Within- and Among-Tree Variation in Flower and Fruit Production in Two Species of Carya (Juglandaceae)

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American Journal of Botany, Vol. 76, No. 7 (Jul., 1989), 1015-1023.

Amer. J. Bot. 76(7): 1015–1023. 1989.

WITHIN- AND AMONG-TREE VARIATION IN FLOWER AND FRUIT PRODUCTION IN TWO SPECIES OF CARYA (JUGLANDACEAE)[1]

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ABSTRACT

The patterns of variability in the production of staminate inflorescences, pistillate flowers, and fruits for *Carya ovata* (Mill.) K. Koch and *C. tomentosa* (Poir.) Nutt. at Hutcheson Memorial Forest (Somerset County, New Jersey) were examined over a four-year period. We sought to determine 1) the patterns of variability in flowering and fruiting (within-trees, among-trees, and between-years), 2) if variable flowering might account for observed nut-bearing patterns, and 3) what were the relative contributions of intrinsic (genetic) and/or extrinsic (environmental) factors in determining flower production and fruit set. In general, our fine-scale analysis of shoots within canopies did not reveal a distinct mast fruiting pattern. While the number of male and female flowers varied significantly (among trees and between years), fruit set was not markedly affected. Variability of flowering and fruiting among shoots within trees was low. Both flowering and fruiting were observed to have a strong genetic and/or microenvironmental basis; however, flowering appeared more plastic and thus more sensitive to yearly environmental vagaries than did fruiting. Favorable environmental conditions at the time of flower differentiation may result in increased flower production; but, this does not necessarily result in increased fruit set. Many pistillate flowers abscise around the time of pollination and fertilization, apparently adjusting fruit set to available shoot resources. Approximately 50% of the pistillate flowers of both species fail to set fruit. Overall, individual trees exhibit their own flowering and fruiting schedules, suggesting the need to account for this level of variability in future studies of mast fruiting.

MANY TEMPERATE TREE species-populations exhibit periodic synchronous production of large seed crops; this phenomenon is commonly referred to as "mast fruiting" (Janzen, 1971; Harper and White, 1974; Waller, 1979; Silvertown, 1980). Much research has been devoted to determining the proximal and ultimate causes for mast fruiting. A wide range of environmental and genetic factors have been found to correlate with large seed crops (e.g., Adriance, 1931; Downs and McQuilken, 1944; Christensen, 1955; Sharp and Chisman, 1961; Sharp and Sprague, 1967; Shaw, 1968; Wolgast, 1978); however, the majority of these studies have tended to be anecdotal or descriptive in approach, or species-level oriented, and therefore unable to statistically assess within- and among-tree variation in flower and fruit production. Thus, while variation in reproduction may be a broadly recognized characteristic of temperate tree populations, it is rarely known what proportion of a population reproduces and whether specific individuals are consistently high or low flower and seed producers. Studies of *Pinus ponderosa* Laws. in Colorado (Linhart et al., 1979; Linhart and Mitton, 1985) found that the majority of cones produced over a six-year period came from the same few trees each year. Likewise, Sork (1983) made the observation that seed production among trees of *Carya glabra* generally followed the same rank order from year to year in a Michigan forest. Alternatively, Carmen, Koenig, and Mumme (1987) found that patterns of acorn production by individual trees, among five western species of *Quercus*, did not respond individualistically but instead tracked the overall population pattern.

Feret et al. (1982) note that quantitative models relating easily measured parameters to fruit crop variability are generally lacking. The development of quantitative models is prob-

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[1] Received for publication 27 April 1988; revision accepted 24 January 1989.

We thank W. E. Manning, T. R. McGuire, and two anonymous reviewers for helpful comments on the manuscript. This research was supported by two grants-in-aid of research from Sigma Xi, the 1986 Torrey Botanical Club Best Graduate Student Research Proposal Award, a Rutgers University Graduate School Student Research Award, two Leathem-Steinetz-Stauber Research Awards administered by the Rutgers University Department of Biological Sciences, three Hutcheson Memorial Forest Summer Stipend Awards, The Morris County Willowwood Arboretum, and a Walter C. Russell Scholarship to B. C. McCarthy.

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ably hampered by the lack of consensus as to the causes and sources of variability within and among masting trees. While Carmen et al. (1987) found no correlation among 14 environmental variables and fruit crop variation, Sharp and Sprague (1967) suggested that variability could be controlled by environmental conditions (i.e., extrinsic factors) during the spring when flowering occurs; however, they also observed differences among trees. This latter observation, one of genetic and/or physiological control (i.e., intrinsic factors), may be more consistent with commonly accepted causes of fruit crop variability (Davis, 1957; Williamson, 1966; Wolgast, 1978; Linhart and Mitton, 1985).

The vast majority of data pertaining to variability in fruit production comes from the study of commercially important tree species. Unfortunately, these cultivated species have been subjected to a tremendous amount of selection through breeding programs and stock grafting to eliminate or reduce alternate bearing which is considered a commercial nuisance. Thus, with few exceptions (e.g., Linhart et al. 1979; Linhart and Mitton 1985), quantitative data for within- and among-tree variability in flower and fruit production in naturally growing forest tree species are generally lacking. Quantitative estimates of flower and fruit production (and patterns of annual variation) are an important first step in facilitating management techniques through selection criteria, understanding basic population structure, and determining the relative influences of environmental and/or genetic components in mast fruiting.

In addition, data on the reproductive allocation of long-lived species are sorely needed in the development and testing of theoretical expectations concerning genetic differentiation vs. plasticity in resource allocation. Except for a few pioneering studies (Pritts and Hancock, 1983, 1985), annuals and herbaceous perennials provide the bulk of our information on the genetic and environmental determinants of reproductive allocation. Until such data become available for a larger number of trees and shrubs, there is not a valid basis for generalizations in regard to life-form, longevity, habitat, and/or life history (Quinn, 1985).

This study was initiated to quantify the abundance of male and female flowers and fruits produced in single populations of *Carya ovata* and *C. tomentosa* (Juglandaceae) in successive years. Specifically, we sought to determine 1) the patterns of variability in flowering and fruiting (within-trees, among-trees, and between-years), 2) if flowering variability might account for differential patterns of fruit set, and 3) the relative contributions of intrinsic (genetic) and/or extrinsic (environmental) factors in determining flower production and fruit set.

MATERIALS AND METHODS—The species selected for this study were *Carya ovata* (Mill.) K. Koch (shagbark hickory) and *C. tomentosa* (Poir.) Nutt. (mockernut hickory). Both species are monoecious and anemophilous, and they occur sympatrically in mixed hardwood stands throughout much of eastern North America. The structure of the staminate inflorescence, pistillate flowers, and fruits has been described in detail by Manning (1940, 1948). Madden and Malstrom (1975) have summarized the floral biology studies of the cultivated pecan (*Carya illinoensis*); the floral biology of *Carya ovata* and *C. tomentosa* have not been studied in great detail but appear to be similar to *C. illinoensis* (personal observation, BCM). In a mature tree the apical buds (terminal or pseudoterminal) of many trees are mixed (i.e., contain both vegetative and reproductive points of growth); the apical bud normally gives rise to a leafy shoot that differentiates terminal pistillate flowers, with vegetative buds axillary to the leaves. Both species are herkogamous; the staminate inflorescences (catkins) are axillary to bud scales at the base of the shoot, and the pistillate flowers are borne distally (at the tip). Catkins are initiated in the early summer of the year prior to the year in which they produce pollen (Woodroof and Woodroof, 1926). Pistillate flowers (each bearing a single orthotropic ovule) are borne in a terminal cluster of 1–5 flowers for most *Carya* spp. and differentiate in early spring after shoot initiation (Shuhart, 1927). After the pistillate flowers develop into fruits, there is no terminal bud on the shoot, and often the enlarged pseudoterminal bud (the uppermost axillary bud) may produce a flowering shoot the following season. The amount of pollen produced at the time that the stigmas are receptive varies, depending on the tree (i.e., dichogamous; unpublished data). Some cultivars of *C. illinoensis* have been shown to exhibit pronounced dichogamy.

The study site for this investigation was the Hutcheson Memorial Forest (HMF) located in Somerset County, New Jersey (40°30′N, 74°34′W). HMF experiences a subcontinental temperate 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 (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 the Triassic red shales

TABLE 1. *Ages and dimensions of* Carya *study trees*

Species	Tree ID	Age (yr)	DBH[a] (cm)	Height (m)
Carya ovata	A	36	17.4	11.5
	B	56	26.3	16.9
	C	57	27.2	13.6
	J	55	21.3	13.5
	K	36	17.0	12.8
Carya tomentosa	D	41	18.4	9.5
	E	74	41.1	14.3
	G	35	29.4	9.9
	H	49	22.1	10.1

[a] Diameter at breast height.

TABLE 2. *Date and rank order of peak pollen shedding*

		1985[a]	1986[b]	1987[b]
Species	Tree	Date (rank)	Date (rank)	Date (rank)
Carya ovata	A	5/10 (1)	5/10 (1)	5/12 (1)
	B	5/14 (2)	5/12 (2)	5/18 (2)
	C	5/15 (3)	5/18 (3)	5/22 (3)
	J	NA	5/20 (4)	5/25 (4)
	K	NA	nd	nd
C. tomentosa	D	5/15 (1)	5/15 (1)	5/16 (1)
	E	5/20 (2)	5/19 (3)	5/25 (3)
	G	NA	5/16 (2)	5/17 (2)
	H	NA	5/25 (4)	5/25 (4)

[a] ±1.5 days.
[b] ±0.5 days.
NA = Data not available (tree not examined that year).
nd = No data because tree was used for other experimental purposes.

of the Piedmont (Wolfe, 1977). These soils may be generally classified as Penn Shaly Silt Loams (Kirkham, 1976).

Nine trees in a wooded hedgerow at the south end of the forest were selected for study. These edge-grown trees, all on the same soil type and with the same aspect, were presumed to have similar microenvironments. All individual trees (Table 1) were dominant canopy specimens that were reproductively mature and observed to produce nuts in 1985. Of the nine trees, five were *Carya ovata* (A, B, C, J, K) and four were *C. tomentosa* (D, E, G, H). Flowering and nut production were monitored for five trees in 1985 (A, B, C, D, E), for eight trees in 1986 (A, B, C, D, E, G, H, J), and for nine trees in 1987 and 1988 (A, B, C, D, E, G, H, J, K). Detailed observations were made in all four years and quantified in 1986 and 1987. It should be emphasized that it was not possible to increase the sample size due to 1) limitations on the construction of sampling towers (described in McCarthy, 1988) 2) the short-duration and labor-intensive nature of the sampling, and 3) the lack of other *Carya* trees in the area with comparable microenvironments.

In 1985, observations on flower and fruit production suggested distinct within- and among-tree (as well as between-species) differences. Observations were quantified in 1986 and 1987 in order to statistically assess patterns and levels of variability in flower and fruit production. In March of these two years, before bud break, ten shoots from the canopy of each tree were randomly selected. As the buds burst and flowers differentiated, the number of pistillate flowers, staminate inflorescences, and number of leaves on each shoot were recorded. Date of peak pollen shedding was also recorded for each tree. Fruit set (fruit initiation) was assessed four weeks after pollen shedding for each tree.

Analysis of variance (ANOVA) procedures (Chatfield and Collins, 1980; Sokal and Rohlf, 1981) were used to assess patterns of flower and fruit variability. Two-way analyses were applied to assess the variation among trees and between years for each species, where the dependent variables for all tests were the number of staminate inflorescences, pistillate flowers, and fruits set. To correct for multicolinearity and heteroscedasticity a $\sqrt{Y + 0.05}$ transformation was used (Sokal and Rohlf, 1981). Two-way multivariate analysis of variance (MANOVA) was applied to assess general differences among reproductive traits across trees, years, and the trees × year interaction (Hand and Taylor, 1987). These analyses were followed by two-way ANOVAs to account for the specific patterns exhibited by the individual dependent variables. All analyses were performed using the GLM procedure provided by SAS (SAS Institute, 1982).

Since we had repetitive measures of the same individual trees at two times, we applied an analysis of repeatability (Falconer, 1981) to shed light on the nature of the reproductive variability. The number of flowers and fruits (i.e., phenotypic variance, V_p) was partitioned into a within-individual component and a between-individual component. The within-individual variance (environmental variance, V_E), refers to that variance arising from developmental or temporary circumstances (i.e., shoot-to-shoot or year-to-year). The between-individual variance (genetic and microenvironmental variance, $V_G + V_M$), refers to that portion of the variance arising from permanent circumstances (variation due to genotype and microenvironment). The repeatability (*r*) represents the correlation between repeated measurements of the same individual. Additionally, *r* sets an upper limit to the degree of heritability (narrow and broad sense).

TABLE 3. *MANOVA results for the effects of tree, year, and tree × year interaction on flower and fruit production for two* Carya *species*.

Species	Source	Parameter[a]			Wilks' lambda[b]	P
		ν_h	ν_e	μ		
Carya ovata	Tree	4	81	3	0.7476	0.0233
	Year	1	81	3	0.7270	0.0001
	Tree × year	3	81	3	0.7520	0.0063
C. tomentosa	Tree	3	72	3	0.3760	0.0001
	Year	1	72	3	0.8715	0.0214
	Tree × year	3	72	3	0.6335	0.0002

[a] The parameters ν_h, ν_e, and μ identify respectively, the degrees of freedom for the hypothesis sum of squares and cross product (SSCP) matrix (H), the degrees of freedom for the error SSCP matrix (E), and the number of variables analyzed.

[b] Wilks' lambda = [det(E)]/[det(E+H)] where H = the type III SSCP matrix for the effect and E = the type III SSCP matrix for tree (species × year).

RESULTS—Observations on date of peak pollen shedding indicate that individual trees, within a species, are remarkably consistent in their rank order for the three years of observations (Table 2). Specifically, tree A was always the first *Carya ovata* to shed pollen followed by trees B, C, and J. Likewise, tree D was always the first *C. tomentosa* to shed pollen followed by trees G, E, and H. Due to the similarity in microenvironments, these data indicate that flowering (and probably fruiting) is strongly genotype-dependent and that analyses should focus on among-tree differences.

Flower and fruit production varied greatly among trees and between years (Fig. 1–3). However, all trees were observed to produce a similar number of pistillate flowers in 1986 ($P > 0.05$; one-way ANOVA). All other reproductive traits varied significantly ($P < 0.05$) between trees, years, and species in a complex fashion. Coefficients of variation (not shown) were consistently highest for fruiting in 1986 and staminate flowering in 1987. Results of the multivariate analyses summarize the overall reproductive variability for both species (Table 3). Two-way MANOVAs assessing variation attributable to trees, years, and tree × year interaction were all significant ($P < 0.05$). Subsequent analysis by two-way ANOVAs for each dependent variable highlighted some interesting trends. For both species of *Carya*, the number of staminate inflorescences was consistently the most variable ($P < 0.05$) among trees, between years, and for the interaction (Table 4). Patterns of pistillate flowering, for both species, were somewhat less clear. The number of pistillate flowers, for *Carya ovata*, was generally constant among trees ($P = 0.76$)

TABLE 4. *ANOVA results for the effects of tree, year, and tree × year interaction on the dependent reproductive variables for two* Carya *species*

Species	Variable	Source	df	SS	F	P
Carya ovata	Stam. infl.	Tree	4	12.0727	4.09	0.0045
		Year	1	11.8361	16.04	0.0001
		Tr × yr	3	12.9065	5.83	0.0012
	Pist. flowers	Tree	4	0.2740	0.47	0.7585
		Year	1	1.4855	10.17	0.0020
		Tr × yr	3	0.9998	2.28	0.0855
	Fruits	Tree	4	0.3353	0.55	0.7027
		Year	1	0.0003	0.01	0.9634
		Tr × yr	3	0.7197	1.56	0.2051
C. tomentosa	Stam. infl.	Tree	3	51.0462	28.47	0.0001
		Year	1	3.0314	5.07	0.0274
		Tr × yr	3	14.0266	7.82	0.0001
	Pist. flowers	Tree	3	1.6869	2.45	0.0703
		Year	1	0.4225	1.84	0.1790
		Tr × yr	3	1.4373	2.09	0.1092
	Fruits	Tree	3	1.1085	2.38	0.0764
		Year	1	0.0216	0.14	0.7103
		Tr × yr	3	2.2864	4.92	0.0037

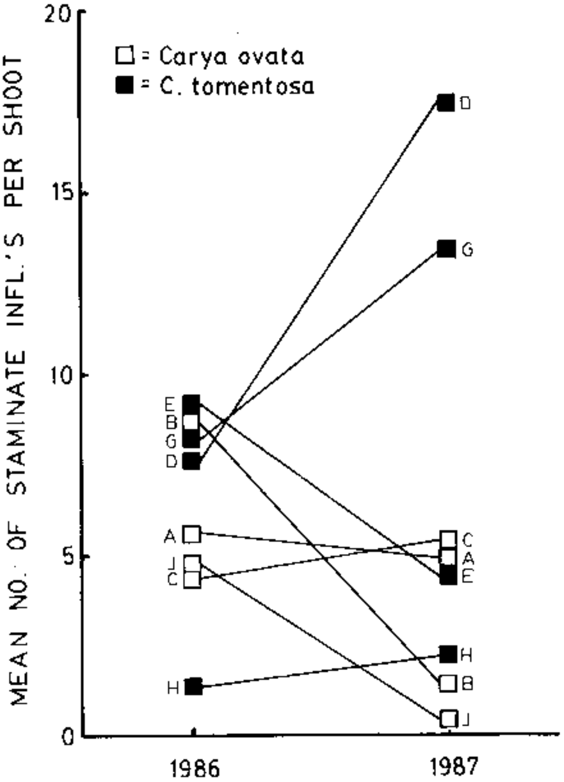

Fig. 1. Mean number of staminate inflorescences produced per shoot in 1986 and 1987. The mean value for each tree is based on a sample size of 10 shoots.

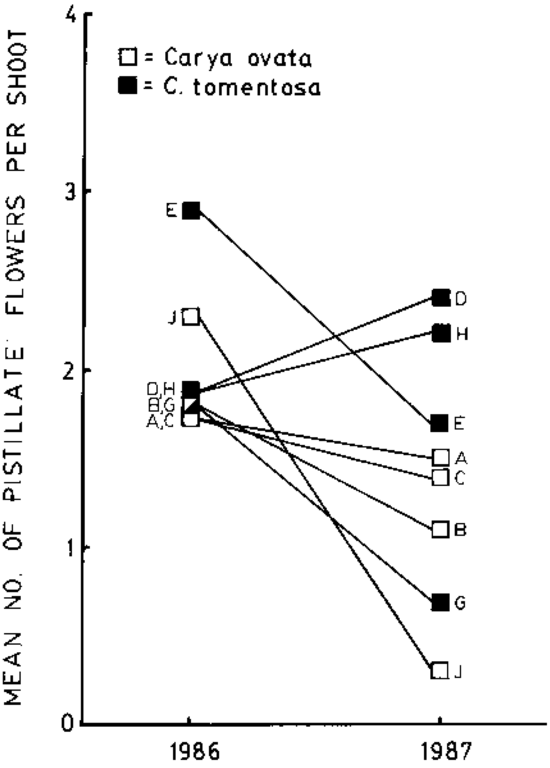

Fig. 2. Mean number of pistillate flowers produced per shoot in 1986 and 1987. The mean value for each tree is based on a sample size of 10 shoots.

but varied significantly ($P = 0.002$) between years; oddly, this latter difference was *not* reflected in differential fruit set between years ($P = 0.96$). The number of pistillate flowers, for *C. tomentosa*, was not statistically different between years ($P = 0.18$) and among trees ($P = 0.07$); however, these probability levels are suggestive of ecologically important differences. The direction and magnitude of response, of individual trees for the measured reproductive variables over the two-year period, are shown in Fig. 1–3. The survival of flowers to fruit set for *Carya ovata* was 39% in 1986 and 54% in 1987; for *C. tomentosa* it was 59% in 1986 and 63% in 1987.

Lastly, the repeatability analysis indicated that for all reproductive variables, for both species, the environmental variance arising from temporary or developmental circumstances (i.e., shoot-to-shoot and yearly environmental variation), was consistently inconsequential (<20%; Table 5). The variance arising from permanent circumstances (genotype and microenvironment) was consistently more important (>80%). While the latter variance has a microenvironmental component that cannot be separated from the genetic component, it is clear that year-to-year environmental differences contributed little to the observed variation in reproduction (Table 5). Thus, the high repeatability estimates ($r > 0.800$) suggest that the variation was due primarily to genotype and/or microenvironment. Since every effort was made to minimize microenvironmental variability we presume that genotype explains most of the total variance associated with $V_G + V_M$.

DISCUSSION—Flower and fruit abundance varied considerably among trees and between years for both species of *Carya* at Hutcheson Memorial Forest. Variation in flowering and fruiting is probably the rule rather than the exception for many forest tree species, owing in part to genetic differences among trees, the tendency to alternate fruit crops as a function of depletion and accretion of resources, and the influence of yearly weather patterns (Matthews, 1963). The relative contribution of each of these factors is additionally impacted by geography, site quality, population genetic structure, etc. in a complex fashion. We suspect

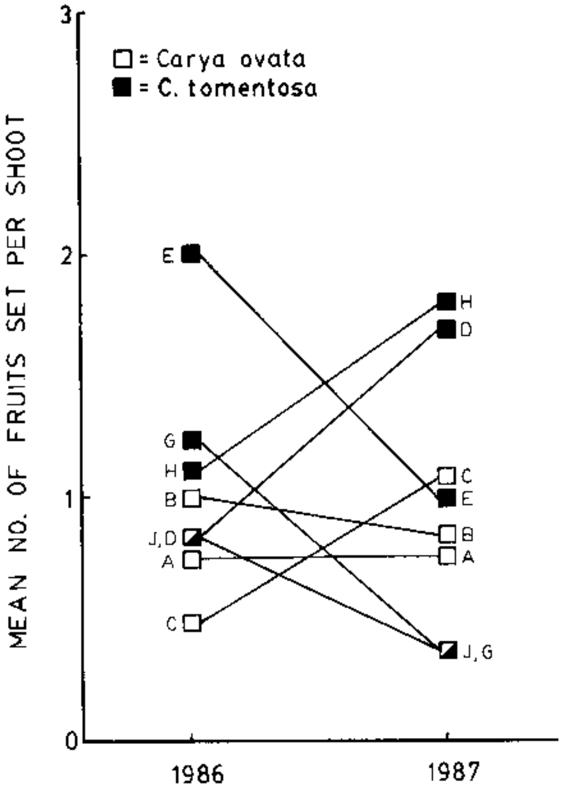

Fig. 3. Mean number of fruits set per shoot in 1986 and 1987. The mean value for each tree is based on a sample size of 10 shoots.

that at least two of these factors contributed to variation at our study site. A previous study of *Carya,* which only assessed variability in fruit production, indicated that all three of the above factors played a role (Nixon, McClain, and Hansen, 1980).

Our data suggest that differences between trees are greater for floral traits (particularly staminate flowering) than for fruiting. Pistillate flower production also varies more between years than does fruit set. Collectively, these data indicate that flowering is probably more sensitive to local and yearly environmental vagaries than is fruit set. This is not to say that floral traits do not have a strong genetic component (which they do have based on our pollen shedding observations), but only that the traits may be more plastic as indicated by significant tree × year interactions. Apparently, a sufficient amount of staminate inflorescences is produced every year for adequate pollination, with occasional years of two- and threefold increases. It is important to note that these years of excess pollen production do not necessarily result in increased fruit set (unpublished data). These highly self-compatible species (unpublished data) may, however, benefit from increased outcrossing events due to increased pollen production. The observed pistillate flower mortality patterns (ca. 50% for both species, compare Fig. 2 and 3) during the stage of pollination to fruit set are consistent with recorded patterns for other hardwood species (Williamson, 1966; Feret et al., 1982). A much greater percentage of mortality (70–98%) would be indicated if one considered the whole predispersal stage from pollination to fruit maturation (Williamson, 1966; Sork, 1983; unpublished data).

Comparisons of flower production within- and between-species highlight additional patterns regarding flowering dynamics. *Within* a species, there is a high degree of concordance between male and female flowering. With the exception of tree G, the direction and magnitude of change (between years) in both male and female flower number is consistent within each tree; i.e., an increase in the number of staminate inflorescences coincides with an increase in the number of pistillate flowers. However, *between* the two species we see that male and female flowering follows different dynamics. From 1986 to 1987 the number of staminate inflorescences increases for three of four *C. tomentosa* but decreases for three of four *C. ovata.* Additionally, the number of pistillate flowers increases in two of four *C. tomentosa* but decreases in four of four *C. ovata.* Taken together, these data suggest that within a species there is apparently a similar response to the influence of environment on flowering but that evolutionary divergence among congenerics probably resulted in differing responses to the environment.

In contrast to other studies of hardwood species (e.g., Feret et al., 1982), flower abundance in *Carya* is not always a good "predictor" of fruit set. While the number of female flowers produced obviously sets an upper limit to the number of fruits that can be set, the converse is not true; many flowers fail to set fruit. In the presence of an adequate pollen supply (unpublished data), and absence of sexual selection, fruit set is apparently adjusted as a function of available resources within a given shoot (study in progress), i.e., regardless of how many pistillate flowers are produced and fertilized per shoot, fruit set remains relatively constant from year-to-year. Our four years of observations on fruit production in *Carya* are somewhat inconsistent with the commonly accepted hypotheses of shifting resource availability affecting fruit crop periodicity; however, as a caveat our small sample size should be recognized.

TABLE 5. *Partitioning of the phenotypic variance for the flower production and fruit set of two hickory species. Each component is given as the actual variance and as a percentage of the total variance based on 10 observations per tree over two measurement periods*

	Carya tomentosa			*Carya ovata*		
Variance	Fruits	Female flowers	Male flowers	Fruits	Female flowers	Male flowers
Total phenotypic (V_P)	0.333 (100%)	0.477 (100%)	29.311 (100%)	0.077 (100%)	0.231 (100%)	5.974 (100%)
Between trees ($V_G + V_M$)	0.281 (84%)	0.452 (95%)	26.556 (91%)	0.068 (88%)	0.215 (93%)	4.791 (80%)
Within trees (V_E)	0.052 (16%)	0.025 (15%)	2.755 (4%)	0.009 (12%)	0.016 (7%)	1.183 (20%)
Repeatability (r)	0.843	0.947	0.906	0.880	0.932	0.802

Alternate bearing of fruits (i.e., 2-year cycle), as suggested by Boisen and Newlin (1910) and Fowells (1965) as being characteristic of the *Carya,* was not clearly observable in this study. The ability to recognize and quantify seed crop periodicity may be closely linked to the scale at which it is examined. The effects of scale on the interpretation of fruit crop variability are only beginning to be explored. Implicit in the study by Carmen et al. (1987) of acorn dynamics are the differing ecological and evolutionary implications for interpretations based on data from individuals, populations, or communities. Previous studies of fruit crop variability have often tended to be of an extensive nature looking at species-level or between-species patterns at one site, or looking for patterns at a broader geographic level (Sharp and Sprague, 1967; Nixon et al., 1980). These approaches do not permit the fine-scale assessment of factors affecting differential reproductive success within and among individuals of a population. An understanding of the physiological, genetic, and environmental influences on reproductive success can only be achieved by intensively examining a smaller number of trees at a sufficiently fine scale for extended periods. Moreover, future research initiatives should focus on examining reproductive variability in terms of the interacting modules (shoots) which comprise the genet (tree). Indeed, it is the behavior of these modular subpopulations that defines the ecological properties of the genet (Harper and White, 1974). The consideration of trees as metapopulations of shoots (White, 1979, 1984) may help in focusing critical attention on current perspectives of reproductive variability (mast fruiting), resource allocation, and the genetic and environmental determinants of variability and allocation in woody plants.

Flowering and fruiting of *Carya* were found to be largely innate and strongly influenced by genotype and/or microenvironment. This observation is consistent with that made by Sharp and Sprague (1967) and Wolgast (1978) in regards to *Quercus* acorn yield being consistently low for some trees and consistently high for others. Linhart and Mitton (1985) determined that a minority of trees consistently produced the majority of cones year after year in *Pinus ponderosa.* There are a number of implications concerning this hereditary element. The first concerns community structure. In general, a given population will contain a range of trees varying in reproductive potential from low to high. Seed dispersal and seedling establishment may be spatially correlated (sensu Janzen, 1970) to those trees of high reproductive potential (i.e., recruitment foci), assuming equal patterns of seed predation across phenotypes. With the presence or absence of disruptive disturbances, patterns of distribution and abundance in time and space may vary considerably. Secondly, our data suggest the importance of considering individual-level variation as well as species-level variation when evaluating the ultimate factors influencing mast fruiting. Janzen (1971) and Silvertown (1980) suggested that periodicity in seed crops may be an evolutionary strategy to starve out seed predators (small mammals and/or insects) in years of low seed output. This hypothesis relies on a more-or-less boom and bust cycle for effectiveness. But, suppose that individual trees, on their own fruiting schedules, are known by predators to be consistently good seed producers. It is less likely that the population size of predators will be significantly altered in this case, and in fact the more prolific phenotypes may be selected against by serving as feeding foci for predators in all years and thus suffering a reduced recruitment in subsequent generations. Assuming that phenotypes (genotypes) with lower seed output have a larger proportion of seeds escaping predation (i.e., trees are visited infrequently by predators because they represent a nonoptimal resource), the absolute number of seeds escaping predation for both low and high seed producing phenotypes may be similar, thus serving to maintain the *Carya* population structure. Lastly, the forest management implications are that individual trees should be observed for several years prior to timber stand improvement or clear-cutting practices. The amount of mast for wildlife can be potentially increased by cutting out genotypes of low seed production, or when clear-cutting, preserving the best genotypes for reseeding and mast food. Retaining the better genotypes will maximize vertebrate conservation efforts by ensuring that there is sufficient mast availability during the poorest nut production years.

LITERATURE CITED

ADRIANCE, G. W. 1931. Factors influencing fruit setting in the pecan. Bot. Gaz. 91: 144–166.

BOISEN, A. T., AND J. A. NEWLIN. 1910. The commercial hickories. U.S. Dept. Agric. Forest Service Bull. 80.

BRAUN, E. L. 1950. Deciduous forests of eastern North America. Hafner, New York.

CARMEN, W. J., W. D. KOENIG, AND R. L. MUMME. 1987. Acorn production by five species of oaks over a seven year period at the Hastings Reservation, Carmel Valley, California. *In* T. R. Plumb and N. H. Pillsbury [eds.], Proceedings of the symposium on multiple-use management of California's hardwood resources, 429–434. Gen. Tech. Rep. PSW-100, U.S. Dept. Agric., Forest Service, Berkeley, CA.

CHATFIELD, C., AND A. J. COLLINS. 1980. Introduction to multivariate analysis. Chapman and Hall, London.

CHRISTENSEN, D. M. 1955. Yield of seed by oak in the Missouri Ozarks. J. Forest. 70: 439–441.

DAVIS, L. D. 1957. Flowering and alternate bearing. Proc. Amer. Soc. Hort. Sci. 70: 545–556.

DOWNS, A. A., AND W. E. MCQUILKEN. 1944. Seed production of southern Appalachian oaks. J. Forest. 42: 913–920.

FALCONER, D. S. 1981. An introduction to quantitative genetics. 2d ed. Longman, London.

FERET, P. P., R. E. KREH, S. A. MERKLE, AND R. G. ODERWALD. 1982. Flower abundance, premature acorn abscission, and acorn production in *Quercus alba* L. Bot. Gaz. 143: 216–218.

FORMAN, R. T. T., AND B. A. ELFSTROM. 1975. Forest structure comparison of Hutcheson Memorial Forest and eight old woods on the New Jersey Piedmont. William L. Hutcheson Memorial Forest Bull. 3: 44–51.

FOWELLS, H. A. 1965. Silvics of forest trees of the United States. U.S. Dept. Agric. Handbook No. 271, Washington, DC.

HAND, D. J., AND C. C. TAYLOR. 1987. Multivariate analysis of variance and repeated measures. Chapman and Hall, London.

HARPER, J. L., AND J. WHITE. 1974. The demography of plants. Annual Rev. Ecol. Syst. 5: 419–463.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. Amer. Naturalist 104: 501–528.

———. 1971. Seed predation by animals. Annual Rev. Ecol. Syst. 2: 465–492.

KIRKHAM, W. C. 1976. Soil survey of Somerset County, New Jersey. U.S. Dept. Agric., Soil Conservation Service.

LINHART, Y. B., AND J. B. MITTON. 1985. Relationships among reproduction, growth rates, and protein heterozygosity in ponderosa pine. Amer. J. Bot. 72: 181–184.

———, ———, D. B. BOWMAN, K. B. STURGEON, AND J. L. HAMRICK. 1979. Genetic aspects of fertility differentials in ponderosa pine. Genet. Res. 33: 237–242.

MADDEN, G. D., AND H. L. MALSTROM. 1975. Pecans and hickories. *In* J. Janick and J. N. Moore [eds.], Advances in fruit breeding, 420–438. Purdue University Press, West Lafayette, IN.

MANNING, W. E. 1940. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruit. Amer. J. Bot. 27: 839–852.

———. 1948. The morphology of the flowers of the Juglandaceae. III. The staminate flowers. Amer. J. Bot. 35: 606–621.

MATTHEWS, J. D. 1963. Factors affecting the production of seed by forest trees. Forest. Abstr. 24: i-xiii.

MCCARTHY, B. C. 1988. A method of access into the crowns of subcanopy and canopy trees. Canad. J. Forest Res. 18: 646–649.

NIXON C. N., M. W. MCCLAIN, AND L. P. HANSEN. 1980. Six years of hickory seed yields in southeastern Ohio. J. Wildlife Managem. 44: 534–539.

PRITTS, M. P., AND J. F. HANCOCK. 1983. Seasonal and lifetime allocation patterns in the woody goldenrod *Solidago pauciflosculosa* Michaux. (Compositae). Amer. J. Bot. 70: 216–221.

———, AND ———. 1985. Lifetime biomass partitioning and yield component relationships in the highbush blueberry, *Vaccinium corymbosum* L. (Ericaceae). Amer. J. Bot. 72: 446–452.

QUINN, J. A. 1985. Genetic differentiation and phenotypic plasticity of resource allocation in plants. Amer. J. Bot. 72: 838.

ROBICHAUD, B., AND M. F. BUELL. 1973. The vegetation of New Jersey. Rutgers University Press, New Brunswick, NJ.

SAS INSTITUTE. 1982. SAS user's guide: statistics. Cary, NC.

SHARP, W. M., AND H. H. CHISMAN. 1961. Flowering and fruiting in the white oaks: staminate flowering through pollen dispersal. Ecology 42: 365–372.

———, AND V. G. SPRAGUE. 1967. Flowering and fruiting in the white oaks: pistillate flowering, acorn development, weather, and yields. Ecology 48: 243–251.

SHAW, M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petrea*) in north Wales. J. Ecol. 56: 565–583.

SHUHART, D. V. 1927. The morphological differentiation of the pistillate flowers of the pecan. J. Agric. Res. 34: 687–696.

SILVERTOWN, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. 14: 235–250.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman, San Francisco, CA.

SORK, V. L. 1983. Mast-fruiting in hickories and availability of nuts. Amer. Midl. Naturalist 109: 81–88.

WALLER, D. 1979. Models of mast fruiting in trees. J. Theor. Biol. 80: 223–232.

WHITE, J. 1979. The plant as a metapopulation. Annual Rev. Ecol. Syst. 10: 109–145.

———. 1984. Plant metamerism. *In* R. Dirzo and J. Sarukhan [eds.], Perspectives on plant population biology, 15–47. Sinauer, Sunderland, MA.

WILLIAMSON, M. J. 1966. Premature abscissions and white oak acorn crops. Forest Sci. 12: 19–21.

Wolfe, P. E. 1977. The geology and landscapes of New Jersey. Crane Russak, New York.

Wolgast, L. J. 1978. Effects of site quality and genetics on bear oak mast production. Amer. J. Bot. 65: 487–489.

Woodroof, J. G., and N. C. Woodroof. 1926. Fruit-bud differentiation and subsequent development of the flowers in the *Hicoria pecan*. J. Agric. Res. 33: 677–685.