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Fruit maturation patterns of *Carya* spp. (Juglandaceae): an intra-crown analysis of growth and reproduction

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Summary. Fruit survival patterns, from fertilization to maturation, were examined for *Carya ovata* and *C. tomentosa* in a New Jersey USA forest. We observed fruiting and shoot growth characteristics over a 3-yr period to determine: (1) the patterns of fruit survivorship (from initiation to maturity) within and among years, (2) the relationships between shoot growth, fruit initiation, and fruit survival to maturity, and (3) the influence of phytophagous insects on fruit survival. We found that within years, smaller infructescences (1–2 fruits) exhibited greater relative survivorship than larger ones (3–4 fruits); however, absolute nut production was greatest for mid-sized infructescences (2–3 fruits). Among years, fruit survivorship varied considerably within populations. Across the 3-yr period we observed average fruit survivorship to be convex, linear, and concave, respectively. Likewise, shoot characteristics (length, width, number of leaves) varied concomitantly (decreasing fruit survivorship was accompanied by decreasing shoot length and number of leaves). Within years, we found no strong relationship between shoot characteristics and infructescence size and survival. The patterns of tree-to-tree variation suggested a strong genetic basis to shoot growth and fruit maturation. However, patterns of variation within and among years also indicated a strong environmental influence on these traits as well. Natural phytophagy by insects was observed to be low (<5%); however, shoot defoliations of 10–25% were not uncommon. Experimental defoliations (ambient, 10–15%, 20–40%, and 75–100%) did not result in reduced survival to maturity. Collectively, the data suggest that year-to-year variability in shoot growth has a greater influence on fruit maturation patterns than within year fruit-shoot relations.

Key words: *Carya* – Fruit abortion – Herbivory – Reproduction – Resource allocation

Plants typically initiate more fruits than are ever brought to full maturity. This observation was probably first noted by Darwin (1877) and subsequently investigated with great intensity by agronomists, foresters, and fruit breeders (Kozlowski 1973; Sweet 1973; Janick and Moore 1975). The causes and implications for mortality between fertilization and fruit maturity in natural plant populations have received considerable attention by evolutionary ecologists (e.g., Lloyd 1980; Stephenson 1980, 1981; Udovic and Aker 1981; Bawa and Webb 1984; Nakamura 1986; Lee 1988). With the exception of a limited number of studies (Williamson 1966; Boucher and Sork 1979) there are few data on the proximal factors contributing to fruit abortion amongst tree species common to eastern North American deciduous forests.

Trees, and plants in general, can be viewed as possessing a finite amount of resources which must be allocated to various functions including maintenance, growth, and reproduction (Harper 1977; Willson 1983). Many tree species exhibit an inverse relationship between vegetative growth and reproductive output (Harper 1977). While there is evidence that alternate-bearing or mast-fruiting trees draw upon whole-tree stored reserves (to some degree) for seed production (Kozlowski and Keller 1966) the vast majority of tree species take their carbohydrates for seed production from associated twigs and subtending leaves (Kozlowski and Keller 1966; Janzen 1971; 1976; Davis and Sparks 1974; Stephenson 1980; Bertin 1982; Watson and Casper 1984; Marquis 1988).

In addition, leaf herbivores can markedly affect plant fitness by lowering the leaf area and altering the patterns of carbon assimilation and nutrient uptake. The effects of high intensity insect defoliation on the growth and mortality of trees has received considerable attention (see reviews by Kulman 1971 and Schowalter et al. 1986). The importance of intra-crown variation in herbivory has received much less attention (Janzen 1976; Stephenson 1980; Bertin 1982; Gorchov 1988; Marquis 1988; Haukioja et al. 1990). Natural levels of low intensity herbivory have been presumed to have negligible effects on plant fitness and demography (Jameson 1963); however,

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there is now evidence to suggest the contrary (Crawley 1985). Few studies have considered the effects of low intensity herbivory on plant fitness at the branch or shoot level (Marquis 1988; Haukioja et al. 1990).

To investigate the intra-crown relationships between growth and reproduction in natural populations of hardwood trees we performed a series of field observations and experiments with *Carya ovata* (Mill.) K. Koch and *C. tomentosa* (Poir.) Nutt. (Juglandaceae). Specifically, we had three objectives: (1) To examine the patterns of fruit survivorship (from initiation to maturity) within and among years; (2) To assess the intra-crown relationships between shoot growth and fruit production; (3) To determine the amount of leaf area lost to phytophagous insects and how changes in shoot characteristics might affect fruit production.

Methods

Study site

Field work was conducted at the Hutcheson Memorial Forest (HMF) located in Somerset County, New Jersey (40° 30′ N, 74° 34′ W). HMF experiences a subcontinental climate with 112 cm of precipitation annually and a mean annual temperature of 11.7 C (Robichaud and Buell 1973). Forests of the region are generally considered as mixed oak or oak-hickory (Robichaud and Buell 1973; Forman and Elfstrom 1975) and were included in the oak-chestnut region of Braun (1950). The forest lies on soils developed from Triassic red shales of the Piedmont (Wolfe 1977). These soils may be generally classified as Penn Shaly Silt Loams (Kirkham 1976). Most of the work was conducted on trees in a wooded hedgerow on the southern border of the forest.

Study species

We chose to examine *Carya* spp. because they are typical constituents of many eastern North American deciduous forests, have fruits and leaves which are sufficiently large to allow experimental manipulation, have fruits which mature within one growing season, and have received considerably less attention than other hardwood species (e.g., *Quercus*). We selected two species so that a comparative approach could be utilized to gain a better understanding of the range and extent of responses.

Carya ovata (Mill.) K. Koch (Shagbark Hickory) and *C. tomentosa* (Poir.) Nutt. (Mockernut Hickory) are common sympatric tree species in many eastern North American forests (Braun 1950; Fowells 1965). Both species are monoecious (bear both male and female flowers) and anemophilous (wind pollinated). In the spring the apical bud normally gives rise to a leafy shoot which may be vegetative or reproductive. Reproductive shoots differentiate terminal pistillate flowers (1–5) with staminate catkins (1-many) borne axillary to the bud scales at the base of the shoot. Fertilization results in a terminal infructescence (cluster) of fruits. General descriptions of *Carya* silvics, life-histories, and details of the reproductive biology can be found elsewhere (Boisen and Newlin 1910; Fowells 1965; Madden and Malstrom 1975; McCarthy and Quinn 1989; McCarthy 1990; McCarthy and Quinn 1990).

Species identifications were made using Manning (1950) and Gleason and Cronquist (1963). Nomenclature follows Gleason and Cronquist (1963). Voucher specimens have been deposited at the Chrysler Herbarium of Rutgers University.

Four shagbark and four mockernut trees were selected for study. The intensive nature of sampling from the crowns of mature trees (20–25 m in height) precluded larger sample sizes. The eight study trees are the same as those described in McCarthy and Quinn (1989, 1990; see Table 1). Trees of both species were of similar size, age, and reproductive status. Observations and experiments were made from sampling towers erected adjacent to each tree (for details see McCarthy 1988).

Fruit survivorship

In May of 1985, 1986 and 1987 all fruiting shoots within the canopy that were accessible from the sampling towers (ca. 30% of the canopy) were censused. Each shoot was marked with an aluminum tag and mapped for its relative position within the canopy. The size of the infructescence (i.e., number of fruits) at fruit set (initiation) was recorded and each shoot was examined for fruit abortions at 20–30 d intervals throughout the remainder of the growing season. A total of 2,023 shoots were examined over the three year period (Table 1).

Fruit survivorship was evaluated by grouping shoots of the same infructescence size (at initiation) and plotting relative survivorship to maturity for the two species. Chi-square goodness-of-fit tests (Siegel 1956) were used to determine if there were differences in survival to day 250 (approximate date of fruit maturation). Kolmogorov-Smirnoff (K–S) two-sample tests (Sokal and Rohlf 1981) were used in multiple pairwise comparisons to determine if different infructescence types had different life spans (Pyke and Thomson 1986).

Shoot characteristics

Each of the censused shoots used to examine fruit survivorship was measured in late summer in each of the three study years. Because of the potential relationship between shoot size and fruit production, the number of leaves produced, shoot length (to nearest 0.1 cm), and shoot width (central diameter to nearest 0.1 mm using a dial micrometer) for each fruiting shoot were recorded. A number of nonfruiting shoots (from the same portion of the canopy) were also selected in 1986 and 1987 (see Table 1 for sample sizes) for morphological comparisons against fruiting shoots. Data were analyzed using the GLM procedure of SAS (SAS Institute 1982). For each species, a standard two factor (trees and years) analysis of covariance (ANCOVA) was used to analyze the variation in shoot characteristics as a function of infructescence size at maturity (covariate). The factor "year" contained three levels (1985, 1986, 1987). Trees were treated as a block because the same four trees within each species were sampled in each year. Shoots were used as the replicate because they were randomly sampled from the canopy each year (i.e., not necessarily the same shoots were sampled each time). Due to the unbalanced design (not all trees sampled in every year), Type-III sums-of-squares are reported as are adjusted (least-squares) means ± one standard error for all treatment combinations (Freund and Littell 1981).

Herbivory observations and simulation experiment

Leaves do not begin to show signs of herbivore damage for one to several weeks following bud-break and leaf expansion (personal observation). To determine the natural levels of herbivory within the canopy, 15 leaves were randomly collected from each study tree in both late June and early September of 1988. Sampling was stratified so as to collect 5 leaves from each of the lower, middle, and upper portions of the crown as well as leaves that were borne on terminal and distal portions of a shoot. Actual leaf area (ALA) was measured using a Li-Cor Leaf Area Meter. Potential leaf area (PLA; in the absence of folivory) was determined by remeasuring all leaves after the holes had been covered with opaque paper and the edges reconstructed using crescent-shaped templates. Leaf area removed (LAR) by herbivores was determined by subtracting ALA from PLA and expressed as a percentage of PLA. LARs between sample dates and species were compared using Mann-Whitney two-sample tests (Sokal and Rohlf 1981).

To determine the relationship between leaf herbivory (presumably affecting shoot resources) and fruit abortion, a simulated defoliation experiment was set up in 1988. Forty shoots, from each of the two study species (80 shoots total), were randomly selected early in the spring immediately after fruit set. Of the 40 fruiting shoots per species, 20 were designated as "low density infructescences" and 20 as "high density infructescences". Low density infructescences were 1-fruited on *Carya ovata* trees and 2-fruited on *C. tomentosa* trees. High density infructescences were 2-fruited on *C. ovata* trees and 3-fruited on *C. tomentosa* trees. The 20 shoots of each infructescence density category were randomly allocated amongst four treatments (thus 5 replicates per treatment): −1LFL (where the terminal odd pinnate leaflet was removed from every leaf on the shoot), −3LFL (the terminal leaflet and two basal leaflets of every leaf on the shoot were removed), −5LFL (the distal-most five leaflets are removed from every leaf on the shoot), and a control (no leaflets removed, ambient herbivory of $<5\%$). Depending on the species, the experimental removals simulated 10–15% LAR (−1LFL), 20–40% LAR (−3LFL), and 75–100% LAR (−5LFL). Experimental defoliations were all made immediately after fruit initiation. Shoots were scored for fruits remaining on infructescences after ca. 90 d. ANOVA (GLM procedure) was used to evaluate treatment effects and compare low and high density infructescence responses for each species separately. Multiple comparisons amongst treatment means were made using Least Significant Differences (LSD).

Results

Fruit survivorship

The survival patterns of the infructescence types for a given species within a given year (Fig. 1A–C) were similar (all pairwise K–S tests NS, $P>0.10$). However, if the average survival patterns of pooled infructescences (within a species) are evaluated across the three years, there are significantly different survival patterns (K–S tests, $P<0.05$). In 1985 (Fig. 1A) all infructescences experienced light mortality early, reached a plateau, and developed all remaining fruits through day 260. Natural fruit drop generally occurs from ca. day 250 onwards. In 1986 (Fig. 1b) the average survival pattern was one of more-or-less constant mortality through time. In 1987 (Fig. 1c) there was very high mortality immediately following fruit set; thereafter, mortality was minimal to maturation. Additionally, there were no significant differences in mean survival patterns between species within a year (K–S tests all NS, $P>0.10$). Collectively, these data indicate that fruit survivorship patterns differ more among years than between species within years.

By day 250 (the approximate date of fruit maturation) of 1985, 1- and 2-fruited shoots of *C. tomentosa* had matured a greater proportion of fruits than 3- or 4-fruited shoots (Chi-square tests, $P<0.05$). In 1986, 1-fruited *C. tomentosa* and 3-fruited *C. ovata* infructescences matured greater and lesser (respectively) fruits proportionally compared to other infructescence sizes (Chi-square tests, $P<0.05$). In 1987, 4-fruited infructescences of *C. tomentosa* produced a lower proportion of mature fruits compared to smaller infructescences (Chi-square tests, $P<0.05$) within that species. Collectively, these data suggest that there is a tendency for smaller infructescences to bring a greater proportion of their fruits to maturity than larger infructescences. However, intermediate-sized infructescences typically brought the greatest absolute number of fruits to maturity in both species (Chi-square tests, $P<0.05$; Table 1).

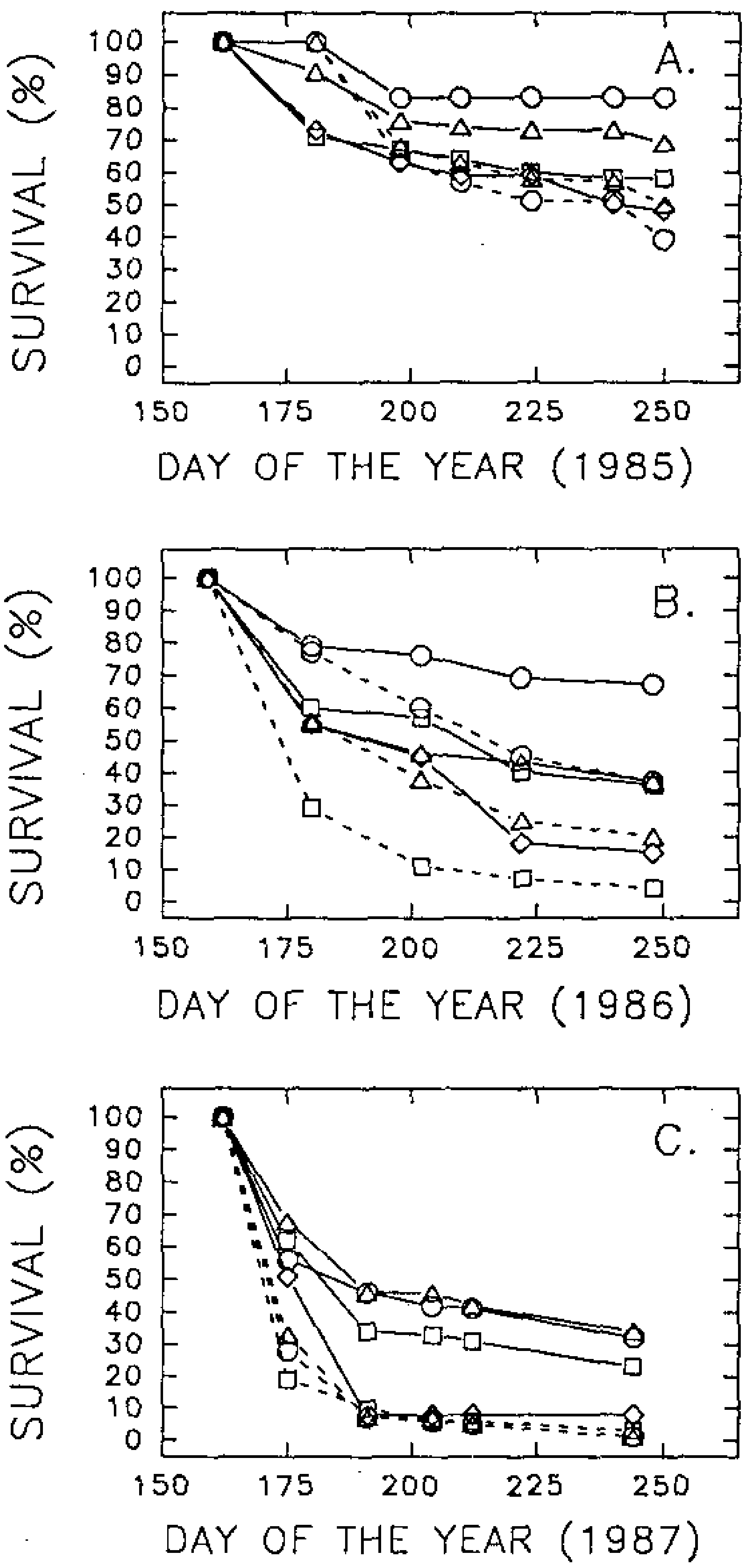

Fig. 1A–C. Fruit survivorship to maturation for 1985 (**A**), 1986 (**B**), and 1987 (**C**). Fruits are grouped by infructescence size at time of initiation and were considered mature by day 250. Dashed lines are *Carya ovata*, solid lines are *C. tomentosa*. Circles, triangles, squares, and diamonds are 1-, 2-, 3-, and 4-fruited infructescences, respectively. Number of shoots in each infructescence category and species are listed in Table 1

Shoot characteristics

Highly significant ($P<0.0001$) differences were observed for the effects of tree and year on all shoot characteristics for both species (Table 2). Infructescence size at maturity

Table 1. Number of shoots sampled (N), fruits initiated, fruits matured, and percentage of fruits surviving to maturity for *Carya ovata* and *C. tomentosa* in each of three successive years (nd = no data)

Species	Infructescence Size	1985 *N*	Number Initiated	Number Matured	% Matured	1986 *N*	Number Initiated	Number Matured	% Matured	1987 *N*	Number Initiated	Number Matured	% Matured
Carya ovata	0	nd	nd	nd	nd	80	0	0	0	40	0	0	0
	1	67	67	26	39	172	172	64	37	141	141	1	1
	2	35	70	35	50	221	242	48	20	180	360	4	1
	3	0	0	0	0	28	84	3	4	11	33	1	3
	Totals	102	137	61		501	498	115		372	534	6	
C. tomentosa	0	nd	nd	nd	nd	55	0	0	0	40	0	0	0
	1	32	32	27	84	40	40	27	68	130	130	42	32
	2	31	62	43	69	157	314	116	37	259	518	176	34
	3	36	72	42	58	118	354	127	36	79	237	55	23
	4	18	72	35	49	34	136	20	15	9	36	3	8
	5	0	0	0	0	10	50	2	4	0	0	0	0
	Totals	117	238	147		414	894	292		517	921	276	

Table 2. Analysis of covariance (ANCOVA) results for shoot characteristics using infructescence size (fruits) at maturity as the covariate

Variable source		df	SS	MS	F	*P*
Carya ovata						
Leaves	Tree	3	26.56	8.85	9.88	0.0001
	Year	2	66.10	33.05	36.88	0.0001
	Tree × Year	5	19.91	3.98	4.44	0.0005
	Fruits	1	2.59	2.59	2.89	0.8930
	Error	964	863.86	0.90		
Length	Tree	3	322.82	107.61	9.45	0.0001
	Year	2	253.60	126.80	11.14	0.0001
	Tree × Year	5	158.35	31.67	2.78	0.0167
	Fruits	1	4.56	4.56	0.40	0.5267
	Error	964	10971.43	11.38		
Width	Tree	3	46.45	15.48	36.73	0.0001
	Year	2	130.31	65.15	154.53	0.0001
	Tree × Year	5	5.26	1.05	2.49	0.0296
	Fruits	1	0.79	0.79	1.89	0.1691
	Error	964	406.45	0.42		
Carya tomentosa						
Leaves	Tree	3	151.02	50.34	21.75	0.0001
	Year	2	246.15	123.07	53.16	0.0001
	Tree × Year	4	0.09	0.02	0.01	0.9998
	Fruits	1	8.98	8.98	3.88	0.0492
	Error	1038	2402.98	2.32		
Length	Tree	3	4164.29	1388.10	51.42	0.0001
	Year	2	1899.60	949.80	35.18	0.0001
	Tree × Year	4	633.07	158.27	5.86	0.0001
	Fruits	1	86.80	86.80	3.21	0.0733
	Error	1038	28023.61	26.99		
Width	Tree	3	322.39	107.46	143.52	0.0001
	Year	2	144.74	72.37	96.15	0.0001
	Tree × Year	4	61.01	15.25	20.37	0.0001
	Fruits	1	0.45	0.45	0.60	0.4373
	Error	1038	777.24	0.75		

(covariate) was generally non-significant ($P > 0.15$) except for the number of leaves ($P = 0.0492$) and perhaps shoot length ($P = 0.0733$) for *Carya tomentosa* (Table 2). With the exception of mean number of leaves per shoot for *C. tomentosa,* all interactions were also significant ($P < 0.05$) indicating the need to examine the response patterns of individual trees as well as those of the population.

In general, year accounted for a greater proportion of the variance than did tree, particularly for *C. ovata.* Trees within a species tended to respond in a fairly similar fashion. For example, the leaves per shoot and shoot length declined significantly ($P < 0.05$) between 1985 and 1986 for all *C. ovata* trees and remained relatively constant into 1987. Shoot width decreased ($P < 0.05$) from 1985 to 1986 and then increased ($P < 0.05$) from 1986 to 1987. Significant interactions arose from the fact that individual trees did not appear to regularly maintain a rank order from year to year (with the exception of tree H which consistently performed poorly). Likewise, *C. tomentosa* trees responded in a collective fashion, with the most obvious exception being observed in shoot length for tree D in 1986.

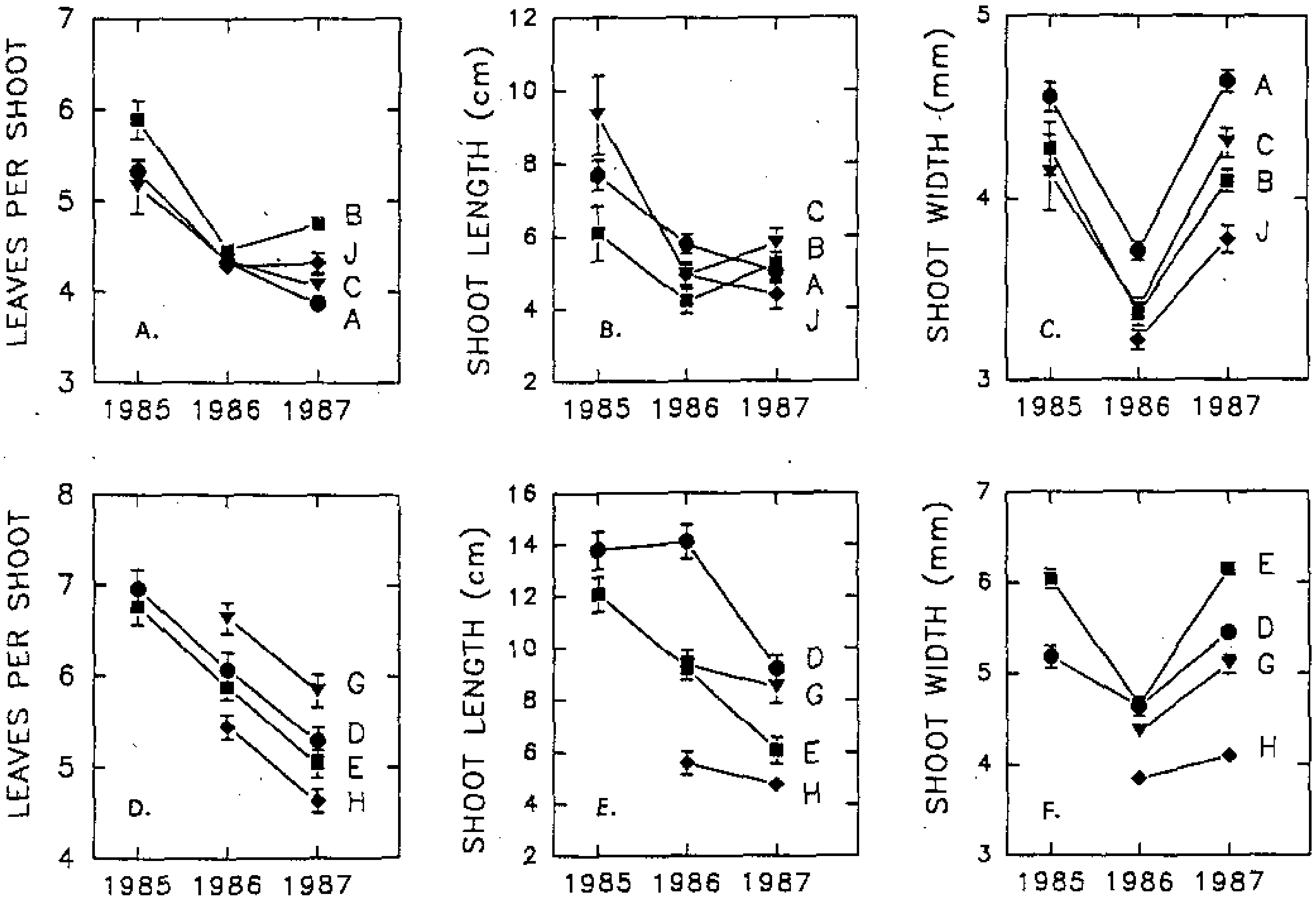

Fig. 2A–F. Mean (±SE) number of leaves per shoot, shoot length, and shoot width arranged by year and tree for *Carya ovata* (**A–C**) and *C. tomentosa* (**D–F**). Note different scales of the dependent variables when comparing species

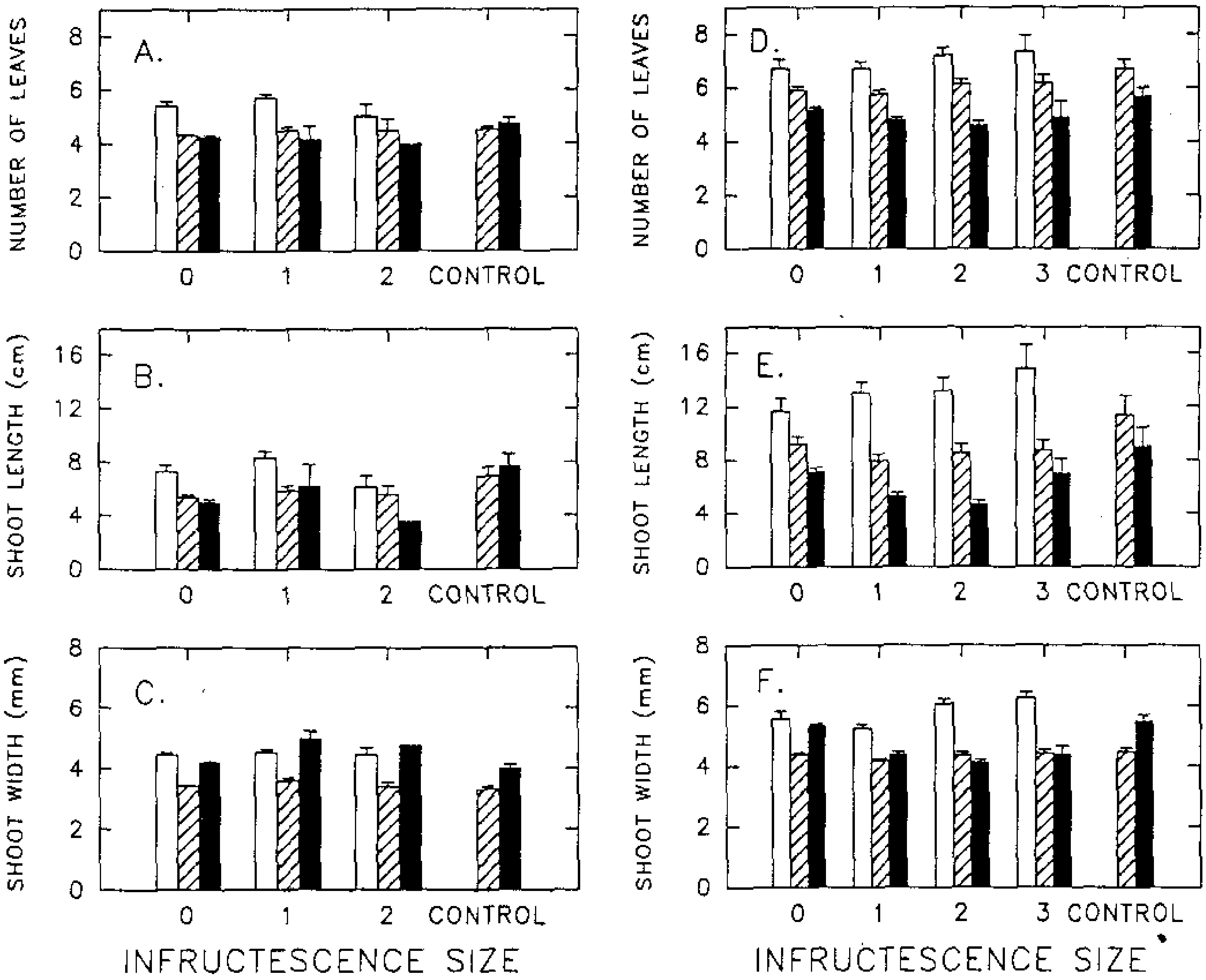

Fig. 3A–F. Mean (±SE) number of leaves per shoot, shoot length, and shoot width arranged by infructescence size at maturity for *Carya ovata* (**A–C**) and *C. tomentosa* (**D–F**). Control groups are vegetative (non-fruiting shoots). The largest infructescence categories for each species are not shown due to small sample sizes (cf. Table 1). Hollow bars, hatched bars, and solid bars are data for 1985, 1986, and 1987, respectively

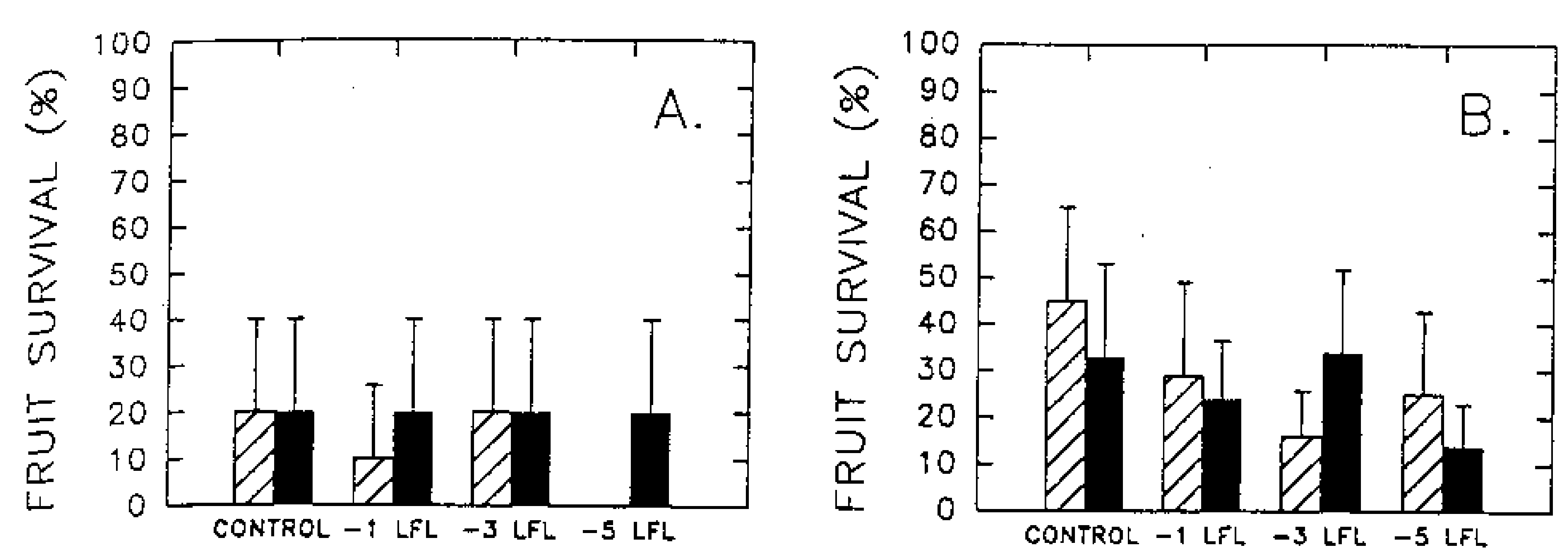

Fig. 4A, B. Mean (±SE) percentage of fruits surviving to maturity under three levels of defoliation and two infructescence densities for *Carya ovata* (**A**) and *C. tomentosa* (**B**). Hatched bars are low density infructescences, solid bars are high density infructescences

The covariate, infructescence size at maturity, was not significantly related to shoot characteristics for *C. ovata*, however, it may have been important with respect to *C. tomentosa* shoot characteristics. Therefore, we examined the relationship between mean shoot characteristics with respect to infructescence size (Fig. 3). The influence of the coavriate for *C. tomentosa* is only important in 1986 for shoot length and in 1987 for shoot length and shoot width. In these years, shoots bringing no fruits to maturity did not differ significantly from non-fruiting control shoots; however, these shoots were generally greater compared to fruiting shoots (Fig. 3).

Herbivory observations and simulation experiment

The mean (±SD) percentage of LAR (leaf area removed) in late June of 1986 was 2.2% (±2.3) for *Carya ovata* and 3.1% (±3.2) for *C. tomentosa*; in September the values were 3.6% (±5.2) and 2.9% (±3.3), respectively. All of these sample distributions were distinctly skewed with numerous leaves having between 5 and 20% LAR. None of the comparisons between dates within a species or between species within dates were significantly different (Mann-Whitney tests, $P > 0.15$).

Significant treatment effects were not observed in the simulated leaf herbivory experiment (Fig. 4, $P > 0.10$ for both 2-factor models). *Carya ovata* did not appear to respond to the treatments at all ($F = 0.31$, $df = 3$, $P = 0.8150$). Fruits surviving to maturity ranged between 0 and 20%. *C. tomentosa* showed a weak trend towards decreasing fruit survival to maturity with increasing leaf area removed ($F = 1.27$, $df = 3$, $P = 0.2877$).

Discussion

Interpretation of fruit maturation patterns based on data from any one year would potentially lead to very different conclusions than those generated by observations over a 3-yr period. *Within* any given year, two general patterns are evident: first, the average survival of *Carya tomentosa* fruits is slightly higher than for *C. ovata*; second, both species tend to exhibit similar patterns of abortion. *Among* years, some important additional patterns emerged. In 1985, the survivorship curve of fruits was convex, i.e., the general pattern was one of high survivorship throughout the maturation period (after a brief period of early mortality). In 1986, the average survivorship curve of fruits was linear, i.e., the general pattern was one of constant mortality throughout the maturation period. In 1987, the average survivorship curve was concave, i.e., there was high mortality after fruit initiation and then a tapering off in mortality rate towards maturity. This latter pattern represents what has typically been described (in one-season studies) for natural populations of woody plants including *Catalpa speciosa* (Stephenson 1980) and *Aesculus pavia* (Bertin 1982). Marked changes in survivorship are indicative of a variable resource environment. This variability may be expressed through a variety of endogenous and/or exogenous mechanisms.

There is considerable evidence to suggest that resources are a major factor in the abortion of fruits both at the level of whole plants (Aalders et al. 1969; Rockwood 1973; Lloyd 1980; Stephenson 1981, 1984; Willson and Price 1980; Lee and Bazzaz 1982; Lee 1988; Queller 1985) and at the more discrete branch level within plants (Janzen 1976; Stephenson 1980; Bertin 1982; Wyatt 1982; Gorchov 1988; Marquis 1988). This study demonstrates that there is a strong relationship between shoot characteristics and fruit survivorship among years (compare Figs. 1 and 3). Regression analysis indicates that as fruit survival patterns changed from 1985 to 1987 there was a concomitant decline in shoot length for both *Carya ovata* and *C. tomentosa* ($r^2 = 0.53, 0.78$; $P = 0.007, 0.004$, respectively). Likewise, the number of leaves also decreased for both species ($r^2 = 0.61, 0.66$; $P = 0.030, 0.003$, respectively). Shoot width was not significantly ($P > 0.05$) correlated with fruit survival across the 3-yr period (due to the shoot width increase in 1987). Haller and Magness (1925), Crane (1931), Amling (1968), Sparks and Brack (1972), Sparks and Heath (1972) and Malstrom and McMeans (1982) all found that there was a distinct relationship between shoot characteristics and fruit production in cultivated apple and pecan trees. Generally, these studies found that longer shoots with more leaves tended to mature more fruits. However, Gross (1982) noted a distinct trade-off between vegetative growth and reproduction after an intense episode of fruiting by two species of *Betula* in natural populations. In a study of the cost of reproduction in *Acer negundo*, Willson (1986) found that the relationship between vegetative growth and reproduction was not always a clear one.

An indirect line of evidence for the effect of shoot resources on fruit maturation patterns (within years) comes from the probabilities of fruit survival to maturity (Fig. 1). Depending upon the species and year, there was a general tendency for larger infructescences to exhibit lower survivorship and percentage of fruits matured. This pattern suggests that fruits within a multiple fruit infructescence may be competing for limited resources. This relationship would be consistent with similar observations made on *Catalpa speciosa* (Stephenson 1980) and *Yucca whipplei* (Udovic and Aker 1981). However, the results of the fruit-shoot relations and the defoliation experiment are not consistent with this interpretation. The results of the defoliation experiment highlight the need to consider multiple and hierarchical causes and mechanisms of fruit abortion. For example, this experiment was performed in 1988, a year in which there were substantial periods of decreased precipitation during some critical periods (e.g., pre-bud burst, fertilization, and kernel filling) of the reproductive cycle of *Carya*. Precipitation was down 47–51% during April, June, and August (based on the 30-yr climatological normal) in New Brunswick, New Jersey (NOAA 1988). In 1988, drought could have had an overriding effect, resulting in decreased fruit maturation, and minimizing the effective response of individual shoots to the defoliation treatments on individual trees. The similarity in survivorship patterns between species within years also suggests a strong environmental influence as does the data from shoot characteristics.

A variety of factors, in addition to drought (e.g., nutrient limitation, predation, competition, etc.) may override the resource relationships found at the level of individual shoots. For example, Boucher and Sork (1979) found that nut predation by *Curculio* and *Conotrachelus* weevils resulted in an early drop of nuts thereby reducing the amount of resources committed to nuts that had no probability of reaching maturity. Surveys of the canopy arthropod fauna (of these same study trees) at Hutcheson Memorial Forest revealed few predatory weevils (Gurien and McCarthy 1987), and their effect on seed production at this site seems negligible. Haukioja et al. (1990) demonstrated that *Betula pubescens* ssp *tortuosa* responded to herbivory as a function of the type and position of damage within the plant. Because growth in *B. pubescens* proceeds largely from resources of the previous year, the effects of herbivore damage may not be seen until a subsequent year. Organization, integration, and carryover effects may be important elements of resource usage in woody plants.

This study differs from previous studies of fruit abortion for two reasons. First, the study species exhibit the "mast-fruiting" habit (i.e., the periodic synchronous production of large seed crops by a tree population; Janzen 1971; Silvertown 1980). Second, there are consecutive years of detailed fruit maturation data at the intracrown level. While there seems to be little doubt that *Carya* are masting species (USDA 1948; Sork 1983), neither species was observed to produce an excessively large seed crop in any of the four years of study at HMF (McCarthy and Quinn 1989; McCarthy 1990) even though the periodicity of large seed crops for these species is supposed to be one to three yr (USDA 1948).
While this study was not designed to examine the var
tion in absolute fruit production amongst trees acr
years, the number of fruiting shoots sampled (Table
provides a relative index to fruit production. These da
represent a total census of all fruiting shoots in a defin
area of the canopy for the study trees and thus can
used to make relative comparisons among years. Int
estingly, the year with the highest fruit survival to ma
uration (1985) was the year with the lowest number
fruiting shoots. In 1986 and 1987, when there was
greater abundance of fruiting shoots, there was general
lower survival to maturity.

Observations and experiments on the pollination a
breeding systems of *Carya ovata* and *C. tomento*
(McCarthy and Quinn 1990) suggest that the number
fruits reaching maturity is not limited by the number
ovules produced or the availability of pollen; both a
generally sufficient and produced in overabundan
There is evidence to suggest that mate selection (v
compatibility relationships) may play a contributing r
in fruit abortion (McCarthy and Quinn 1990). Eviden
presented here suggests that year-to-year variation
growth (perhaps due to whole tree resources, enviro
ment, etc.) may have a greater influence on fruit matur
tion patterns than resources at the shoot level. Shoots a
initiated before fruits are produced, and thus the frui
are subject to a defined resource level. Larger shoo
result in greater fruit production. This resource level c
be altered by herbivores, but not necessarily result
pronounced fruit abortion (other factors like enviro
ment may have an overriding influence). The maturati
time of *Carya* nuts is long (ca. 100–150 days) in con
parison to other reproductive stages, and during the tir
needed to reach maturity, the fruits are subjected to
range of potentially changing resources (e.g., herbivor
and variable environment (e.g., drought). Serial adjus
ment (Lloyd 1980) may be important during the ear
stages of reproduction. Both species of *Carya* have
complex integrated reproductive system which could
subject to intrinsic adjustments at multiple stages. Ho
ever, extrinsic forces seem to result in a high degree
uncertainty thus necessitating an overproduction
fruits.

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