

Relationship of Alternate Bearing Intensity in Pecan to Fruit and Canopy Characteristics

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Abstract. Alternate bearing is a major economic problem for producers of pecan nuts [*Carya illinoensis* (Wangenh.) K. Koch], yet a fundamental understanding of alternate bearing remains elusive. Nut yields (over a period of up to 78 years) from a commercial-like orchard of 66 cultivars was used to calculate alternate bearing intensity (*I*). Best-fit regression analysis indicates no association between *I* and fruit ripening date (FRD) or nut volume; although, there was moderate association with post-ripening foliation periods (PRFP) in that *I* tends to decrease as the length of the PRFP decreases. Multiple regression models indicated that FRD and nut volume were poor predictors of *I*: however, PRFP possessed significant inverse predictive power. Late-season canopy health, as measured by percentage of leaflet retention, decreased as FRD approached early-season ripening. Late-season photoassimilation rate was higher on foliage of trees with late FRDs than those with mid- or early-season ripening dates. These data provide new insight into the complex nature of alternate bearing in pecan and provide evidence for modifying the existing theories of alternate bearing of pecan.

Many polycarpic tree species exhibit strong biennial alternations in cropping (Monselise and Goldschmidt, 1982). In respect to pecan, this biennial cycling in flowering can also become an irregular cycle exhibiting various degrees of interannual alternations. This phenomenon is termed “alternate bearing” and is typically enhanced and synchronized by a dominating biotic or abiotic stress factor that in turn triggers high amplitude cycling of both yields and revenue from trees, orchards, farms, and regions (Gemoets et al., 1976; Wood, 1993, 1995). Alternate bearing is therefore often regarded as the economically most important biological problem of pecan husbandry in the United States (Amling and Amling, 1983).

The solution to this alternate bearing problem is embedded within the physiological processes associated with flowering and fruit-set. Crops from individual trees typically alternate between large and small crops, with relatively large crops exhibiting low nut quality (i.e., “on” year) and small crops exhibiting high nut quality. However, pecan differs in a fundamental manner from many alternate bearing crop species in that individual trees sometime bear two or three consecutive “on” crops of moderate to high yields before exhibiting a

pronounced “off” year (Sparks, 1974). Thus, alternate bearing by pecan trees can display pronounced “irregularity.” Understanding the alternate bearing phenomena is therefore fundamentally important to the optimization of husbandry strategies.

A study by Pearce and Dobersek-Urbanc (1967) of methods to quantify the bienniality aspect of alternate bearing, the most pronounced form of irregular bearing, concluded that this phenomenon is quantifiable by the measure “*I*.” Although production irregularity is affected by random environmental variations, such as weather, *I* remains a highly useful measure of irregularity, has a near normal distribution and is largely insensitive to production trends. Thus, *I* is commonly used for measuring alternate bearing in tree crops.

The basic physiology of alternate bearing in pecan is unknown. Its limited study has produced two generalized theories—the “Carbohydrate Theory” (CT) and the “Phytohormone Theory” (PT) (Barnet and Mielke, 1981). Neither theory has been clearly defined in terms of specific floral evocation, induction, or developmental processes. Of the two, the CT is most commonly advocated (Wood, 1991). It purports that flowering, and subsequent cropping, is fundamentally controlled by the tree’s dormant season carbohydrate pool. Conversely, PT purports that flowering, and subsequent cropping, are fundamentally controlled by flower suppressing or promoting phytohormone-like substances produced by fruit, leaf tissues, or both.

After the identification by Smith and Waugh

(1938) of a linkage between root carbohydrate levels and fruiting, followed by supporting findings by others (Sparks and Brack, 1972; Wood, 1989; Worley, 1978, 1979a, 1979b), CT has become the foundation on which essentially all husbandry strategies of pecan are based (Wood, 1991). The discovery of phytohormone-like substances produced by pecan fruit and foliage (Wood, 1982), plus moderation of alternate bearing by removing fruit prior to kernel filling (Reid et al., 1993; Smith and Gallot, 1990; Smith et al., 1993; Wood, 1995), provides evidence of a key regulatory role for endogenous phytohormone-like substances and perhaps an ancillary role for the endogenous carbohydrate pool. A similarly shared regulatory role, for carbohydrates and phytohormone-like substances, is hypothesized for several other tree fruit crops [i.e., apple (*Malus ×domestica* Borkh.), olive (*Olea europaea* L.), pistachio (*Pistacia vera* L.), avocado (*Persea americana* Mill.), and mango (*Mangifera indica* L.)] (Monselise and Goldschmidt, 1982).

The general CT predicts that fruit-set is proportional to the dormant season carbohydrate pool and implies that pool size is proportional to late-season net photoassimilation capacity of the tree’s canopy. Thus, it is commonly assumed that cultivars ripening fruit relatively early in the growing season, or possessing a longer post-ripening foliation period, will accumulate a larger photoassimilate pool and therefore exhibit a lower intensity of alternate bearing than those ripening relatively late in the season. Because of ramifications pertaining to breeding strategies, cultivar selection, and husbandry strategies, this putative relationship merits validation. We report here an estimation of the relationship between alternate bearing intensity (*I*) and fruit ripening date (FRD), nut volume, and length of the post-ripening foliation period (PRFP).

Materials and Methods

Alternate bearing as related to fruit ripening, nut volume, and post-ripening foliation period. Alternate bearing intensities (*I*) in this study are from Conner and Worley (2000), who recently reported *I* for 66 pecan cultivars based on up to ≈75 years of production data from trees grown at Tifton, Ga. (on the Gulf Coast Coastal Plain). These data reflect yield performance for both relatively young trees (with data collection beginning at age 9 to 20 years) and old trees (with data collection beginning at ages from 9 to 30+ years). *I* was determined for young trees using yield data from age 9 to 20, whereas *I* for older trees was used based on at least 20 consecutive years of yield data. These trees received commercial-like cultural and pest management inputs typical of those in the southeastern United States during the life of the trees. These identical trees were measured in the autumn of 2001 for date of fruit ripening (date when >50% of fruit exhibited split shuck sutures; FRD), post-ripening foliation period (date of 75% canopy defoliation minus date of fruit ripening; PRFP), and in-shell nut volume (based on 100 nuts per tree). Alternate bearing

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intensity indexes, or I , were regressed against FRD, PRFP and nut volume for trees of two age classes: “younger” trees (i.e., calculations based on yields from 9- to 20-year-old trees) receiving fungicide sprays for the control of pecan scab; and “older” trees (i.e., calculations based on nut yields from 9- to 30+-year-old trees) receiving the same fungicide sprays for the control of pecan scab. Nut volume tends to be stable, within a genotype, when mature trees receive good culture (Sparks, 1992). The cultural and pest management programs used on these trees through the years varied, but were generally conducted according to Georgia Cooperative Extension Service recommendations for commercial pecan orchards.

Copious anecdotal evidence indicates that the magnitude of alternate bearing intensity is a relatively stable defining characteristic of a particular cultivar (ex. ‘Desirable’ typically exhibits a low I whereas ‘Chickasaw’ exhibits a high I , regardless of where or how the cultivar is commercially cultivated); and that relative differences in alternate bearing severity between any two cultivars tends to be highly similar in commercially cultivated orchards. Thus, the above described relationships between I and FRD and PRFP was also tested for a second cultivar population. Fruit ripening date and leaf fall data from this nearby site (i.e., Byron, Ga.; ≈ 140 km from Tifton; also on the Gulf Coast Coastal Plain, and also in the same U.S. Dept. of Agriculture (USDA) Plant Cold Hardiness Zone of 8a) were collected over a 5-year period (Wood et al., 1997). The two locations are nearly identical with regard to both elevation, climate, weather and cultural practices. Additionally, several years of observations by the authors indicated that both absolute and relative FRDs vary little between the two locations. Data were analyzed with the SAS statistical system (SAS Institute, Cary, N.C.) for linear, quadratic, and cubic regression components and for best-fit multiple regression models. This cultivar population was segregated into two nut volume classes before regression analysis of I against PRFP. Cultivars were segregated into “large” [those at least as large as ‘Stuart’ (>13.5 cm³)] and “small” [those smaller than ‘Stuart’ (<13.5 cm³)] volume classes.

Relationship between canopy health and ripening date. An ≈ 18 -year-old cultivar collection, grown under drip irrigation, was evaluated for canopy health and fruit ripening dates in 2000 and 2001. The orchard included two replications of 81 cultivars and received fertility, disease, and arthropod control measures according to Georgia Cooperative Extension Service recommendations for commercial pecan orchards. Trees were evaluated twice weekly from early September until mid-November to determine the time of fruit ripening (date when $>50\%$ of fruit exhibited split shuck sutures; FRD). They were again evaluated on a single date in mid-November for canopy health based on the percentage of leaflets remaining on shoots (percentage of total leaflets remaining on 10 shoots randomly sampled 3 m aboveground on the eastern side of the canopy). FRD and canopy health were regressed using SAS as described above.

Foliage photoassimilation rates (A) of trees with FRDs, ranging from 1 week prior to the autumn equinox to ≈ 6 weeks afterwards, were also measured from the above described cultivar collection. A was measured on the apical-most leaflet of the apical-most compound leaf on three randomly selected terminal shoots 2 m aboveground on the eastern side of the canopy. Measurements were taken from 0900 to 1200 hr using a LI-COR 6400 (LI-COR, Lincoln, Nebr.) portable open-system photosynthesis apparatus (Wood, 1988). Measurements were made at a photosynthetic photon flux of 1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, at ≈ 400 ppm CO₂, on attached foliage from trees receiving ≈ 50 L water per day via drip irrigation. A was regressed against fruit ripening date using SAS regression techniques as described above.

Results and Discussion

Alternate bearing as related to ripening dates of cultivars. I derived from younger and older tree populations of the same cultivar were highly associated ($R^2 = 0.89$; Fig. 1); thus, the degree of irregular bearing exhibited by an individual cultivar was very similar, regardless of tree age.

I of the “younger tree” or “older tree” population of cultivars at the Tifton orchard reflected FRDs ranging from 5 d before the equinox to 42 d after the equinox (a 47-d range) (Fig. 2A), whereas the “older tree” population consists of cultivars ripening from 11 d after the equinox to 43 d after the equinox (a 32-d range) (Fig. 2B). These dates encompass $>90\%$ of the variation in ripening dates exhibited by pecan cultivars (Sparks, 1992).

There was little or no linkage between I and FRD ($R^2 < 0.02$, and $P > 0.20$), regardless of tree age class (Fig. 2). These data indicate that the nature of genetic control over alternate bearing is such that its intensity, I , is only loosely linked to date of fruit ripening. For example, ‘Moneymaker’ and ‘Barton’ are early ripening genotypes, yet their I values were much greater than ‘Sumner’ and ‘Farley’, which are late ripening genotypes. Other evidence supporting a weak genetic relationship between I and FRD is the observation (by the senior author) that a well-tended tree exhibiting unusually early fruit ripening (in Jaumave, Tamaulipas, Mexico; ripening in mid-July, ≈ 60 + d ahead of most cultivars and ≈ 120 d before leaf fall) also exhibits severe alternate bearing. Because alternate bearing is not necessarily diminished in early-ripening genotypes, breeding efforts to effectively overcome alternate bearing must also include additional traits.

Alternate bearing as related to duration of post-ripening foliation period of cultivars. Regression analyses indicated that 23% of the variation in I of the “younger tree” population was positively associated with length of the PRFP (Fig. 3A). Thus, the shorter the post-ripening period the less the intensity of alternate bearing. This relationship between I and PRFP was even stronger (with PRFP accounting for 43% of the variation in I) in the “older tree” population (Fig. 3B).

Analysis of cultivars in common between the Tifton orchard and the Byron orchard (i.e., having 5 years of data on the length of the post-ripening foliation period of several cultivars) confirmed the relationship between I and PRFP as described above (data not shown) and the

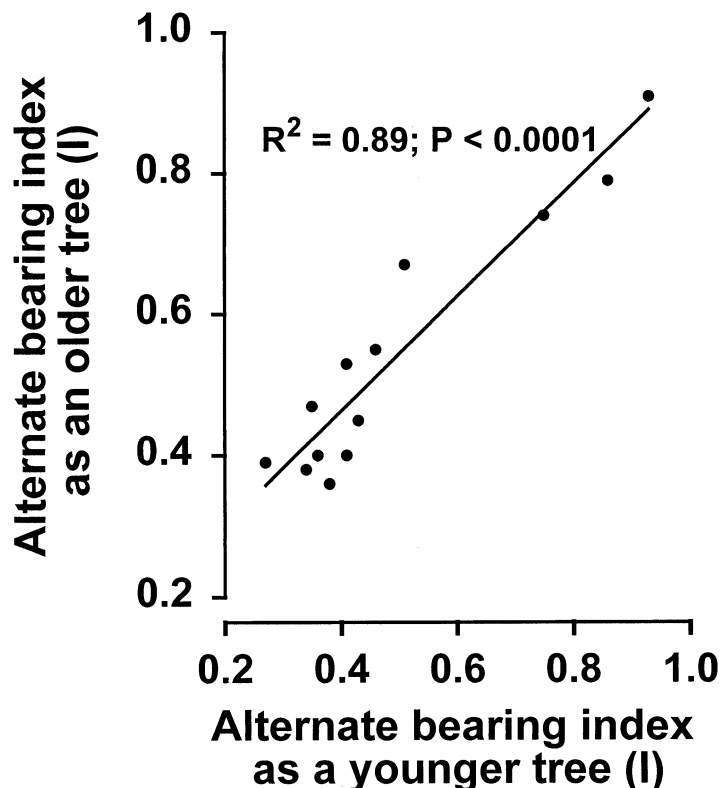


Fig. 1. Linear regression of the relationship of alternate bearing intensity (I) exhibited by relatively old trees (i.e., chronologically) to I exhibited by relatively young trees of the same cultivar.

lack of relationship between *I* and FRD (data not shown). When these cultivars were segregated into “small nut volume” vs. “large nut volume” classes and the relationship between *I* and PRFP determined, there were only slight associations ($R^2 < 0.11$; $P > 0.30$) with “small nut volume” cultivars in either the “younger tree” or the “older tree” populations (data not shown). However, with the “large nut volume” population there was a much stronger association between *I* and PRFP for “younger”, “older”, and “all” tree populations (Fig. 4). In the case of the “younger trees”, 58% of the variation in *I* was positively associated to the length of PRFP (Fig. 4A), whereas 38% was associated in the “older tree” population (Fig. 4B).

Again, with cultivars possessing nuts with large volumes, the longer the post-ripening foliage period, the greater the intensity of alternate bearing. There was a much weaker relationship with cultivars possessing small volume nuts. Thus, these observations involving data from two different orchards and tree populations agree with each other in regards to the association between “*I* and FRD” and “*I* and PRFP”.

Alternate bearing as related to nut volume. An evaluation of the “younger” and “older” populations of cultivars for the relationship between *I* and nut volume revealed an absence of linear or quadratic associations within either the “younger” or “older” tree populations (Fig. 5). Thus, breeding efforts to minimize *I* must necessarily take into account factors other than nut size (i.e., possibly nut-set per cluster, percentage of fruiting shoots, oil content of kernels, leaf area to kernel mass ratio, leaf photosynthetic efficiency, etc.).

Multiple regression models. Incorporation of all combinations of FRD, PRFP, and nut size as independent variables in multiple regression models failed to generate a model possessing reasonable statistical significance (i.e., $P > F = \leq 0.20$; models not shown) for predicting *I*. This was true for both “younger” and “older” tree populations. However, it is noteworthy that PRFP was much more predictive than were FRD or nut size. Thus, models for prediction of alternate bearing intensity must also include traits not evaluated in this study (i.e., perhaps nut cluster size, oil content of kernels, photosynthetic efficiency of foliage, leaf area to fruit mass ratio).

Fruit ripening date and canopy health and photoassimilation. Canopy health, as measured by the percentage of foliage present in the lower canopy in mid-November, was closely associated with the date of fruit ripening (Fig. 6A). About 52% of the variation in canopy health was associated with FRD, with health increasing with latter fruit ripening dates. Cultivars ripening fruit early in the fruit ripening period (about the time of the autumn equinox) exhibited canopies that were largely defoliated by mid-November, whereas those ripening fruit late in the fruit ripening period (i.e., 6 to 8 weeks after the autumn equinox) exhibited canopies that were well foliated.

When specimen leaflets of the lower canopy were measured in mid-November for photoassimilation rate it was discovered that “A” declined in a curvilinear manner as FRD approached the autumn equinox (Fig. 6B). About 76% of the variation in A was associated with FRD. Foliage from trees exhibiting late-season fruit ripening possessed A rates 3- to 5-fold greater than rates of foliage from trees ripening fruit around the time of the autumn equinox. Thus, late-ripening cultivars tend to maintain more canopy later in the growing season and

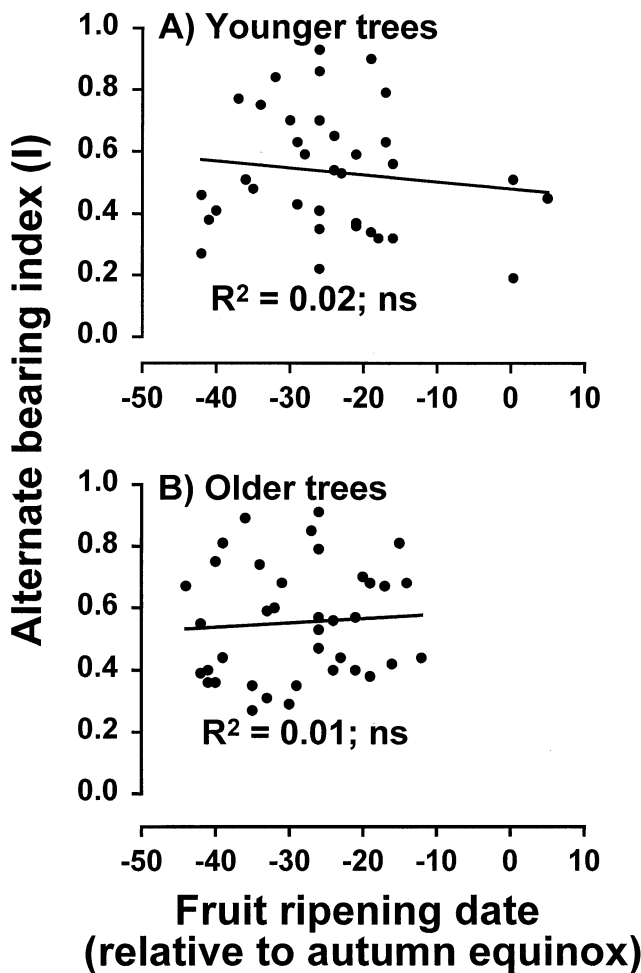


Fig. 2. Linear regression of alternate bearing intensity (*I*) to date of fruit ripening (FRD) of several pecan cultivars cultivated over a 75-year period at Tifton, Ga. Regressions are for: (A) “younger trees” (age 9 to 20 years), and (B) “older trees” (age 9 to 30+ years). R^2 s are nonsignificant at $P < 0.25$. Positive numbers for fruit ripening dates are dates earlier than the autumn equinox whereas negative numbers are dates after the autumn equinox.

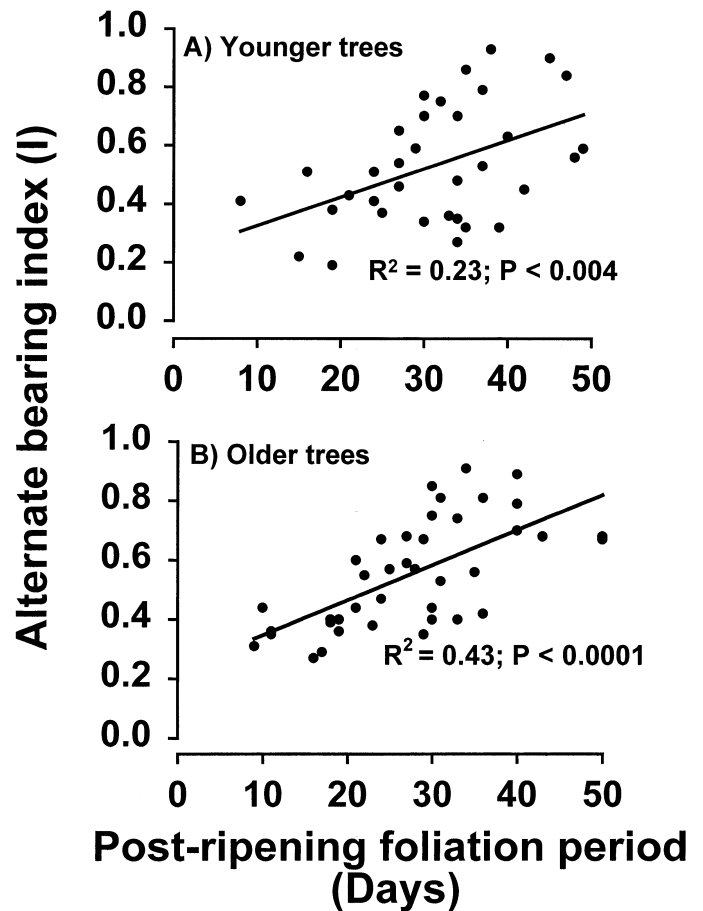


Fig. 3. Linear regression of the relationship of alternate bearing intensity (*I*) to the duration of the post-ripening foliage period (PRFP) of pecan cultivars. Regressions are for: (A) “younger trees” (age 9 to 20 years), and (B) “older trees” (age 9 to 30+ years).

also maintain a higher rate of photoassimilation than do early ripening cultivars.

Reconciliation with salient alternate bearing theories. These data provide new and unexpected insight into alternate bearing of pecan. Although not a critical test of the two predominate theories of alternate bearing, these data illustrate phenomena to which a viable theory must be reconciled. Thus, the two prominent theories merit an evaluation within the context of these findings.

The CT purports that it is the magnitude of the tree's carbohydrate reserves that controls flowering, crop set, and variations in alternate bearing. This theory is derived from observations showing that: 1) cropping is closely linked to dormant season assimilate reserves, especially those in roots (Smith and Waugh, 1938; Sparks, 1974; Waugh and Smith, 1936; Wood, 1989; Worley 1979a, 1979b); 2) reductions in canopy health or longevity, enhance the intensity of alternate bearing, whereas long-lived and healthy canopies result in greater return fruit set (Hinrichs, 1962; Worley, 1979a, 1979b); 3) crop-set by certain early-ripening cultivars is greater than that of certain late-ripening cultivars when crop load is thinned in the previous year (Smith et al., 1986); 4) trees and limbs appear to possessing a certain source : sink (leaf : fruit) equilibrium

that exhibits a relatively low alternate bearing intensity (Wood, 1991); 5) there is a high positive correlation between fruit set and growth of shoots and leaves (Gossard, 1933); and 6) return bloom is often only mildly reduced in crop years following a large nut crop largely devoid of kernels (Davis and Sparks, 1974). Thus cultural and pest management practices enhancing canopy health and retention usually reduce alternate bearing intensity, but do not eliminate the cycling phenomena (Conner and Worley, 2000). The CT functions well as a "conceptual tool" on which husbandry practices are based.

It is commonly accepted, in the case of pecan, that alternate bearing is tightly linked to: 1) date of fruit ripening relative to the length of the growing season; 2) duration of kernel filling; and 3) lipid content of kernels (Sparks, 1974). Pecan fruits typically ripen >40 d later than most other deciduous trees (Sparks, 1974)—during the last one-third of the growing season. During this time photosynthetically active radiation levels rapidly decline as leaves senesce and abscise in preparation for winter (Wood, 1988).

Conversely, the PT identifies phytohormones as the primary factor(s) controlling flowering, crop set, and alternate bearing. The PT (Barnet and Mielke, 1981) is supported by

observations that: 1) return bloom is usually inversely related to the size of the previous crop and with return bloom becoming greater as the duration of the presence of developing fruit diminishes—even much earlier than the initiation of cotyledon filling (Wood, 1989); 2) the removal of fruit during "late water stage" (immediately prior to the initiation of significant kernel filling) of development has a large positive impact on return bloom before there is significant deposition of kernel dry weight (Crane et al., 1934; Reid et al., 1993; Smith and Gallot, 1990; Wood, 1989); 3) water stage fruit contain substantial amounts of gibberellin-like substances (Wood, 1982), a phytohormone known to inhibit flowering in certain other tree species (Greene, 2000) [thus serving as the basis of the pecan management practice of mechanically reducing crop load in which kernels exhibit little or no development (Reid et al., 1993; Smith et al., 1986; Smith and Gallot, 1990)]; 4) shoots, branches, and limbs can cyclically bear on opposite cycles (Wood, 1991); 5) there is little or no difference in concentration of total carbohydrates in 1-year-old shoots where flowers are produced for the following crop season (Smith et al., 1986; Wood and McMeans, 1981); and 6) pistillate flowers are physiologically differentiated by early August (i.e., 2–3 weeks before the initia-

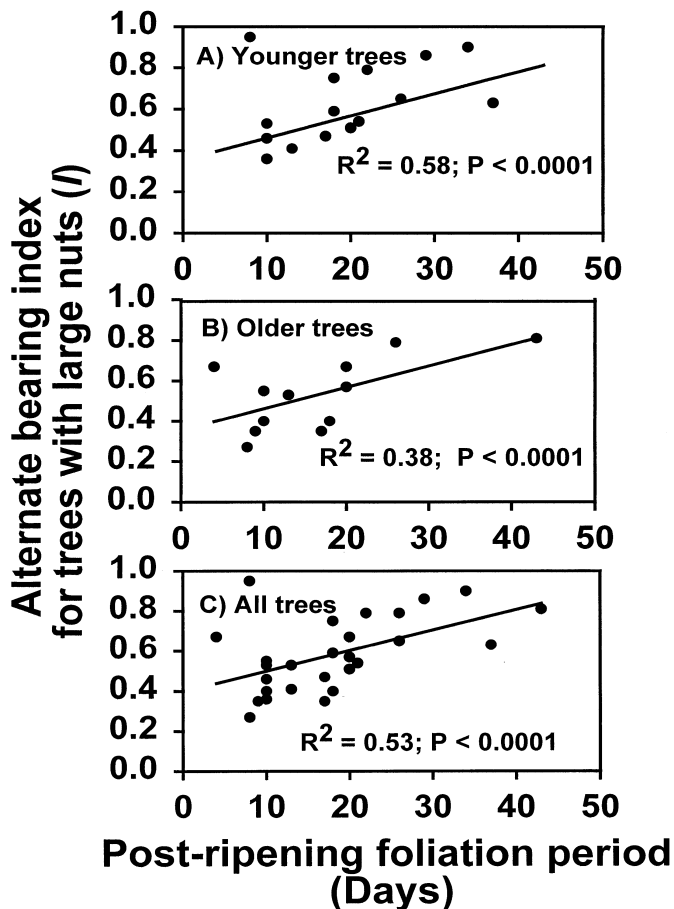


Fig. 4. Linear regression of the relationship of alternate bearing intensity (I) to the duration of the post-ripening foliation period (PRFP) of pecan cultivars characteristically possessing large-size nuts ["large" = >13.5 cm³ per in-shell nut (i.e., >'Stuart'). Regressions are for two tree-age populations (i.e., "younger trees" and "older trees"; where A) younger = 9 to 20 years; B) older = age 9 to 30+ years; and C) "all" is for both age groups combined).

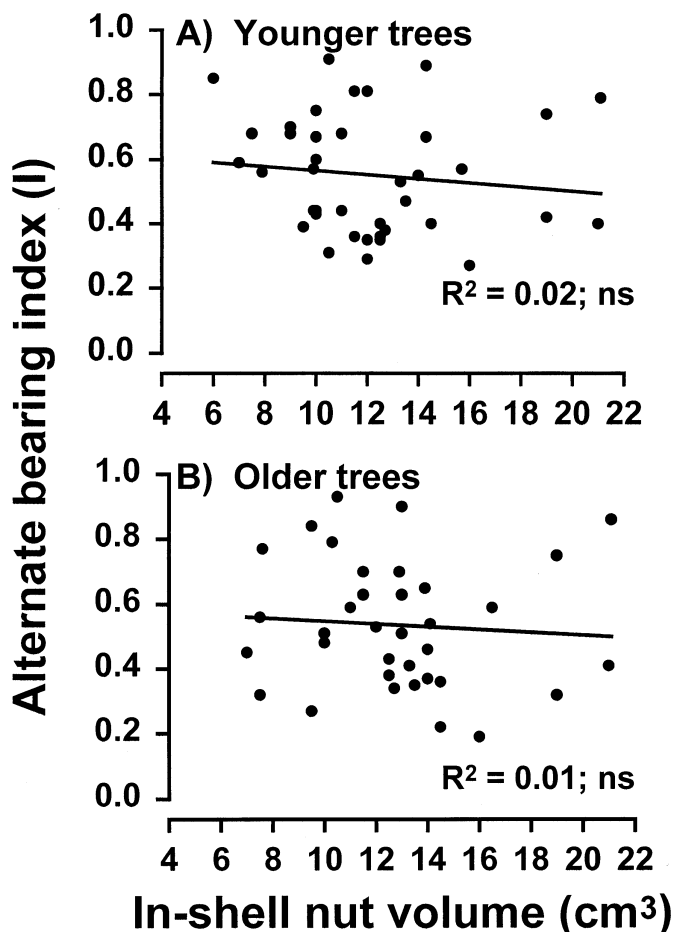


Fig. 5. Linear regression of the relationship of alternate bearing intensity (I) to characteristic nut volume of pecan cultivars. Regressions are for: A) "younger trees" (age 9 to 20 years), and B) "older trees" (age 9 to 30+ years).

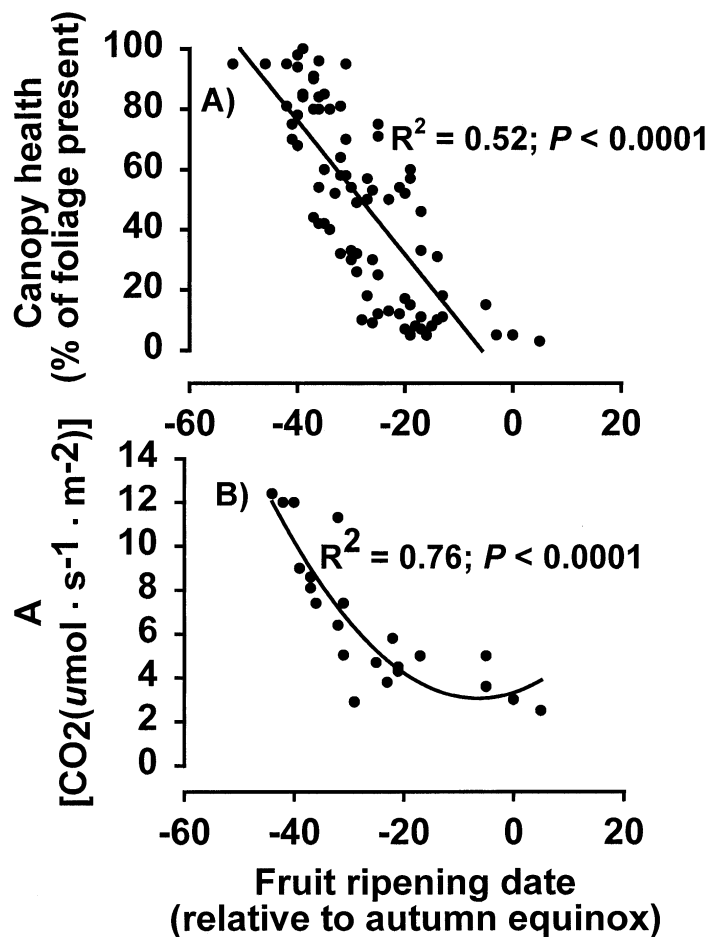


Fig. 6. Regression of the relationship of A) canopy health and B) photoassimilation to fruit ripening date. Positive numbers for fruit ripening dates are dates earlier than the autumn equinox whereas negative numbers are dates after the autumn equinox.

tion of kernel filling) of the year preceding their initiation (Amling and Amling, 1983; Wood 1995). The classical PT attributes year-to-year variations in flowering, crop-set, and alternate bearing intensity, to one or more flowering inhibitors produced by developing fruit, foliage, or both.

It is noteworthy that regardless of the mechanism controlling alternate bearing, physiologically differentiated pistillate flowers require vernalization if they are to develop into flowers the following growing season (Amling and Amling, 1983).

Data from the present study do not necessarily disagree with the CT, but it does require revision of thinking in regards to how carbohydrate reserves may be regulated in pecan. The CT implies that, for a diverse population of cultivars, there should be a strong statistical linkage between alternate bearing intensity and factors that either enhance or prevent the buildup of carbohydrate reserves in storage tissues during the dormant season. Thus, factors such as date of fruit ripening and duration of the post-ripening foliage period, especially for large nut-size cultivars, would be expected to be closely linked to alternate bearing intensity due to their perceived likelihood of influencing carbohydrate reserves.

The present study indicates little or no linkage between *I* and FRD, yet at least a

moderate linkage with PRFP. Curiously, this linkage is opposite of that commonly perceived—in that cultivars with a short PRFP tend to exhibit the least degree of alternate bearing and those with a long PRFP exhibit a higher *I*. The above described data on canopy health and photoassimilation indicates that this *I*-PRFP linkage could be attributed to a greater photosynthetic output of the tree's canopy. Trees ripening fruit in late season also tended to retain canopy and have higher late-season photoassimilation rates than those ripening in early season. Therefore, early fruit ripening appears to advance the initiation of leaf senescence (especially from the standpoint of photoassimilation) and late fruit ripening appears to delay or retard the onset of senescence. Thus, trees with a short PRFP may possibly benefit from a greater accumulation of assimilate reserves in storage tissues which influence flower initiation or development. This explanation is supported by the observation that fruit enhance net photosynthesis and delay senescence of adjacent foliage of pecan (Wood, 1988). Thus, the CT is not necessarily inconsistent with these results. However, the lack of relationship between *I* and in-shell nut volume, and the associated greater sink mass of large volume nuts, remains paradoxical unless the ability of the tree to satisfy the carbohydrate storage pool in the tree is largely unrelated to

the magnitude of the demand of developing nuts for photoassimilates. Additionally, this lack of effect of large sized nuts (with large kernels) on *I* is evidence that the enhancing effect of mechanical fruit thinning, at the beginning of kernel filling, on return flowering and fruit-set is not solely related to the alleviation of kernel demand for photoassimilates, and may indeed be unrelated.

When these data are reconciled with the existing PT, there are both consistencies and inconsistencies. The lack of association between *I* and FRD is consistent with the existing theory in that the action of a fruit produced hormonal floral inhibitor is likely to be essentially independent of the time of fruit ripening. There is inconsistency in that cultivars with a short PRFP tend to have at least a moderate linkage to *I* and to extended canopy health and photoassimilation. Thus, the classical PT, in which phytohormone-like flowering inhibitors putatively function as the sole regulator of alternate bearing, appears untenable.

These results indicate that the classical PT explaining flowering in pecan is probably invalid unless there is a late-season flowering promoter produced by non-senescent late-season foliage, by developing fruit, or both. Either way, the generalized classical theory requires revision. Results also require that the classical CT be revised to explain how *I* is unrelated to nut size and is not substantially moderated by a long post-ripening period of foliage and is also substantially reduced by a short post-ripening foliage period. These results indicate that alternate bearing in pecan is best explained by a model synthesizing aspects of both theories; to include key regulatory roles for both phytohormones and carbohydrates. These findings also impart a degree of importance to the effect of late ripening dates for maintaining canopy health that was previously unrecognized. It also points out a major problem with the concept that alternate bearing will be substantially moderated by ensuring a long post-ripening foliage period solely via usage of early-ripening cultivars.

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