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Research Report

The Influence of Elevated CO_2 on the Photosynthesis, Carbohydrate Status, and Plastochron of Young Peach (*Prunuspersica*) Trees.

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Abstract. The plastochron, defined as the time interval between the initiations of two successive leaves, can also indicate the development of successive phytomers along a shoot. Previous work has shown that crop load impacts the plastochron in field-grown peach (*Prunuspersica*) trees, which led us to hypothesize that the plastochron of peach trees may be sensitive to the carbon status of the tree. To testthis hypothesis, a 38-day growth chamber study was conducted to determine if elevated CO_2 (800 $\mu mol \cdot mol^{-1}$) speeds up the plastochron of young peach trees relative to their growth in ambient (400 $\mu mol \cdot mol^{-1}$) CO_2. The leaf lamina lengths were measured every other day to generate leaf growth rate curves that were fitted against a classic Gompertz growth curve to estimate the time of the initiation of each leaf, which in turn, was used to estimate the plastochron. Additionally, in order to non-destructively gauge the effects of CO_2 concentration on plant performance during the experiment, net leaf CO_2 assimilation and stomatal conductance measurements were taken approximately half way through and at the end of the 38-day experiment. Doubling the ambient CO_2 concentration had no effect on the plastochron, even though the leaf CO_2 assimilation rates, leaf starch and total nonstructural carbohydrate concentrations were greater in trees grown in elevated CO_2. In addition, there were no significant treatment differences in incremental shoot growth or the number of lateral syleptic shoots.

Additional key words: carbon assimilation rate, leaf appearance rate, metamer, phyllochron

Introduction

An understanding of the underlying physiological mechanisms that drive organ growth is necessary for physiologists and plant modelers to accurately assess and predict the environmental impacts on plant development. Factors that affect plant developmental rates may alter the timing of ontogenetic events such as flowering, as well as the dynamics of canopy development and competition for resources between organs (Tremmel and Patterson, 1994). Modeling the growth of vegetative organs in fruit crops is of particular interest, since excessive vegetative growth is costly in energy and reduces fruit quality and yield (DeJong and Day, 1991). The L-PEACH functional-structural computer model simulates 3D peach (*Prunuspersica*) tree growth and architecture, as well as carbohydrate assimilation and allocation (Da Silva et al., 2011; Lopez et al., 2008; Allen et al., 2005); however, a weak point of this model is the lack of an experimentally-based rationale for determining the timing of the addition of new organs to growing shoots.

L-PEACH and most other functional-structural plant models are constructed based on phytomers, repetitive subunits defined as segments containing a node, leaf, axillary meristem and internode (White, 1979). When constructing a model of a growing plant from phytomers it is necessary to accurately time the appearance rate of each constituent, which is likely dependent upon a complex combination of genetics, environmental influences and cultivation practices. Phytomer emergence rate can be measured easily as the leaf appearance rate (LAR), the number of emerged leaves over a period of time. The reciprocal of LAR is the plastochron, originally defined as the unit of time corresponding to the interval between the initiations of two successive leaf primordia on a stem apex (Askenasy, 1880; Erickson and Michelini, 1957). It is impossible to measure the initiation of leaf primordia without damaging the stem apex, so for the purposes of this study we employed the alternate definition of the term plastochron: the duration between two recurring events during plant growth. In this study, the plastochron was determined as the time interval between the appearances of two successive

leaves that were 0.5 cm in length.

Studies on the plastochron have been well documented in annual species, but less so in woody perennials. Temperature is believed to be the most important environmental factor that influences the plastochron (Cao and Moss, 1989), followed by day length and radiation (Bertero, 2001). Water, nitrogen supply and shoot type/axis may also affect the plastochron, but to a lesser extent (Frank and Bauer, 1996; Longnecker and Robson, 1994; Kervella et al., 1995; Silk, 1980).

Carbon availability also appears to impact the plastochron in peach trees. In a field experiment with mature fruit-bearing peach trees, the plastochron of the tagged shoots of fully-cropped trees was significantly longer than for defruited trees (Davidson, 2014). In other words, it took more time for successive leaves to appear on the shoots of trees that bore heavy crops, presumably because of the presence of nearby fruit competing for carbohydrates. This led us to hypothesize that the plastochron of peach trees is sensitive to the carbohydrate status of the tree.

Evidence that the plastochron can be influenced by the carbon status of the plant varies among species. Slafer and Rawson (1997) conducted a phytotron study with two cultivars of wheat exposed to 360 and 720 μmol·mol^{-1} of CO_2 and found that elevated CO_2 had little to no effect on the rate of leaf primordia initiation and LAR. Shöenfield et al. (1989) also found negligible differences in the plastochrons (plotted in thermal time) of wheat grown at 350 and 700 μmol·mol^{-1} CO_2. Contrary to these studies, CO_2-enriched soybean plants were reported to have greater leaf initiation rates and growth rates (Rogers et al., 1984; Hofstra and Hesketh, 1975). Baker et al. (1989) conducted a growth chamber study to determine the effects and interactions of CO_2 concentration and air temperature on the development, growth, total nonstructural carbohydrate (TNC) content and final seed yield of soybeans grown in either 330 or 660 μmol·mol^{-1} CO_2. Interestingly, both CO_2 enrichment and an increased air temperature decreased the main stem plastochron interval, and the higher air temperature resulted in an increased final node number.

Other studies also suggest that the effect of CO_2 on the plastochron may be coupled to temperature (Tremmel and Patterson, 1994; Ackerly et al., 1992). Ackerly et al. (1992) found that in *Abutilon theophrasti* (velvet leaf), an elevated CO_2 concentration increased the leaf initiation rate at 28°C, resulting in an increase in whole-plant leaf area. The *Amaranthusretroflexus* (redroot pigweed) leaf initiation rate increased with temperature, and elevated CO_2 increased both the leaf area and leaf initiation rate at 28°C, but decreased it at 38°C. Tremmel and Patterson (1994) also studied the effects and interactions of atmospheric CO_2 concentration (350 and 700 μmol·mol^{-1}) and two temperature regimes (average day/night of 26°/19°C and 30°/23°C) on LAR and the leaf initiation rate in soybean (*Glycine max*) and five weeds, which included C3 and C4 grasses as well as dicot weeds. Johnsongrass (*Sorghum halepense*) LAR was unaffected by elevated CO_2 exposure. Quackgrass (*Elymusrepens*) produced leaves more rapidly at elevated CO_2 in the high temperature treatment. Elevated CO_2 and higher temperatures significantly increased the plastochron rate of soybean, redroot pigweed and sicklepod (*Senna obtusifolia*), the latter of which also increased its branch production in these conditions. The velvet leaf plastochron was unaffected by CO_2 in this study, which contrasts with aforementioned findings published by Ackerly et al. (1992).

Based on these previous studies it appears that the effect of elevated CO_2 and, by extension, plant carbohydrate status on the plastochron varies among plant species. Furthermore, data on perennial woody species are lacking. Therefore, the objective of this study was to observe the plastochron of peach grown in growth chambers maintained at either ambient (400 μmol·mol^{-1}) or elevated (800 μmol·mol^{-1}) CO_2 to test the hypothesis that the increased plastochron observed on heavily fruiting trees in the field could be a function of tree carbohydrate status. In order to non-destructively gauge the effects of ambient CO_2 concentration on plant performance, net leaf CO_2 assimilation (A) and stomatal conductance (g_s) measurements were taken approximately halfway through and at the end of the 38-day experiment. Upon harvest, data on canopy biomass, leaf area and specific leaf area (the ratio of leaf area to dry mass) were collected. To determine the carbon status of the trees, dried leaf tissue was analyzed for starch and TNC content.

Finally, it is important to note that the results obtained in this study are also useful for research in the context of global warming. Atmospheric CO_2 has increased from 284 μmol·mol^{-1} to 397 μmol·mol^{-1} since 1832 (Wheeler and von Braun, 2013), which has resulted in an increase in global temperature and affected plant growth rate (Sanchez et al., 2014).

Materials and Methods

Plant Materials and Growth Conditions

This experiment was conducted from March 5 to April 11, 2012, in growth chambers located at the UC Davis Controlled Environment Facility. One-year-old peach trees, var. Elberta on Nemaguard rootstock, were used in this experiment. The trees had an average height of 76 cm. Upon arrival from a commercial nursery, the canopy of the trees consisted of a trunk and only 3-4 shoots from the previous year, a few flowers (which were removed), and no emerged vegetative shoot buds. Twenty trees were potted in 16 L pots in fritted clay, and on March 5, the trees were divided between two reach-in growth chambers (PGR15, Conviron,

Canada) with either an ambient CO_2 concentration (~400 $\mu mol \cdot mol^{-1}$) or an elevated CO_2 concentration of 800 $\mu mol \cdot mol^{-1}$. All other environmental settings were the same for both chambers; temperatures were set at 27/20°C day/night and humidity was set at 50%. During the 14-hour light period the light flux densities were maintained at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ through the use of five 400-watt metal halide lamps, five high-pressure sodium lamps and six 60-watt incandescent bulbs. Watering was to field capacity, by letting the surplus water drain, every other day for the first two weeks then daily for the remainder of the experiment. One liter of full-strength Hoagland's solution was added to each pot once per week. The trees were given one week to acclimate to growth chamber conditions before data collection commenced.

Analysis of the Leaf Appearance Rate and the Plastochron

Data collection began on March 12 and was performed every other day until the end of the experiment. The lamina lengths of each leaf on two marked shoots per tree were measured with a simple metric ruler. The leaf length data 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 measurements of very small leaves it was impossible to capture the exact initiation point of the leaf without causing damage, and furthermore, the leaf sometimes appeared between the data collection days. Therefore, leaf appearance was normalized to the time when each new leaf was 0.5 cm long. This leaf appearance time was estimated by fitting each incremental leaf length to a classical growth curve using a 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 is related to the lower asymptote, and t is the time in hours (Gompertz, 1825). The fitted Gompertz curve was then used to determine the time taken by the leaf to reach 0.5 cm (Fig. 1).

To determine the plastochron, the appearance times of each leaf on a given shoot were plotted against their rank on that shoot and fitted with a line. Therefore, the plastochron for that shoot was estimated as the slope of the fitted line, estimated over two-day intervals (because the data were collected every two days) during the experiment and then averaged to obtain a plastochron for a particular two-day period.

Leaf Gas Exchange Measurements

CO_2 assimilation and stomatal conductance measurements were made after three weeks and again at five weeks (March 26 and April 11) of the 38-day experiment using a portable gas exchange system (LI-6400, Li-Cor Inc., Lincoln, NE, USA). Each tree was sampled (one leaf per tree) using mature source leaves (leaf 5). The portable gas exchange system was set to a reference CO_2 concentration of 400 or 800 $\mu mol \cdot mol^{-1}$ (depending on the treatment) and leaves were held in the gas exchange chamber for two minutes under the same irradiance as they experienced in the growth chamber (1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The vapor pressure deficit was maintained at <1.2 kPa by varying the flow rates. The molar fractions of water vapor remained constant, and leaf temperatures were maintained at 27°C. The CO_2 assimilation and stomatal conductance data were analyzed by analysis of variance using JMP version 10 (SAS Institute Inc., Cary, NC, 1989-2010). P values were calculated using a LS means Student t-test at $\alpha = 0.05$.

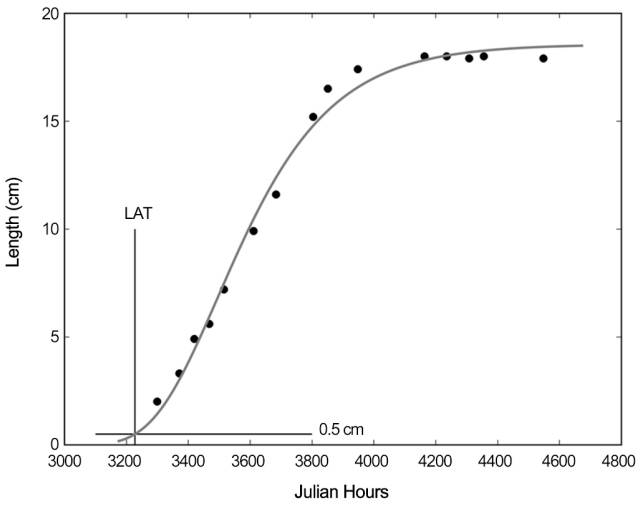

Fig. 1. An example of the Gompertz growth curve fitted to peach leaf growth rate data to estimate the normalized leaf appearance time (LAT), defined as the appearance of a leaf with a length of 0.5 cm.

Measurement of Plant Growth

At the end of the experiment the height of each tree was measured and the newly grown canopy was harvested, separating the leaf biomass from the stem biomass. Syleptic shoots are neoformed lateral shoots that can grow from current-year vegetative buds on proleptic shoots. The number of syleptic shoots along each of the 40 tagged proleptic shoots was counted and recorded. The fresh leaf and stem biomass was dried at 50°C and weighed. Leaf area (LA, cm^2) was estimated non-destructively from measurements of leaf lamina length (L, mm) using the equation: $LA=0.1889L^2+0.2735L$. This equation was obtained by a polynomial fitting of leaf length and area measurements from randomly selected leaves representing six size classes (small to large) harvested from non-tagged shoots (120 leaves per treatment). These leaves were scanned using a portable scanner (CanoScanLiDE 110, Canon, Tokyo, Japan) and an image analysis

Table 1. Growth characteristics of trees grown in chambers with ambient and elevated CO_2

Variable	CO_2 (400 μmol·mol^{-1})	CO_2 (800 μmol·mol^{-1})	*P*-value
Plastochron (h)	34 ± 1.6[z]	35 ± 1.4	0.468
Tree height (cm)	99.9 ± 2.2	95.9 ± 2.2	0.20
Leaf dry weight (g)	37.4 ± 2.4	42.7 ± 2.4	0.14
Stem dry weight (g)	12.5 ± 0.7	14.2 ± 0.7	0.10
Leaf length (mm)	12.4 ± 0.1	11.7 ± 0.1	0.07
Leaf area (cm^2)	32.8 ± 0.6	29.54 ± 0.533	0.09
Specific leaf area (cm^2 g^{-1})	181.4 ± 8.2	164.1 ± 8.21	0.37
Shoot length (cm)	29.5 ± 1.1	28.4 ± 1.0	0.431
Number of syleptics	5.3 ± 0.7	4.8 ± 0.74	0.61
% Total nonstructural carbohydrates (mass fraction)	0.1036 ± 0.0064	0.140 ± 0.0063	0.004
% Starch (mass fraction)	0.051 ± 0.0053	0.080 ± 0.0054	0.005

[z]Mean ± S.E (n=20).

program (ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA) that calculated leaf area. The leaf area data were analyzed with an ANOVA (JMP version 10) to estimate the effects of the elevated CO_2 treatments. The leaf area sample leaves were dried at 50°C and weighed to calculate the specific leaf area (SLA) for each size class using the equation: SLA=leaf area (cm^2)/leaf weight (g).

The tree heights, as well as the mean leaf and shoot dry weights of all harvested trees, were calculated for each treatment. Mean shoot length and number of syleptic shoots were also calculated, and the leaf area per tree was estimated by collecting a pooled sample of leaves on two randomly-selected shoots per tree. *p*values were calculated using a LS means Student t-test at $\alpha = 0.05$.

Total Nonstructural Carbohydrates and Starch

Leaf starch and TNC contents were determined from the harvested leaves. TNCs were defined as the sum of total glucose, free sucrose and free fructose. Five equal samples (by mass) of dried leaf tissue were taken from two trees per treatment. These samples were ground, combined and thoroughly mixed prior to tissue analysis.

The samples were extracted using a modified method (Smith, 1969) for soluble carbohydrates and enzymatically hydrolyzed with amyloglucosidaseat 55°Cfor starch and total glucose. Measurement was by HPLC with mass selective detection at the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California, Davis, CA (ANR Analytical Lab, 330 2006).

The starch and TNC contents were statistically analyzed as a completely randomized design with five repetitions. The values in Table 1 represent the least significant differences detected by the ANOVA with one standard error from the mean. P values were calculated using a LS means student t-test at $\alpha = 0.05$.

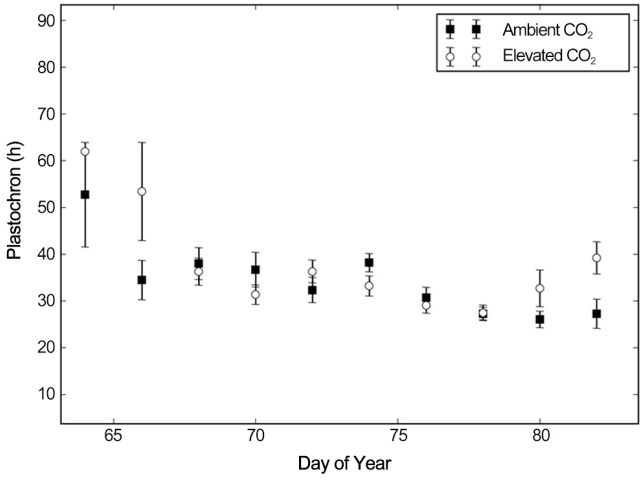

Fig. 2. The plastochron, measured at two-day intervals, in ambient (400 μmol·mol^{-1}) and elevated (800 μmol·mol^{-1}) CO_2 treatments. Error bars represent SE (n=20) of the mean.

Results

At the start of the experiment the plastochron in the ambient and elevated CO_2 treatments was slightly longer than it was during the rest of the experiment. After several days the plastochron in both treatments stabilized to approximately 36 hours. The plastochron remained relatively constant until the end of the experiment, when it increased slightly in the elevated CO_2 treatment. Overall, elevated CO_2 had no significant effect on the plastochron (Fig. 2, Table 1).

On the first day of measurement, the leaf CO_2 assimilation rates (*A*) differed between treatments, with means of 21.4 and 13.6 μmol·m^{-2}·s^{-1} for the elevated and ambient CO_2 treatments, respectively (Table 2). By week 5, the values of

Table 2. Leaf CO_2 assimilation rates (A; $\mu mol \cdot m^{-2} \cdot s^{-1}$) in ambient and elevated CO_2 conditions taken after three and five weeks of the experiment

Date	CO_2 (400 $\mu mol \cdot mol^{-1}$)	CO_2 (800 $\mu mol \cdot mol^{-1}$)	*P*-value
Mar 24, 2012	13.6 ± 0.60[z]	21.4 ± 0.63	<.0001
Apr 11, 2012	10.5 ± 0.75	13.4 ± 0.76	0.019

[z]Mean ± S.E (n=20).

Table 3. Leaf stomatal conductance (g_s; $mol \cdot m^{-2} \cdot s^{-1}$) values in ambient and elevated CO_2 conditions taken after three and five weeks of the experiment

Date	CO_2 (400 $\mu mol \cdot mol^{-1}$)	CO_2 (800 $\mu mol \cdot mol^{-1}$)	*P*-value
Mar 24, 2012	0.29 ± 0.04[z]	0.40 ± 0.04	0.069
Apr 11, 2012	0.22 ± 0.03	0.21 ± 0.03	0.785

[z]Mean ± S.E (n=20).

A decreased to 13.4 and 10.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the elevated and ambient CO_2 treatments, respectively.

The differences in A were related to numerical differences in stomatal conductance (g_s), but the variation between leaves was quite large. While the leaf g_s was 28% greater in the elevated CO_2 treatment compared to the ambient CO_2 treatment (0.40 and 0.29 $mol \cdot m^{-2} \cdot s^{-1}$, elevated and ambient treatments respectively) these differences were not statistically significant. At week 5, the leaf g_s was decreased in both treatments, with a larger decline in the elevated CO_2 treatment, but the values were not significantly different (0.21 and 0.22 $mol \cdot m^{-2} \cdot s^{-1}$ CO_2 in the elevated and ambient treatments, respectively (Table 3).

Elevated CO_2 did not significantly affect the incremental biomass production. The leaf and stem dry weights were slightly higher in elevated CO_2than in the ambient CO_2 treatment, but these differences were not significant (Table 1). Leaf area, specific leaf area, tree height and the number of syleptic shoots were slightly greater in ambient than elevated CO_2conditions,but these differences were also not significant (Table 1). On the other hand, the leaves of trees grown in elevated CO_2 had significantly higher concentrations of starch and TNCs (Table 1).

Discussion

The plastochron was slightly slower during the first few days of the experiment, particularly in the elevated CO_2 treatment, compared to the remainder of the study where it stabilized at around 36 hours. We speculate that this temporary increase was probably due to a slow emergence from dormancy and acclimation to growth chamber conditions in these young trees.

After the initial measurements, high CO_2 had no apparent effect on the plastochron. This lack of sensitivity to CO_2 concentration was similar to the results found in studies of wheat (Slafer and Rawson, 1997; Shönfeld et al., 1989), Johnsongrass, velvet leaf (Tremmel and Patterson, 1994), and soybean (Ackerly et al., 1992). However, these results were unexpected given that, in a previous field study of cropped and non-cropped trees, the plastochron was significantly increased by the presence of heavy crop loads that most likely decreased the amount of carbohydrates available for shoot growth (Davidson, 2014).

We hypothesized that by doubling the available atmospheric CO_2, photosynthesis would increase and therefore more sugars would be available for shoot growth in plants in the high CO_2 treatment compared to the ambient CO_2 treatment. While the leaf CO_2 assimilation rates and leaf carbohydrate contents were higher in the elevated CO_2 treatment trees (Tables 1 and 2), these increases appeared to have no effect on the plastochron or the incremental increase of shoot biomass (Table 1). Furthermore, plants in the elevated CO_2 treatment had qualitative differences in growth compared to those in ambient CO_2, developing slightly smaller leaf areas, shorter leaf lengths, and lower specific leaf areas in addition to being shorter and having fewer syleptic shoots. This contrasts with reported results for soybean, in which elevated CO_2 increased leaf area as well as the aboveground biomass and final seed yield, while decreasing the plastochron (Baker et al., 1989). Likewise, when investigating the interactive effects of elevated CO_2 (350 and 700 $\mu mol \cdot mol^{-1}$) and water availability on two-year-old peach seedlings, Centritto (2002) reported a 33% increase of total dry mass, but a significant reduction in SLA under elevated CO_2 conditions.

In our study there was a large drop in A and g_s from week 3 to week 5 in the elevated CO_2 treatment (Table 3). At the end of the experiment, A was still significantly different between treatments; however, the differences were less pronounced than at week 3. This may be related to the similar shoot biomasses of trees in both conditions at the end of the experiment (Table 1).

After 55 days of subjecting young peach seedlings to elevated and ambient CO_2 treatments, Centritto (2002) found

that while the daily A rates were not different between treatments in the early morning or evening, during the middle of the day there were significant differences. Centritto reported no significant differences in A-C_i (C_i internal CO_2 concentration) curves between CO_2 treatments and consequently no statistical differences in the J_{max}, V_{max}, and A_{max} parameters that describe photosynthetic capacity. As in our study, Centritto (2002) found no differences in stomatal conductance between plants grown in ambient or elevated CO_2. Centritto (2002) speculated that a downward acclimation of A may have developed through secondary metabolic adjustments related to the source-sink dynamics, particularly the plants' ability to increase N uptake concurrently with the increase in carbohydrate production (Drake et al., 1997). A downward acclimation of A may be the result of feedback mechanisms that occur in response to increased rates of carbon uptake in leaf tissue that disrupt the source-sink functional balance (Centritto 2002). Consequently, the potential increase in plant growth rate from a higher carbon uptake in elevated CO_2 may be reduced to a rate determined by N uptake (Farage et al., 1998).

In retrospect, the unexpected lack of a shoot growth or plastochron response to elevated CO_2 may be a function of conducting this experiment in growth chambers. In the growth chamber treatments the carbohydrate status of the trees may not have been limiting for shoot growth, whereas in the field it is widely understood that heavy crop loads can limit shoot growth (Berman and DeJong, 2003; Grossman and DeJong, 1998, 1995) and the plastochron (Davidson, 2014), presumably because of intense within-tree competition for carbohydrates (Grossman and DeJong, 1994). Indeed, Davidson (2014) reported significant differences in plastochron values for peach epicormic shoots; 74.2 hours for unthinned trees and 59.9 hours for non-cropped trees. Leaf length and leaf area were also significantly greater for non-cropped trees.

The plants in this growth chamber experiment received cumulative daily leaf light exposures (14 hours at 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of highly scattered light) at a level approaching the light saturation limit of peach leaf photosynthesis (Rosati et al., 1999). This light level was higher and less variable than the natural leaf light exposure in a field tree canopy over a day (Rosati et. al., 1999; DeJong and Doyle 1985). Additionally, it was unlikely that root growth was limited in this experiment because when the plants were harvested we noted that the roots had not completely filled the pot; however, it is possible that theassimilated carbon could have been used for increased respiration or carbon accumulation in the roots. In fact, high source-carbon availability provided by the elevated CO_2 conditions could have affected the patterns of canopy versus root growth. The relationship of root growth versus carbon availability has been recently studied in walnuts by Contador et al. (2015), who argued that root growth was negatively affected during the periods where carbohydrates were mainly allocated to reproduction. Unfortunately, in the present study no measurements of root respiration and total root weight were taken, and thus this hypothesis could not be tested. The tree nutrition was most likely not limiting since the weekly addition of full-strength Hoagland's solution should have been more than adequate to supply their nutritional needs.

The fact that the measured leaf assimilation rates in both the elevated and ambient CO_2 chambers declined over the course of the experiment, and that the leaves in the high CO_2 chamber declined more than in the ambient CO_2 chamber, aligns with the hypothesis that photosynthesis may have been sink-limited in both chambers. The canopy photosynthetic rates could have been more than adequate to meet potential shoot growth rates in both the ambient and elevated CO_2 growth chamber conditions. Thus, the growth chamber experiment was more of a test of whether the plastochron and shoot growth rates could be stimulated by an oversupply of available carbohydrates whereas the field experiment with different crop loads examined whether the plastochron could be limited by a lack of available carbohydrates. Based on the results of this experiment, the answer to the first test is clearly that both the plastochron and shoot growth in young peach trees cannot be stimulated to grow above a certain growth potential by increasing the availability of photosynthates. On the other hand, previous field experiments support the idea that the plastochron, as well as overall shoot growth, can be slowed down by competition for carbohydrates from fruit sinks.

The results obtained in this study are also interesting in the context of global warming because they provide evidence on tree performance under variable CO_2 concentrations, while atmospheric temperature remained unchanged. No change in plastochron initiation was observed in this study, therefore there is no direct effect of CO_2 on plastochron initiation; however, because the increase of CO_2 is linked with an increase in atmospheric temperature in the current global warming context, there is still a possibility that high CO_2 could interact with temperature to affect plastochron initiation. Further studies in this area may include treatments where atmospheric temperature varies under high CO_2 concentrations and thus tests whether the plastochron of peach trees is affected by global warming.

Conclusions

We hypothesized that by doubling the available atmospheric CO_2, photosynthesis would increase and therefore more sugars would be available for shoot growth in the high CO_2 treatment compared to the ambient CO_2 treatment. While leaf CO_2 assimilation rates, leaf starch, total nonstructural carbohydrate concentrations were greater in the trees grown in high CO_2, these increases appeared to have no effect on

the plastochron or incremental shoot biomass. Furthermore, plants in the elevated CO_2 treatment tended to have slightly smaller leaf areas, shorter leaf lengths, and lower specific leaf areas, in addition to being shorter trees and having fewer syleptic shoots than trees grown in ambient CO_2, although these differences were not significant. Based on the results of this experiment, both the plastochron and shoot growth in young peach trees cannot be stimulated to grow above a certain growth potential by increasing the availability of photosynthates.

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