“Late Winter/Early Spring” Xylem Sap Characteristics Influence Pecan Crop Load

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Abstract. Alternate bearing (AB) by individual trees is a major biological problem faced by pecan [*Carya illinoensis* (Wangenh.) K. Koch] nut producers. The linkage between flowering and subsequent cropload with xylem sap characteristics at the time of floral bud swelling and expansion is unknown. Multiyear field studies of mature ‘Cheyenne’ and ‘MoneyMaker’ trees, in “on” or “off” phases of AB, were evaluated regarding this linkage. Xylem sap flowing from trunks of ‘Cheyenne’ trees just before, and at the time of, budbreak (i.e., “late winter/early spring”) consisted of a variety of simple sugars. These were hexoses (fructose and glucose), a disaccharide (sucrose), polysaccharides (raffinose and stachyose), and sugar alcohols (xylitol and sorbitol). Sucrose was the overwhelmingly dominant simple carbohydrate at this growth stage, comprising 55% to 75% of the total molar composition, regardless of tree bearing status or sampling time during the seasonal transition from late winter to early spring as buds swell, break, and begin to produce shoots and flowers. Both sap flow volume and concentration of individual carbohydrates were much greater in “on” phase than “off” phase trees. “On” phase xylem sap contained ≈ 19.9 -fold more sucrose than sap from “off” phase trees. The concentration of all sap carbohydrates was much greater at flow inception, declining quickly as buds transition from “bud swell” to “budbreak” and subsequent “shoot growth.” Depending on crop year, individual “on” phase ‘Cheyenne’ trees (≈ 25 years old) exhibited flow volumes 5.5- to 20.2-fold greater than “off” phase trees. In-shell nut yield by both ‘Cheyenne’ and ‘MoneyMaker’ trees (110 years old) increased hyperbolically with increasing “late winter/early spring” sap flow volume. Sap flow from ‘Cheyenne’ and ‘MoneyMaker’ resulted in near maximum nut yield when flow volume per xylem tap peaked was at ≈ 10 L/tree and ≈ 15 L/tree, respectively, over a 16-day sampling period. These findings are suggestive that sucrose, and possibly other simple carbohydrates, moving acropetally toward axillary bud meristems of shoots during “late winter/early spring” at about the time of “bud swelling” influences the final phase of floral development and therefore subsequent cropload.

Alternate bearing is a natural trait exhibited by the reproductive modules (i.e., shoot, branch, limb, and tree) of many tree species. This trait likely improves the probability of species survival in their native habitats but poses a major biological problem in horticultural enterprises as a result of excessive interannual variability in yield and quality of nutmeats. Alternate bearing in pecan is influenced by the tree’s processing of environmental and/or endogenous cues consistent with an autonomous flowering pathway involving phytohormones (Amasino, 2010; Rohla et al., 2007a, 2007b; Smith et al., 2007; Wilkie et al.,

2008; Wood, 2011) and carbohydrate reserves (Wetzstein and Sparks, 1983).

Three distinct sequential phases of pistillate flower development appear involved in regulation of AB in pecan (Wood, 2011). These are: 1) foliar production of a phloem translocated florigen that initiates chromatin-modifying inductive processes in young bud primordia; 2) an interplay of foliar and fruit produced phytohormones acting on the primordia to regulate a second phase of chromatin modification; and 3) regulation of the final phase of chromatin modification by concentration of one or more non-structural carbohydrates (e.g., sucrose) acting in the environment of the axillary meristems during, or just after, vernalization preceding anthesis (Wood, 2011). Like with many other tree-fruit species (Schmidt et al., 2009), florally induced bud primordia on heavy cropload trees (i.e., “on” year of AB cycle) are likely exposed to different phytohormonal environments than are primordia of induced buds on light cropload trees (i.e., “off” year of AB cycle). This is also likely true for sugar concentration within the environment of the

floral bud meristem in that sugar signaling is thought to play a key role in flowering (Gibson, 2003, 2005) through a complex interplay with phytohormones regarding their effects on gene expression (Leon and Sheen, 2003).

Non-structural simple carbohydrates can affect gene expression (Koch, 1996; Leon and Sheen, 2003; Li et al., 2003a, 2003b) and appear involved in one or more processes controlling pecan floral initiation (Smith and Waugh, 1938; Sparks, 1975; Wood, 1989; Wood et al., 2004; Worley 1979a, 1979b). For example, sugars appear to be major regulators of floral genes involved in certain vernalization and subsequent floral initiation and evocation processes (Wetzstein and Sparks, 1983; Wood, 1989, 1995). This raises the possibility that simple sugar components within the primordial environment exert a major regulatory role sufficient to influence chromatin-modifying events controlling floral initiation and evocation processes. If so, sugars supplied by xylem sap during the late winter to early spring transition period before and during budbreak likely influence floral initiation and evocation.

Positive pressure within a tree’s above-ground stem structure leads to late winter xylem sap flow. This pressure and flow is near maximum when there is substantial diurnal fluctuation of stem temperature above and below freezing (Marvin and Ericson, 1956; Marvin and Greene, 1951; Wiegand, 1906). Johnson et al. (1987) found xylem sap pressure, and subsequent sap flow, in relatively dormant late winter trees to depend on the xylem sap’s sucrose component. If sucrose affects dormant season sap pressure and flow in pecan, then the subsequent diurnal rhythmic-like pumping of sucrose-enriched sap into the apoplastic space of swelling buds likely influences gene regulation within floral meristems and therefore the final stage of floral initiation—i.e., Phase III (Wood, 2011). This might partially explain how carbohydrate reserves influence AB and raises the possibility that sufficient exposure to one or more simple carbohydrates made available just before budbreak, through early season sap flow, substantially regulates the “on” vs. “off” bearing state of pecan trees. The nature of this relationship is presently unknown for pecan and other angiosperms. This study assesses the relationship between xylem sap flow and its constituent simple carbohydrate composition at the time of spring budbreak to the subsequent cropload AB phase of pecan trees.

Materials and Methods

Relationship of sap flow to “on” versus “off” bearing status. An orchard population of ≈ 25 -year-old ‘Cheyenne’ trees growing in a commercial-like research orchard at Byron, GA, was studied for the relationship between cropload and “late winter” sap flow and sugar composition. The location (lat. +32°39’54” N, long. +83°44’31” W) is in a humid climatic zone with an average elevation of

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≈156 m (509 ft). The dominant orchard soil is a Lucy loamy sand (loamy, Kaolinitic, thermic Arenic Kandiudult). The site has a freeze-free growing period of ≈280 d with annual precipitation of ≈1.3 m (51 inches). Orchards were managed according to the Georgia Extension Services guidelines for pests, fertilizers, etc. (Hudson et al., 2007). Trees also received subsurface drip irrigation with drip emitters rising to the soil surface at 1-m intervals to supplement tree water needs. Parallel irrigation lines ran the length of tree rows, positioned ≈1.2 m on either side of tree trunks. Drip emitters delivered water at 3.78 L·h⁻¹ for ≈8 to 12 h·d⁻¹, depending on water needs, throughout the growing season. Irrigation lines were within an herbicide strip maintained in a vegetation-free state using glyphosate (Monsanto, St. Louis, MO). Trees received annual broadcast applications of nitrogen, potassium, phosphorous, magnesium, and calcium as needed, based on previous July leaf analysis, at principal leaf development growth stage “11” (Finn et al., 2007). Canopies also received foliar sprays of micronutrients (zinc, nickel, copper, manganese, iron, and boron) during canopy expansion (growth stage “11–17”) each spring. Orchard management included routine foliar sprays of pesticides to control pecan scab caused by *Fusicladosporium effusum* (winter) and various arthropod pests. Pest management practices produced fruits with little pecan scab damage and little or no fruit drop or fruit damage as a result of arthropod pests.

‘Cheyenne’ trees were individually rated for cropload (heavy vs. little or none) in late Aug. 2007 and two extreme bearing groups (i.e., “on” vs. “off”) were identified, consisting of 15 trees exhibiting little or no crop (“off”) and 15 trees with relatively heavy nut crops (“on”). Trees were assessed the next spring for sap flow and sugar composition and in the fall for in-shell nut yield. These parameters were measured for 3 consecutive years (2008, 2009, and 2010). Sap flow from each of the 30 trees was measured by drilling a single 1.3 cm × 8-cm hole into the trunk, 0.5 m above the ground on the east side of the tree, and collecting naturally extruding sap through a plastic tube insertion to a depth approximating that of the outermost xylem ring (so as to prevent possible contamination from phloem sap). Sap was collected “late winter/early spring” in a polypropylene container and exudate (described here as “flow”) volume measured daily throughout late March to early April, from before bud swell to bud-break, with subsamples frozen at -20°C until sugar analysis by high-performance liquid chromatography (HPLC). Nut yield was based on subsampling of nuts lying on the ground by placing four pie-shaped sectors, one at each of the four cardinal directions, beneath the canopy, and using the appropriate expansion factor to estimate total weight of nuts on the ground after mechanical shaking of trees.

The experimental design consisted of two bearing class treatments (“on” vs. “off”) replicated 15 times (n = 30) within a randomized

complete block structure. Blocking was by proximity of the nearest “on–off” tree pairs growing under similar light conditions during the previous growing season. Measurement parameters were in-shell nut yield and sap flow volume with data being analyzed through analysis of variance (ANOVA) at $P \leq 0.05$ and relationships further described through curvilinear regression analysis by year. For simple non-structural carbohydrate in excreted sap, analysis through least squares ANOVA with sap collection date nested within bearing phase based on sap exudate composition collection 1 and 16 d after the beginning of sap flow from drill holes. Treatment means were separated using Tukey’s honestly significant difference with $P \leq 0.05$.

The relationship between cropload and “late winter/early spring” sap flow was also estimated for ≈110-year-old, ≈30 m tall ‘Money-maker’ (a severe AB cultivar) trees growing at the previously described location. Trees were managed as described previously but without irrigation. The orchard was on a Norfolk loamy fine sand (fine loamy, kaolinitic, thermic Typic Kandiudult). Sixty-five trees were randomly selected from a 15-ha orchard population of trees and monitored over 2 years for sap exudation and cropload. Sap monitoring was as described previously for ‘Cheyenne’ trees. Cropload of ‘Money-maker’ trees was visually estimated based on early September fruit load within the lower half of the tree canopy [1 = no crop (0 to 1 kg/half-tree); 2 = light crop (2 to 25 kg/half-tree); 3 = moderate crop (26 to 50 kg/half-tree); 4 = heavy crop (51 to 100 kg/half-tree); 5 = exceptionally heavy crop (greater than 100 kg/half-tree)] and then indexing to actual historical yields of these similar trees of the same cultivar type and age to provide cropload resolution equivalent to the cropload levels most relevant to alternate bearing. Estimates were in 2009 and 2010. Measurement parameters were in-shell nut yield and sap flow volume with data analyzed by curvilinear regression analysis by year after testing for a normal distribution by the Shapiro-Wilk-W test for goodness of fit.

Carbohydrates. Non-structural carbohydrate analysis focused on relatively common hexoses, disaccharides, polysaccharides, and sugar alcohols. Analysis was through HPLC (Thermo SCM1000 Spectra System, Logan, UT) with an Alltech Evaporative Light Scattering Detector [ELSD-800 detector (Deerfield, IL)] using a Prevail™ Carbohydrate ES Column (250 × 4.6 mm; 5 μm; Alltech) with a mobile phase consisting of acetonitrile: acetone (75:25) at 100% for 25 min at a flow rate of 1.0 mL·min⁻¹. Sap samples were filtered through a SAX ion-exchange preparatory column (Bond Elute; Varian, Santa Clara, CA) and then diluted 3-fold with distilled water and 10 μL of diluted sample analyzed by HPLC. Analyzed sugars and sugar alcohols were xylitol [retention time (RT) = 7.0 min, fructose (RT = 7.6 min), sorbitol (RT = 8.4 min), glucose (RT = 9.0 min), sucrose (RT = 10.5 min), raffinose

Table 1. Relationship of alternate bearing (AB) phase, expressed as in-shell nut yield, and “late winter/early spring” sap exudation from ≈25-year-old ‘Cheyenne’ pecan trees.

Initial alternate bearing phase ^a	In-shell nut yield (kg/tree)	Sap exudation (L/tree)
2008 (Year t_{+0}) ^b		
On	59.52 a ^c	4.54 a
Off	5.49 b	0.82 b
2009 (Year t_{+1})		
On ^w	7.49 b ^c	0.21 b
Off	59.25 a	4.24 a
2010 (Year t_{+2})		
On	71.46 a	3.62 a
Off	10.67 b	0.41 b

^aTrees were categorized as being in either the “on” or “off” bearing phase of AB in 2007 with 2008 (t_{+0}) serving as the index year for 3 years of cropping.

^bFirst yield year = 2008 = t_{+0} ; second yield year 2009 = t_{+1} ; third yield year = 2010 = t_{+2} .

^cTreatment means followed by different letters (i.e., a non-common letter) are significantly different at $P \leq 0.05$ level by analysis of variance.

^wTrees that were in the “off” phase in 2008, but in the “on” phase in 2009, and vice versa.

Fig. 1. Relationship between volume of “late winter/early spring” xylem sap exudates (x) and subsequent in-shell nut yield (y) produced by ≈25-year-old ‘Cheyenne’ pecan trees later in the growing season. Relationships are for 3 consecutive years. The relationship was best described by hyperbolic functions. For 2008 (A): $y = (6.891^{e+1} x) / (1.190^{e0} + x)$, $R^2 = 0.41$, $P = 0.05$; for 2009 (B) $y = (7.383^{e+1} x) / (9.755^{e-1} + x)$, $R^2 = 0.73$, $P = 0.05$; and 2010 (C) $y = (8.336^{e+1} x) / (6.528^{e-1} + x)$, $R^2 = 0.44$, $P = 0.05$. Sap flow is that amount collected from a single 1.3-cm bore hole 8 cm deep into the xylem over a 16-d period at the beginning of sap flow in from 13 Mar. to 29 Mar.

(RT = 13.7 min), and stachyose (RT = 16.6 min)] based on the same retention times exhibited by both pure and mixed samples of these reference carbohydrates. Tree sap was analyzed for these simple carbohydrates in 2008, 2009, and 2010 with only data for 2008 reported, although 2009 and 2010 data are very similar in regard to simple carbohydrate composition and relationship to sap flow and yield.

Results

Relationship of sap flow to “on” versus “off” bearing status. ‘Cheyenne’ trees identified during the fall of 2007 as either “on” or “off” cropped in 2008 ($Year\ t_{+0}$) with pronounced opposite phase in-shell nut yield differences (Table 1). $Year\ t_{+0}$ “on” trees had a harvested in-shell nut cropload 11.8-fold greater than that of $Year\ t_{+0}$ “off” trees. The associated late winter mean sap excretion was 5.5-fold greater in these $Year\ t_{+0}$ “on” trees than in $Year\ t_{+0}$ “off” trees. In the second year ($Year\ t_{+1}$), the former $Year\ t_{+0}$ “on” trees were “off” and vice versa with a 5.5-fold in-shell yield difference and with the $Year\ t_{+1}$ “on” trees exhibiting a late winter sap excretion 20.2-fold greater than current year ($Year\ t_{+1}$) “off” trees. This relationship was also evident in the third crop year ($Year\ t_{+2}$) with $Year\ t_{+2}$ “on” tree in-shell nut yield being 6.7-fold that of $Year\ t_{+2}$ “off” trees with sap flow of $Year\ t_{+2}$ “on” trees being 8.8-fold that of $Year\ t_{+2}$ “off” trees. ‘Cheyenne’ trees therefore exhibited the biennial form of AB so typical of almost all commercial pecan cultivars but with cropload being positively related to volume of sap excreted from tree trunks during the late dormant season in late winter.

Relationship of sap flow to subsequent in-shell nut cropload. The relationship between late winter exudation of xylem sap and subsequent in-shell nut crop for ‘Cheyenne’ trees was both positive and curvilinear, exhibiting

a moderate hyperbolic relationship in all 3 years ($R^2 = 0.41$ in 2008; $R^2 = 0.73$ in 2009; and $R^2 = 0.44$ in 2010) (Fig. 1). A relatively small increase in volume of xylem sap exudate up to ≈ 2.5 L/tree led to substantial increases in in-shell nut yield after ≈ 5 L/tree in-shell nut yield only slightly increased as sap flow increased. In the case of ≈ 110 -year-old ‘Moneymaker’ trees, there was also a hyperbolic relationship ($R^2 = 0.85$ in 2009 and $R^2 = 0.73$ in 2010; Fig. 2). Cropload was near maximum in 2009 and 2010 with a sap flow of 15 L/tree over the 16-d collection period. These data indicate that in-shell nut yield of pecan is positively related to sap exudation volume occurring during the late winter to early spring transition, just before budbreak.

Carbohydrates. The excreted sap of ‘Cheyenne’ pecan trees was comprised of several classes of carbohydrates that include hexoses (fructose and glucose), a disaccharide (sucrose), polysaccharides (raffinose and stachyose), and sugar alcohols (xylitol and sorbitol) with sucrose being on average 63% to 76% of the total simple carbohydrate composition, depending on bearing status (Table 2). The concentration of each of these carbohydrates, except for xylitol, was greater in the sap exudates of “on” phase trees than for “off” phase trees. In the case of sucrose, by far the dominate simple carbohydrate, the excreted sap of “on” phase trees contained 19.9-fold more sucrose than did “off” trees. Similar, or greater, differences were evident in the other measured monosaccharides and polysaccharides, but not in the sugar alcohols. Carbohydrate composition was much greater during the initial phase of sap flow than 16 d later (Table 2) with sugar concentration declining over time (data not shown). Average sucrose concentration was as great as 16.9 mM ($5.8\text{ mg}\cdot\text{mL}^{-1}$) of sap in “on” trees during the first day of sap excretion, being 19.2-fold greater than the sucrose concentration in “off” trees on Day 1. Similarly, total

Fig. 2. Relationship between volume of “late winter/early spring” xylem sap exudates (x) and subsequent in-shell nut yield (y) produced by ≈ 100 -year-old ‘Moneymaker’ pecan trees later in the growing season in 2 consecutive years. The relationship was best described by a hyperbolic function. The relationships for 2009 and 2010 are: (A) cropload (y) = $(5.874e^{+0}x)/(3.402e^{+0}+x)$, $R^2 = 0.85$; (B) cropload (y) = $1.739 + (1.715e^{+1}x)/(7.626e^{+1}+x)$, $R^2 = 0.73$. Cropload rating scale: 1 = no crop (i.e., 0 to 1 kg/tree); 2 = light crop (i.e., 2 to 25 kg/tree); 3 = moderate crop (i.e., 26 to 50 kg/tree); 4 = heavy crop (i.e., 51 to 100 kg/tree); 5 = very heavy crop (i.e., greater than 100 kg/tree). Estimate is total tree cropload based on assessment of the load on the lower half of the fruiting canopy. Sap flow is that amount collected from a single 1.3-cm bore hole 8 cm deep into the xylem over a 16-d period at the beginning of sap flow from 13 Mar. to 29 Mar.

Table 2. Influence of alternate bearing phase (“on” versus “off”) and time of “late winter/early spring” xylem sap exudation (1 d after tapping versus 16 d after tapping) on concentration of carbohydrates within exuded xylem sap of ≈ 25 -year-old ‘Cheyenne’ pecan trees.

Treatment ^a	Simple carbohydrate composition of exuded sap (mM)							Total
	Sucrose	Fructose	Glucose	Raffinose	Stachyose	Xylitol	Sorbitol	
Alternate bearing phase								
On	8.706	0.222	0.666	1.598	0.165	0.066	0.055	11.477
Off	0.438	<0.056	<0.056	<0.017	<0.015	0.066	<0.043	0.690
	***y	***	*	***	***	NS	*	***
Time after initial sap flow ^a								
1 d	8.852	0.278	0.666	1.615	0.165	0.131	0.055	11.762
16 d	0.292	<0.056	<0.056	<0.017	<0.015	<0.066	<0.054	0.556
	***	***	*	***	***	*	*	***
Interaction								
On + 1 d	16.857 a ^w	0.44 a	1.388 a	3.179 a	0.330 a	0.131 a	0.110 a	22.439 a
On + 16 d	0.584 b	<0.056 b	<0.056 b	<0.017 b	<0.051 b	<0.066 b	<0.055	0.848 b
Off + 1 d	0.584 b	<0.056 b	0.056 b	<0.017 b	<0.015 b	<0.066	<0.054	0.848 b
Off + 16 d	<0.029 b	<0.056 b	<0.056 b	<0.017 b	<0.015 b	<0.066 b	<0.054	0.029 b

^a“On” trees = substantial cropload in 2008; “off” bearing trees = little or no crop in 2008. Analyzed sap was compared for carbohydrates for samples collected from trees on Day 1 and Day 16 in “late winter/early spring” as buds are swelling.

^bMeans differed by analysis of variance such that means were significantly different: ***0.001, **0.01, *0.05, NS = nonsignificant at $P \leq 0.05$.

^cExcreted sap collected either 1 d or 16 d after tapping of the tree trunk.

^dTreatment means followed by different letters (i.e., a non-common letter) are significantly different by Tukey’s honestly significant difference at the $P \leq 0.05$ level.

simple carbohydrates in “on” trees on Day 1 was 22.9-fold greater than that of “off” trees in Day 1 and “on” trees at Day 16 was still 5.8-fold greater than were “off” trees on Day 1. These data indicate that the xylem sap of pecan trees is comprised of a variety of simple carbohydrates, but with sucrose being the dominant source of reduced carbon flowing within the xylem and probably apoplastic spaces of shoots, just before budbreak in late winter.

Discussion

Temperate zone trees tend to cluster into one of two sap exudation classes (Type-TD vs. Type-TI). Type-TD trees (e.g., *Acer*, *Carya*, and *Juglans* spp.) exhibit strong temperature dependent sap exudation in “late winter/early spring,” whereas exudation by Type-TI trees (e.g., *Populus*, *Bitola*, *Vitis* spp.) is relatively temperature independent (Wiegand, 1906). The nature of sap flow from the pecan trees observed in the present study is consistent with temperature-dependent, Type-TD flow behavior as reported for *Carya* spp. by Wiegand (1906). Observations here indicate that the greater the sucrose concentration, or possibly that of other di- and polysaccharides (e.g., galactosyl-oligosaccharides of the Raffinose family oligosaccharides such as raffinose and stachyose), in xylem vessels during the “late winter/early spring” transition, the greater the sap pressure and greater the subsequent sap flow. It is noteworthy that in *Acer* sp., equal molar sugar hexoses (e.g., glucose and fructose) do not elicit nearly as much sap pressure (Johnson et al., 1987). Sucrose, a non-reducing sugar, is unlikely to interact non-enzymatically with xylem sap proteins; plus only a few key sucrose-hydrolyzing enzymes (Van Bel et al., 2008) likely control the flow of this form of reduced carbon. This may explain why sucrose is the primary carbon carrier in the “late winter/early spring” xylem sap of pecan.

The sap exudation mechanism depends largely on gas bubbles in fibers and sucrose in xylem sap (Johnson and Tyree, 1992). Like with *Acer* species, it is likely that the rhythmic diurnal temperature changes in pecan stems during late winter influence these gas bubbles, which in turn influence movement of sucrose and other simple carbohydrates into the xylem sap of pecan. Tyree (1983) notes that lack of subfreezing temperatures decreases the rate of sap flow over time. This was also apparent in the pecan trees studied here, because flow rate diminished over the collection period and as night temperatures warmed and failed to drop to freezing. He also notes that sap flow rate in large trees is closely linked to temperature changes taking place in small shoots; in a like manner, observations of sap flow in ‘Cheyenne’ and ‘Moneymaker’ trees was greatest when diurnal air temperature changes were also greatest. Tyree (1983) also noted that sap flow is unrelated to root pressure. Although there is limited late winter or early spring sap exudation from pecan stumps severed during

late winter (e.g., by cutting trees during orchard thinning) with diurnal swings in temperature, subsequent flow is a small fraction of that occurring when trunks are severely injured or tapped.

The high sap flow and relatively high sucrose concentration of xylem sap during the several days preceding budbreak is suggestive that this rhythmic diurnal pulsation of a high-energy carbon source, coming out of stem storage sites, is potentially influencing key growth and developmental processes of pecan. This sucrose is theoretically available for movement through both apoplastic and symplastic routes into axillary buds of shoots where subsequent sucrose enrichment of the bud meristem environment potentially influences the final phase (Phase III) of chromatin modifications needed for flowering (Wood, 2011). The observation here of a significant statistical difference in high sap flow and sugar (especially sucrose) concentration between what became “on” trees and the inverse in what became “off” trees is suggestive that one or more simple non-structural carbohydrates (especially sucrose) regulate the final phase of floral initiation occurring around the time of budbreak and therefore influence AB physiology. Observations in pecan of strong linkage between AB severity and previous growing season canopy health and photoassimilation productivity (Smith and Waugh, 1938; Sparks, 1975; Wetzstein and Sparks, 1983; Wood, 1989; Wood et al., 2004; Worley 1979a, 1979b) and by evidence that the final floral evocation processes (i.e., Phase III chromatin modifications) are intimately associated with tree carbohydrate reserves (Wetzstein and Sparks, 1983) support this conclusion. Additionally, this is consistent with findings for other species where sugars, especially sucrose, can regulate gene expression (Koch, 1996; Leon and Sheen, 2003; Li et al., 2003b). The relatively large change in cropload in consequence of sap flow (Figs. 1 and 2) is suggestive that the final floral initiation processes (Phase III) are sensitive to relatively small changes in sugar exposure.

Alternate bearing occurs at several levels (e.g., tree, branch, and shoot) within the tree and appears controlled by physiological events occurring during three regulatory phases during the annual growth cycle (Wood, 2011). Data here are suggestive that the last major factor influencing AB physiology is exposure of axillary meristems, within 1-year-old shoots, to sucrose (i.e., concentration and duration) provided by xylem sap flowing just before and during budbreak. Whether sucrose exposure would enable completion of the final phase of flowering necessarily depends on the degree of floral inhibition/promotion occurring during Phase II during the previous growing season as a consequence of the interplay between flowering promotes and inhibitors arising from developing fruit and foliage and as also influenced by the environment. Thus, if Phase II processes potentially enable flowering by axillary buds, then subsequent exposure to simple carbohydrates (e.g., sucrose) appears to enable completion of Phase III processes. Alternatively,

if Phase II processes fail to prepare the developing axillary bud for eventual possible flowering (i.e., floral-inhibiting hormones dominate over promoters), then high sucrose during Phase III, about the time of subsequent year budbreak, would not be expected to enable flowering. This potentially accounts for the variability observed in the present study regarding the relationship between sap flow and subsequent cropload. Based on the suppressive ability of developing fruit on Phase II flowering processes, especially in the case of “short shoots,” it may be that the impact of the above described sucrose effect is greatest for long shoots (Wood et al., 2004).

This study indicates that the volume of xylem sap flow, and associated concentration of sucrose and total simple carbohydrates, during the “late winter/early spring” transition period, when buds are swelling, is an indicator of subsequent in-shell nut cropload and by association spring floral load. This raises the possibility that sucrose made available from tree storage sites is the primary factor acting during this transitional period to trigger final chromatin modifications associated with floral meristems. These findings emphasize the importance of orchard managers implementing horticultural strategies favoring canopy health and photoassimilation productivity during the post-ripening period of the previous growing season, thus favoring greater storage of simple carbohydrates and ensuring late winter availability of sucrose and perhaps other simple carbohydrates needed for the final phase of floral initiation. It also 1) raises the possibility that pressure injection of sucrose into the xylem, just before or during bud swelling, will increase flowering; and 2) raises the question as to whether the sap exudation class of temperate zone AB tree species is Type-TD and whether non-AB tree species are Type-TI trees.

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