Relationship of Reproductive and Vegetative Characteristics of Pecan to Previous-season Fruit Development and Postripening Foliage Period

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Abstract. Alternately bearing 'Cheyenne' pecan [*Carya illinoensis* (Wangenh.) K. Koch] trees were studied to assess the temporal aspects of previous season fruit development on several reproductive and vegetative traits of horticultural importance. Action spectra were generated and used to identify the relative sensitivities of these traits to the temporal aspects of fruiting. Based on date of maximum rate of change in sigmoidal models fitted to these action spectra, the relative sensitivity of certain important growth and developmental parameters to fruit removal time was number of distillate flowers per terminal shoot > number of distillate flowers per flower cluster on lateral shoots > length of terminal shoots > percentage of lateral shoots with fruit = catkins per terminal shoot at top of the tree > percentage of terminal shoots with fruit > catkins per standard terminal shoot > shoots produced per 1-year-old branch > percentage of 1-year-old shoot death. Maximum rates of change for these reproductive and vegetative parameters were typically during the dough stage of ovule development; however, substantial change also occurred for several parameters over a much wider developmental window. No evidence was found for a hormone-like translocatable factor from developing fruit that either promotes or inhibits flowering. Extending the time from nut ripening to leaf drop increased production of staminate and distillate flowers the following year and appeared to increase fruit set.

Fruit production by individual trees and orchards of pecan is typically variable, exhibiting a strong tendency for bienniality at the tree and orchard level with epicycles of varying periods at regional levels (Wood, 1993b). The corollary is an impediment to the industry and growers due to unstable production, diminished nut quality during the "on" years, impaired marketing, and diminished economic returns.

The mechanisms regulating biennial bearing are unknown, appear to be complex, and are apparently ubiquitous in pecan. Differentiation of pistillate flowers is reported to occur by early August of the year preceding their initiation, with vernalization before the onset of rest being an absolute requirement for floret formation (Amling and Amling, 1983). The primary endogenous regulator has been theorized to be a) the level of carbohydrate reserves within the tree (Monselise and Goldschmidt, 1982; Smith and Waugh, 1938; Wood, 1989; Worley, 1979a, 1979b); b) endogenous hormone-like growth regulators produced by the fruit or foliage (Barnet and Mielke, 1981), similar to the seed inhibitor produced by some apple cultivars (Chan and Cain, 1967); or c) a dual mechanism based on carbohydrate levels within the tree and phytohormone balances (Smith et al., 1986; Wood, 1991). From a commercial perspective, the first and last hypotheses have proven satisfactory because factors favoring the accumulation of photoassimilates, such as rootstock (Wood, 1989), foliage retention and health (Himrichs, 1962; Worley, 1971, 1979a, 1979b), and source: sink ratio (Crane et al., 1934; Reid et al., 1993; Sparks and Brack, 1972; Smith and Gallott, 1990; Smith et al., 1993) greatly moderate the amplitude of the biennial cycle.

Clear evidence for a direct regulatory role for hormone-like substances as primary regulators of flowering@ pecan is lacking (Monselise and Goldschmidt, 1982; Wood, 1991). Much of the

evidence supporting carbohydrates as the primary regulator can also be interpreted to fit a phytohormonal model. Studies have not been performed in pecan to separate the relative roles of carbohydrates and phytohormone-like substances as primary regulators. One such test would be the blocking of phloem transport between developing fruit and associated developing buds. Because most axillary buds in pecan are capable of producing pistillate and staminate flowers (Wood and Payne, 1983) if allowed to complete development, their isolation from factors being directly translocated from developing fruit would be expected to influence flowering, since carbohydrate levels in shoots do not appear to be associated with flowering (Smith et al., 1986; Wood and McMeans, 1981).

The degree of alternation has also been hypothesized to be diminished in cultivars possessing early fruit ripening (Smith et al., 1986); this is attributed to there being more time for the tree to accumulate carbohydrate reserves before leaf fall (Smith et al., 1986). This conclusion was based on a positive association exhibited by three cultivars with different ripening dates. A critical test of the hypothesis necessitates a determination of the influence of the length of the postripening foliage period on flowering within a single alternately bearing cultivar.

The present study assesses several interrelated factors contributing insight into the alternate bearing of pecan. These include the dynamics of the temporal relationship between developing fruit and subsequent year reproductive and vegetative characteristics, the presence of a translocatable fruit-associated hormone-like promoter or inhibitor of flowering, and the effect of the extension of the postripening foliage window on fruiting.

Materials and Methods

Studies were conducted using 'Cheyenne' (growing on a 'Curtis' seedling rootstock) pecan trees growing in an orchard in central Georgia. 'Cheyenne' is a common commercial cultivar in the United States, is excessively prolific, and is a prime example of a

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severe alternately bearing cultivar. The study orchard was managed as a commercial orchard with water supplemented via drip irrigation (186 liters/tree per day) and was managed for nutrient elements and pests according to Georgia Cooperative Extension Service recommendations (Crocker, 1986). Tree spacing was at 9 × 9 m. The various experiments were as follows.

Experiment 1: Influence of defruiting date on reproductive and vegetative growth. Treatment trees had nearly maximum fruit set with essentially 100% of terminal shoots and about 50% of lateral shoots supporting fruit. Trees were 10 years old and largely maintained free of significant insect (incidental populations of yellow aphids) or pests and pecan scab during the study period.

The influence of defruiting time, or fruit development stage, on reproductive and vegetative growth characteristics in the subsequent growing season was determined by hand removal of all developing fruit at biweekly intervals from late June to early October and included a nondefruited treatment where fruit were allowed to naturally ripen on the tree. Experimental design was completely randomized, consisting of three replicates per defruiting date and one tree per experimental unit ($n = 27$ trees). Fruit were evaluated for developmental and growth characteristics at the time of defruiting. Trees were evaluated the following growing season for the effects of fruit removal date on number of pistillate flowers and catkins per terminal and per lateral shoot, percentage of terminal and lateral shoots with return bloom of distillate flowers, number of pistillate flowers per flower cluster on terminal and lateral shoots, length of terminal shoots, number of catkins per terminal shoot growing at the top of the tree, shoots produced per 1-year-old branch, and percentage of 1-year-old shoot death. Means were based on a random sampling of 50-100 subjects. Pearson correlation coefficients and regression models were determined using SAS-PC (SAS Institute, 1988). Analysis of the responses was based on a sigmoidal model whenever appropriate (TableCurve, 1991).

Experiment 2: Influence of date of phloem girdling on flowering. Shoots were used to test the hypothesis that a fruit-associated hormone-like translocatable factor is produced in developing fruit that promotes or inhibits flower formation in shoots originating from axillary buds. The experiment consisted of four treatments in which terminal shoots were selected at biweekly intervals from mid-May until fruit ripening. Treatments were ungirdled fruiting shoots, ungirdled nonfruiting shoots, partially girdled fruiting shoots, and partially girdled nonfruiting shoots. Fifteen or more shoots were selected per treatment per date per tree. The experiment consisted of a completely randomized design comprised of four replicates with individual trees serving as replicates. Shoots were girdled by removing a 5-mm-wide section of phloem and bark from about 5 mm above the second primary bud below either the fruiting cluster or the apical bud. This girdle extended two-thirds around the circumference of the shoot, being directly between the bud in question and the fruiting cluster or apical bud. All buds above the treatment shoots were removed by pruning before budbreak the following spring to force the development of the bud immediately below the girdled zone. Nongirdled shoots were also pruned at a location similar to the girdled treatments. Return bloom was monitored the following spring for treatment differences. SAS-ANOVA was performed on treatments per treatment date.

Experiment 3: Influence of extension of foliated postripening period on return bloom. The hypothesis that flowering is primarily regulated by photoassimilate levels was further evaluated by observing return bloom of trees as a result of extending the amount of time available from nut ripening until leaf fall for the accumulation of photoassimilates. Study trees were selected from a

population of trees to result in "on" bearing in the year of treatment. Differential fruit ripening was achieved by treating trees in late January with 2% hydrogen cyanamide (Dormex; Trostburg, Germany). This accelerated budbreak and other phenological processes, resulting in the advancement of fruit ripening by about 3 weeks (Wood, 1993a). Leaf drop in hydrogen cyanamide-treated trees occurred at the same time as in nontreated trees. The experiment therefore consisted of two treatments: a) trees with advanced ripening date and b) trees ripening normally. The advanced ripening date treatment provided a time window about 3 weeks longer than the untreated trees for accumulation of photoassimilates (about 7 weeks vs. 4 weeks) before natural leaf drop. The experiment was a completely randomized design comprised of two treatments with twelve replicates per treatment. Trees were monitored for return bloom and fruit set the following growing season.

Fig. 1. Growth characteristics of 'Cheyenne' pecan fruit. Growth curve functions were described by the following sigmoid functions: $f(x) = a + b / \{ 1 + \exp [- (x - c) / d] \}$; (A) Nut volume ($r^2 = 0.99$, $\alpha \leq 0.01$), where $a = 24.6$, $b = -22.9$, $c = 224.3$, $d = -5.2$; (B) fruit fresh weight ($r^2 = 0.99$, $\alpha \leq 0.01$), where $a = -0.6$, $b = 23.3$, $c = 227$, $d = 16.9$, and dry weight ($r^2 = 0.99$, $\alpha \leq 0.01$), where $a = -9.5$, $b = 71.2$, $c = 221$, $d = 18.1$; (C) kernel fresh weight ($r^2 = 0.99$, $\alpha \leq 0.01$), where $a = 0.99$, $b = 213.8$, $c = 227$, $d = 15.7$; and kernel dry weight ($r^2 = 0.99$, $\alpha \leq 0.01$), where $a = 0.07$, $b = 1.8$, $c = 265$, $d = 7.1$.

Results and Discussion

Experiment 1: Fruit growth characteristics. While the general developmental characteristics of pecan fruit have been documented (Hammar and Hunter, 1946; Woodroof and Woodroof, 1927), the growth and developmental phases-specific to 'Cheyenne' fruit have not and are presented to illustrate clearly the relationship between developmental events of fruit at the time of defruiting or girdling treatments and the subsequent relationship to reproductive and vegetative processes. Fruit growth of pecan is slow during the first few weeks after pollination (about 25 Apr.); thus, volume increase from pollination until late July [Julian date (JD) about 210] was slight (Fig. 1A). There was substantial acceleration in volume growth during August (maximum at JD-227 with 0.40 ml/day) with a concurrent and proportional increase in ovule growth.

Maximum fresh (290 mg/day) and dry (80 mg/day) weight accumulation rates for fruit tissues (excluding the developing ovule) were on JD-230 for fresh weight and JD-220 for dry weight (second week of August, Fig. 1B). As is typical for pecan, the expanding ovule was filled with an aqueous solution (termed liquid endosperm) during its enlargement period. This pressurized

liquid is especially noticeable during the latter portion of this expansion period, which is immediately before and during shell hardening, and is typically termed water stage.

During shell hardening, the endosperm is rapidly absorbed by the two developing cotyledons when they initiate (gel stage through dough stage) their rapid accumulation of dry weight. This accumulation by developing cotyledons continued until about 2 weeks before kernel ripening (as identified by involucre dehiscence or shuck split). Dry matter accumulation, and therefore demand for photoassimilates, was especially great during cotyledon growth (cotyledon growth stage). The rate of accumulated fresh weight was maximum (65 mg/day) at JD-244 (first week of September) and of dry weight (63 mg/day) at JD-270 (last week of September, Fig. 1C).

Functional relationships of reproductive structures to defruiting. All of the reproductive and vegetative growth parameters measured in this study, except date of budbreak, exhibited strong continuous functional relationships with defruiting date. SAS-GLM analysis of the data indicated significant ($\alpha \leq 0.01$) linear, quadratic, and cubic relationships for all measured parameters except budbreak date. These functional relationships were there-

Fig. 2. Action spectra describing the functional relationship between percentage of terminal shoots producing pistillate flowers (A) and the number of distillate flowers per fruiting terminal (B) to date of total defruiting during the previous growing season. Arrow depicts the beginning of cotyledon growth (gel stage) of the pecan kernel. Response equations for both parameters are sigmoidal where $f(x) = a + b / \{ 1 + \exp [-(x - c) / d] \}$. For parameter A, $r^2 = 0.99$ at $\alpha \leq 0.01$, where $a = 2.6$, $b = 93.6$, $c = 249$, $d = -6.7$, and for B, $r^2 = 0.95$ at $\alpha \leq 0.01$, where $a = 2.6$, $b = 1.6$, $c = 232$, $d = -14.6$. Dashed lines indicate the 95% confidence limits.

Fig. 3. Action spectra describing the functional relationship between number of catkins produced on standard (mid-canopy) terminal shoots (A) and on the shoots at the top of the tree (B) to date of total defruiting during the previous growing season. Arrows depict the beginning of cotyledon growth (gel stage) of the pecan kernel. Response equations for both parameters are sigmoidal, where $f(x) = a + b / \{ 1 + \exp [-(x - c) / d] \}$. For parameter A, $r^2 = 0.95$ at $\alpha \leq 0.01$, where $a = 0.4$, $b = 44.3$, $c = 252$, and $d = -18.7$; and for B, $r^2 = 0.98$ at $\alpha \leq 0.01$, where $a = 16.2$, $b = 258.2$, $c = 237$, $d = -15.1$. Dashed lines indicate the 95% confidence limits.

Fig. 4. Action spectra describing the functional relationship between percentage of secondary shoots producing distillate flowers (A) and the number of pistillate flowers produced per fruit cluster (B) to date of total defruiting during the previous growing season. Arrows depict the beginning of cotyledon growth (gel stage) of the pecan kernel. Response equations for both parameters are sigmoidal, where $f(x) = a + b/[1 - \exp \{-(x - c)/d\}]$. For parameter A, $r^2 = 0.98$ at $\alpha \leq 0.01$, where $a = 63.1$, $b = -64.4$, $c = 234$, $d = 10.0$, and for B, where $r^2 = 0.99$ at $\alpha \leq 0.01$, where $a = -0.14$, $b = 3.1$, $c = 229$, $d = -17.7$. Dashed lines indicate the 95% confidence limits.

fore well described ($r^2 = > 0.95$; $\alpha \leq 0.01$) by a sigmoid-type transition model $\{y = a + b/[1 + \exp \{-(x - c)/d\}]\}$ where a = upper asymptote, b = slope at inflection point, c = inflection point (point of maximum rate of change), and d = lower asymptote (Figs. 2–5).

The flowering characteristics of terminal shoots were greatly influenced by defruiting date during the previous growing season (Fig. 2), as has been reported by Reid et al. (1993) for ‘Mohawk’, ‘Gormely’, and ‘Giles’ pecan. The percentage of terminal shoots producing distillate flowers was a distinct function ($r^2 = 0.99$, Table 1) of defruiting date (Fig. 2A) and was also highly correlated ($r^2 = 0.78$ – 0.97) with all other measured growth parameters (Table 1) except budbreak date. (Budbreak correlations are excluded from table since there were no differences with treatments.) It was most closely associated with the number of catkins per terminal, implying that the production of male and female flowers are very closely linked.

The influence of date of defruiting on return flowering of terminal shoots was such that the percentage of fruiting shoots declined only slightly (9%, from 100% to 91%) with later defruiting until between late August and early September (JD-237 and 252).

This corresponded to the period in which the ovule became fully expanded and the cotyledons were just beginning rapid accumulation of photoassimilates (20–26 mg/day in dry weight, Fig. 1C). Subsequent defruiting dates resulted in the number of distillate flowers declining to the point that by the third week of September [JD-265 (shortly after the end of the dough stage)] there was only about 12% return flowering (Fig. 2A) with essentially no return bloom from later defruiting dates. Daily rates of loss in return flowering of terminal shoots was maximal at about 2% per day during early September (JD-249), which corresponded to immediately after the end of the dough stage (Figs. 1A and 2A).

The number of distillate flowers produced per terminal shoot also declined with delayed defruiting. Distillate flowers per cluster declined from 4.25 to about 2.7, with defruiting dates ranging from

Fig. 5. Action spectra describing the functional relationship between vegetative characteristics of shoots to date of total defruiting of trees during the previous year. Parameters are length of terminal shoots (A), number of shoots produced per 1-year-old branch (B), and shoot mortality (C). Arrows depict the beginning of cotyledon growth (gel stage). Response equations are sigmoidal, where; $f(x) = a + b/[1 - \exp \{-(x - c)/d\}]$. For parameter A, where $a = 2.8$, $b = 10.2$, $c = 238$, $d = -25.0$ ($r^2 = 0.96$, $\alpha \leq 0.01$); for B, where $a = 1.5$, $b = 0.9$, $c = 255$, $d = -16.4$, ($r^2 = 0.94$, $\alpha \leq 0.01$); and for C, where $a = 1.0$, $b = 55.8$, $c = 270$, $d = 3.7$ ($r^2 = 0.97$, $\alpha \leq 0.01$). Dashed lines indicate the 95% confidence limits.

JD-181 until 252 and with the maximum rate of change at JD-232 (Fig. 2B). This time of maximum change corresponded to the shell hardening period, or just a few days before the end of the liquid endosperm stage. A similar response was observed by Reid et al. (1993) with 'Gormely', 'Mohawk', and 'Giles' and by Sparks and Brack (1972) with 'Stuart'. These data expand on the work of these authors by providing an accurate linkage between the maximum rate of change for the number of pistillate flowers and fruit development and does so for a strongly cycling cultivar. In the present study, the number of nuts per cluster (pistillate flowers per cluster for terminal branches) was also highly correlated ($r^2 = 0.64$ to 0.93) with most other measured growth parameters, but was most closely associated with length of terminal shoot (Table 1), thus supporting earlier reports that, within a tree, pistillate flowers per shoot are closely related to shoot length (Gossard, 1933; Sparks and Heath, 1972; Woodroof et al., 1928).

The production of staminate flowers in the subsequent year was also regulated by defruiting time in the previous year (Fig. 3). The number of catkins (containing staminate flowers) per terminal branch at mid-canopy height and per terminal branch at the top of the tree (these are especially long branches) exhibited a negative functional curvilinear relationships with defruiting date. Although the number of catkins produced on especially long terminal branches at the top of the trees was about 6-fold greater than that from standard fruiting terminals, the relationships were very similar in that maximum loss of catkins occurred at JD-253 (just after the end of the dough stage) for standard terminal shoots (0.52 catkins per day) and at JD-237 (during the dough stage) for those long terminals at the top of the tree (four catkins per day). These data indicate that the development and growth of catkins on the long terminals at the top of the trees are more sensitive to defruiting than those produced from standard terminals along most of the trees perimeter. The number of catkins on terminal shoots was highly correlated with the other growth parameters measured in this study and was especially associated with length of terminal shoots (Table 1).

The relationship between flowering in lateral shoots (Fig. 4A) was analogous to that in terminal shoots except that the maximum percentage of lateral shoots producing pistillate flowers was about 63% (vs. 100% for terminals) and was substantially influenced by date of defruiting about 24 weeks earlier than were terminal shoots. The maximum rate of change in percentage of fruiting lateral shoots was a decline of 1.25% per day at JD-234, corresponding to the gel stage of kernel development (fourth week of August), whereas the date of maximum change for terminal shoots

was JD-249 (Fig. 2A). Defruiting between JD-237 and 252 (dough stage) or later resulted in essentially no return bloom on lateral shoots. These data therefore indicate that the processes associated with pistillate flower development in lateral shoots are substantially more sensitive to the effects of previous season overfruiting than are terminal shoots. This parameter was highly associated ($r^2 = 0.96$) with the percentage of terminal shoots producing pistillate flowers in the same year (Table 1).

The number of distillate flowers per flower cluster produced on lateral shoots that flowered the year after defruiting was also closely associated with date of defruiting (Fig. 4B). Distillate flowers declined from a maximum of nearly three per cluster in late June (JD-181) to none by the fourth week of September (JD-265). The maximum rate of decline was immediately before the initiation of the gel stage (at JD-229). A comparison of the time of maximum rate of change in the production of pistillate flowers per flower cluster produced on either terminal or lateral shoots indicated that these processes in terminal shoots maybe more sensitive to defruiting-related stresses than are lateral shoots; however, the difference is small and may simply be an artifact of the analysis. This parameter was highly correlated with the other measured growth parameters (Table 1) but was most closely associated with the percentage of terminals producing distillate flowers ($r^2 = 0.96$).

Functional relationships of vegetative structures. The measured vegetative parameters exhibited close functional relationships with defruiting date. Length of terminal shoots declined almost linearly from a maximum (13 cm) for defruiting in late June to a minimum (4 cm) when defruited by late September (JD-265) or later (Fig. 5A). The maximum rate of loss of shoot length was about 11 mm per day at JD-239, just at the initiation of the gel stage. Length of terminal shoots was closely associated ($r^2 = 0.93$) with distillate flowers per cluster and percentage of terminals producing pistillate flowers (Table 1).

The number of shoots (terminal and lateral) produced per 1-year-old branch also declined as date of defruiting was delayed (Fig. 5B). This decline went from about 2.3 to 1.5 by the time of natural fruit dehiscence, or ripening, in late October (JD-300). The maximum rates of change occurred about 3 weeks after the end of the dough stage (at JD-254). Number of shoots per branch was closely associated with all other growth parameters (Table 1); for example, 91% of the variation in this parameter could be accounted for by the length of the terminal shoots.

One-year-old shoots of trees exhibited high incidence of death in some treatments by the spring following defruiting. This death, when expressed as a percentage of total terminal and lateral shoots,

Table 1. Pearson correlation coefficients among reproductive and vegetative growth characteristics of 'Cheyenne' pecan.

Parameter ²	N/C	SL	C/S	C/T	S/T	DS	F/ST	FST
FT	0.78*	0.93*	0.97*	0.94*	0.93*	-0.86*	0.96*	0.96*
N/C	---	0.93*	0.82*	0.92*	0.84*	-0.64*	0.83*	0.91*
SL)		---	0.95*	0.99*	0.91*	-0.81*	0.92*	0.94*
C/S)			---	0.96*	0.92*	-0.90*	0.90*	0.88*
C/T				---	0.92*	-0.82*	0.93*	0.96*
S/T					---	-0.84*	0.89*	0.93*
DS						---	-0.75*	-0.72*
F/ST							---	0.96*
FST								---

FT = Percentage of terminal shoots producing female flowers; N/C= number of fruit per flower cluster; SL = length of fruiting terminal shoot C/S = number of catkins per midcanopy terminal shoot; C/T= number of catkins per terminal shoot from top of the tree; S/T = number o-f shoots per terminal; DS = percentage of dead shoots (terminal plus laterals); F/ST= number of fruit per fruiting secondary shoot; FST = percentage of secondary terminals producing female flowers.

*Significant at $\alpha \leq 0.01$.

exhibited a positive curvilinear relationship with increasing date of defruiting (Fig. 5C) to the point in which about 55% of such shoots had died by budbreak (about 28 Mar.) of the following season. The highest frequency of death occurred on trees where fruit were allowed to ripen and drop naturally from the trees. This disorder was not exhibited by trees defruited before early September (JD-252), or rather during or shortly after the dough stage. The rate of death greatly accelerated as the cotyledons accumulated dry weight and the kernel expanded. The rate of increase in death increased nearly linearly and dramatically from JD-260 to 275, with percentage being maximum at the cessation of kernel filling. Death occurred sometime between mid October and budbreak the following year, with dead shoots exhibiting an appearance of cold injury. Smith et al. (1993) reported an increase in cold injury with increased fruiting stress, but trees were exposed to an early and sudden November freeze (-12°C) while trees were still fully foliated. Cold injury to trees in the present study seems unlikely since the following fall–winter–spring was relatively mild; in fact, there were only a few days when temperatures dropped as low as -3°C , even at night. Isolations from damaged tissues produced an abundance of *Phomopsis* sp., a fungus that has been associated with fungal leaf scorch on pecan (Wood et al., 1994). This raises the possibility that this organism might be causing shoot death previously attributed to cold injury. This shoot death exhibited strong negative associations with all other growth parameters (Table 1).

Differential sensitivity to defruiting date. The dynamics of the gradient of change in the functional relationships of reproductive and vegetative parameters to defruiting date were generally maximal during the dough stage; however, the gradients of changes were such that rates during the liquid endosperm and shell hardening stages were usually only slightly less (Figs. 1–5). The gradient of change for most parameters was, therefore, relatively small with there being an absence of a sharp or pronounced change with defruiting date. The most narrowly defined window was the percentage of terminal shoots producing distillate flowers, with nearly all of the change occurring in something less than 28 days (Fig. 2). These slopes are taken as evidence against either a sudden burst (or spike) in production of a phytohormone-like regulator or sudden production or activation of hormone receptors.

Based on the time of maximum rates of change in functional relationships, reproductive and vegetative parameters exhibited differential sensitivity to defruiting date. These were typically during the dough stage and were such that sensitivities to defruiting were number of pistillate flowers per terminal shoot > number of

distillate flowers per flower cluster on lateral shoots > length of terminal shoots > percentage of lateral shoots with fruit = catkins per terminal shoot at top of the tree > percentage of terminal shoots with fruit > catkins per standard terminal shoot > shoots produced per 1-year-old branch > percentage of 1-year-old shoot death (Fig. 2).

Experiment 2: Influence of date of phloem girdling on flowering. The production of staminate and distillate flowers by buds subordinate to fruiting clusters or apical buds was greater on terminal shoots without fruit (about 55% and 27%, respectively) the previous year than on terminals with fruit (about 8% and 0%, respectively, Table 2). This is consistent with the strong alternate bearing nature of ‘Cheyenne’ pecan inasmuch that terminal shoots that were vegetative the previous season are typically fruiting during the subsequent season, whereas those fruiting the previous season are typically without fruit. There was no detectable effect of partial girdling (even at $\alpha \leq 0.10$), regardless of date of girdling, on subsequent year’s flowering by either fruiting or vegetative shoots.

These data indicate the likely absence of a fruit-produced inhibitor or promoter of flowering. The large zone of severed phloem (67% of circumference of shoot) did not reestablish a connection after girdling; thus, once severed, the translocation of fruit-produced substances to the already developed bud immediately below the girdled zone of phloem would have been unlikely, since lateral transport of assimilates from the phloem to the bud via transverse rays would have been minimal or nonexistent during the period of little to no bud growth (Zimmerman, 1974). The absence of statistical, or even numerical, differences in the occurrence of distillate flowers produced from previously fruiting shoots (Table 2), the absence of a girdling effect on staminate flowers of previously fruiting shoots, and the existence of a translocation barrier from about the time of fertilization until fruit ripening is evidence for the likely nonexistence of a fruit-produced phytohormone-like growth regulator that functions as a direct regulator of flowering the following year. Since the physiological differentiation of distillate flowers occurs by early August, before the beginning of the dough stage, phloem girdling treatments before this time would have been expected to have influenced return flowering if a fruit produced phytohormone were directly involved. While these data do not disprove the phytohormone hypothesis (Barnett and Mielke, 1981), they appear to substantially diminish its plausibility.

Experiment 3: Influence of extension of foliated post-ripening period on return bloom. Trees with foliage for 7 weeks between nut

Table 2. Influence of partial girdling of phloem immediately above buds of either fruiting or vegetative shoots of ‘Cheyenne’ pecan in an “on” year on percentage of shoots supporting flowers the following year.^a

	Julian date of treatment								
Treatment	131	153	188	215	229	243	257	271	292
	Staminate flowers (%)								
Fruiting/ungirdled	10 b ^y	17 b	7 b	7 b	7 b	3 b	3 b	7 c	7 b
Fruiting/girdled	10 b	10 b	7 b	7 b	7 b	3 b	7 b	7 c	7 b
Vegetative/ungirdled	57 a	51 a	50 a	57 a	43 b	53 a	67 a	57 a	54 a
Vegetative/girdled	53 a	57 a	60 a	53 a	47 b	53 a	50 a	53 b	47 a
	Pistillate flowers (%)								
Fruiting/ungirdled	0 b	0 b	0 b	3 b	0 b	0 b	0 b	0 b	0 b
Fruiting/girdled	0 b	0 b	0 b	0 b	0 b	0 b	0 b	0 b	0 b
Vegetative/ungirdled	30 a	30 a	30 a	27 a	20 a	23 a	30 a	23 a	27 a
Vegetative/girdled	33 a	23 a	23 a	33 a	20 a	30 a	30 a	30 a	23 a

^aThe girdled zone of phloem was 5 mm $\times$ 67% of short circumferences.

^bTukey’s studentized range (HSD) test; different letters within a treatment date are statistically different at $\alpha \leq 0.05$.

Table 3. Influence of extending the fruit postripening foliated period during “on” year on flowering and nut production in ‘Cheyenne’ pecan in an “off” year.

Treatment ^z	Catkins per shoot (no.)	Pistillate flowers per shoot (no.)	Shoots with catkins (%)	Shoots with pistillate flowers (%)	Nuts per tree (g)
Normal leaf retention	12 b ^y	2.5 b	6 b	3 b	151 a ⁱ
Extended leaf retention	26 a	2.9 a	10 a	5 a	226 a

^yExtension of postripening foliated period was achieved by treating trees with 2% hydrogen cyanamide (Dormex) during the previous January, resulting in about a 3-week advancement in budbreak and a proportional advancement in nut ripening. Normal leaf retention was for about 4 weeks, whereas extended retention was for about 7 weeks.

^zTreatment differences based on ANOVA with $\alpha \leq 0.05$; different letters reflect differences.

ⁱStatistical differences at $\alpha \leq 0.10$.

ripening and leaf fall produced more catkins and pistillate flowers per terminal shoot that produced flowers than those with foliage for 4 weeks (Table 3). These trees also had a greater percentage of their shoots producing catkins and pistillate flowers and ($\alpha \leq 0.10$) produced a larger crop of in-shell nuts per tree during the subsequent “off” year. These data therefore provide a test of the conclusion by Smith et al. (1986) that earlier ripening cultivars are more likely to exhibit less cycling; hence, the amount of time a tree has available for replenishing carbohydrate levels between the end of fruit growth and leaf abscission favorably influences next year’s fruit production. This also supports observations by Worley (1979) that photoassimilates accumulated in the fall are especially important to return flowering. These data are therefore consistent with the hypothesis that tree carbohydrate levels function as the primary regulator of flowering. Furthermore, the data indicate that, within a specific cultivar, the extension of the foliated period will increase next year’s production.

Conclusions

These data provide the first reported description of the action spectra of the relationship of several important horticultural traits that influence crop yield to time of total fruit removal, thus providing new insight into the relationship between these traits and previous season fruiting-related physiological processes. These data also provide insight into the nature of the primary regulators of flowering in pecan.

The results of these three studies are consistent with the hypothesis that flowering in pecan is primarily regulated by the availability of photoassimilates, with the role of endogenous phytohormone-like regulators being ancillary. For example, the strong correlations between increasing date of defruiting and decreasing values for key reproductive and growth parameters are highly compatible with a regulatory role for photoassimilates (Figs. 2–5, Table 1). While such a response does not necessarily disregard a primary role for phytohormone-like promoters or inhibitors, the additional lack of direct evidence for a flower-regulating phloem translocatable factor originating from the developing fruit evaluated in this study (Table 2) lends further credibility to the photoassimilate hypothesis. The plausibility of this conclusion is further enhanced by the observed production of more staminate and pistillate flowers per flowering shoot, more flowering shoots, and more nuts produced on trees having 3 weeks longer to replenish photoassimilate reserves before leaf fall (Table 3). A critical role for carbohydrates in the flowering process is further based on the observation that pecan trees have poor return bloom following diminished leaf area in the previous fall (Himrichs,

1962; Worley, 1971), and often produce a reasonably good crop of pistillate flowers that later abort before fruit set (Sparks and Brack, 1972), especially when produced on shoots of low vigor or short shoots (Sparks and Heath, 1972).

If phytohormone-like growth regulators were directly involved in flowering in pecan, then these data indicate that the effect of such regulators would likely be cumulative up until early August, when pistillate flowers are reported to be differentiated (Amling and Amling, 1983). This is because the action spectrum produced in this study, based on variable defruiting dates, failed to detect a sudden effect of a promoter or inhibitor on return flowering or any other growth parameters.

These data also carry practical ramifications regarding the emerging cultural practice of regulating alternate bearing via fruit thinning in years of excessive fruit loads. For example, this thinning operation should be done at the earliest practical opportunity to minimize the detrimental impact of the present season’s crop on next season’s reproductive and vegetative growth. Mechanical thinning is currently implemented just before the initiation of the dough stage, when the fruit have just attained a size and weight that facilitates good separation from the tree when shaken. The delay of thinning to this later date appears to be effective for many cultivars and is likely to result in only a slight reduction in the percentage of terminal shoots fruiting the following year (Fig. 2A). However, these data also indicate that delaying thinning to just before the dough stage is not likely to be without a significant negative impact on other important reproductive and vegetative parameters. Thinning should ideally be accomplished several weeks before the gel or dough stages of fruit development; however, to accomplish this the present mechanical techniques would require alteration (due to the need for a massive fruit for mechanical thinning to be successful) or the development of chemically based strategies. These general conclusions support those reported by others (Reid et al., 1993; Smith et al., 1993, 1986; Sparks and Brack, 1972) based on thinned trees where fruit were either removed from one-half of the tree or somewhat uniformly throughout the canopy. In a thinning study by Reid et al. (1993), it was observed that the greatest return bloom of ‘Mohawk’ and ‘Giles’ by thinned shoots occurred when thinned shortly after pollination; this is similar to that typically observed in apple (*Malus domestica* Borkh.) (Williams, 1979). Data from the present study corroborates this conclusion for terminal and secondary shoots, with the sensitivity to date of fruit removal being much greater for lateral than terminal shoots.

These data are consistent with the hypothesis that it is the sink vs. source relationship associated with reproductive and vegetative growth that largely regulates fruit set; consequently, endog-

enous factors mediated by tree carbohydrate levels appear to regulate flowering. These data do not exclude the likelihood that the endogenous factors linking fruit growth and development with carbohydrates include phytohormone-like substances. Orchardists should therefore adopt management strategies that ensure an abundance of healthy foliage if alternate bearing is to be minimized without fruit thinning.

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