF (2000) Apical control of branch growth and angle in woody plants. *Am J Bot* 87:601–607
- Wilson BF, Kely MJ (1994) Shoot growth from the bud bank in black oak. *Can J For Res* 24:149–154

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.