

DEMOGRAPHY OF A SHADE-TOLERANT TREE (*FAGUS GRANDIFOLIA*) IN A HURRICANE-DISTURBED FOREST

WILLIAM B. BATISTA,^{1,3} WILLIAM J. PLATT,¹ AND RAUL E. MACCHIAVELLI^{2,4}

¹Department of Plant Biology, Louisiana State University, Baton Rouge, Louisiana 70803 USA

²Department of Experimental Statistics, Louisiana State University, Baton Rouge, Louisiana 70803 USA

Abstract. We examined the demographic responses of *Fagus grandifolia* to Hurricane Kate (1985) in an old-growth Southern mixed-hardwood forest in northern Florida. Matrix population models were used to contrast pre- and post-hurricane population trends (1978–1992) with predictions of four hypotheses of the persistence of this shade-tolerant species in hurricane-frequented forests (resistance, recovery, release, and complementation). Although growth and mortality schedules changed as a result of the hurricane, the asymptotic population growth rate did not change significantly and did not depart significantly from $\lambda = 1$ (stability) in either the pre- or the posthurricane periods. Long-term trends simulated for varying hurricane frequencies also projected stability in population size. These results supported the resistance hypothesis. Elasticity analysis showed that, while recruitment had a minor influence, survival of medium-sized trees was the most critical character influencing population growth. Similar patterns of life history sensitivity are common among other trees, suggesting that traits related to survival of large understory individuals would often be under high selection pressure. Among these traits, those associated with hurricane resistance could also be advantageous in forests subjected to light to moderate disturbance. Thus, resistance to canopy disruption could have remained linked to shade tolerance during expansions and contractions of the distribution of *F. grandifolia*.

Key words: beech; demography; disturbance; *Fagus grandifolia*; Florida; hurricane; matrix population model; Southern mixed-hardwood forest.

INTRODUCTION

The combination of shade tolerance, limited response to high levels of light, and long life-span is typically associated with trees in closed-canopy forests (Marks 1975, Bazzaz 1979, Swaine and Whitmore 1988). One of the most exemplary shade-tolerant species is *Fagus grandifolia* Ehrh. (American beech), a deciduous tree common in temperate forests of eastern North America (Braun 1950). The autoecology of this species has been studied extensively. Light is not required for germination of seeds (Rudolf and Leach 1974) or sprouting of root buds of *F. grandifolia* (Jones and Raynal 1988). Seedlings and saplings survive and grow in shade (Harcombe et al. 1982, Platt and Hermann 1986, Jones and Raynal 1987, Canham 1988, Tubbs and Houston 1990, Poulson and Platt 1995), probably due to their low respiration rate and high photosynthetic efficiency at low light (Loach 1967, Wood and Turner 1971), as well as their pattern of ramification that minimizes self-shading and investment in

supporting structures (Canham 1988, Küppers 1989). Small *F. grandifolia* have higher growth rates in small gaps than under canopy trees (Canham 1988, 1990, Poage and Peart 1993, Poulson and Platt 1995). However, growth rates in gaps are not correlated with light level, possibly due to low light-saturation intensity (Loach 1967), limited seasonal extension growth (Moore 1909), and relatively low morphological plasticity (Canham 1988, 1989, Poulson and Platt 1995). Individuals of *F. grandifolia* can live longer than many species with which they co-occur (Altman and Dittmer 1962, Tubbs and Houston 1990, Poulson and Platt 1995). In addition, community-level analyses of temperate forests have suggested that *F. grandifolia* usually reaches the canopy in small gaps. Relative abundance of this species has been proposed to increase during periods of low rate of canopy disturbance and decline when the rate of canopy disturbance is high (MacGowan 1937, Blaisdell et al. 1974, Forcier 1975, Barden 1980, Harcombe et al. 1982, Runkle 1982, Glitzenstein et al. 1986, Canham 1988, 1990, Poulson and Platt 1989, 1995, Platt and Schwartz 1990, Brisson et al. 1994, Peters and Platt 1995).

Notwithstanding its proposed association with low rates of canopy disturbance, *Fagus grandifolia* often is a major component in hurricane-frequented hardwood forests along the Atlantic and Gulf coasts from New England to eastern Texas (Foster 1988, Platt and Schwartz 1990, Merrens and Peart 1992, Bill and Har-

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³ Present address: Departamento de Ecología, Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, 1417 Capital Federal, Argentina.

⁴ Present address: Departamento de Agronomía y Suelos, Universidad de Puerto Rico-RUM, P.O. Box 5000, Mayaguez, Puerto Rico 00681.

combe 1994, Batista and Platt 1997). In particular, Southern mixed-hardwood forests located along the Coastal Plain of the northern Gulf of Mexico, from northern Florida to eastern Texas, consistently have *F. grandifolia* among the dominant species (Quarterman and Keever 1962). Each stand of these forests is likely to be affected several times per century by moderately intense tropical storms (maximum sustained wind-speeds 100–160 km/h, Batista and Platt 1997). These storms damage overstory trees, create multiple tree fall gaps, expand the fraction of the forest area in gaps, and increase the light levels under the canopy. Following the storms, damaged overstory trees exhibit decreased growth rates, while understory trees not damaged by fallen trees are released (Batista and Platt 1997). In these forests, *F. grandifolia* coexists with both evergreen (*Magnolia grandiflora*, *Pinus* spp.) and deciduous (*Liquidambar styraciflua*, *Quercus* spp., *Carya* spp., *Nyssa sylvatica*) overstory species, and with many understory species (e.g., *Ostrya virginiana*, *Carpinus caroliniana*, and *Ilex opaca*) (Gano 1917, Quarterman and Keever 1962, Blaisdell et al. 1974, Delcourt and Delcourt 1974, Marks and Harcombe 1981, Glitzenstein et al. 1986, White 1987, Platt and Schwartz 1990, Vankat 1990, Ware et al. 1993, Batista and Platt 1997).

How does *Fagus grandifolia* persist under a regime of frequent canopy disruption? We addressed this primarily demographic problem by examining the responses of a population of *F. grandifolia* to a moderate-intensity hurricane in a Southern mixed-hardwood forest. For our analysis, we distinguished two phases in the dynamics of the forest: the “open” canopy, and the “closed” canopy periods. The open-canopy phase was defined as that starting with a hurricane, over which some large fraction of the forest area was in multiple treefall gaps. Immediate and delayed tree deaths caused by the hurricane were included in the mortality of this period. The closed-canopy phase was defined as that occurring some time after the most recent hurricane, when the canopy had reformed and a comparatively large proportion of the forest was under canopy or in small, single-treefall gaps. These two phases were assumed to alternate in time in some long-term stochastic sequence. Admittedly, our analysis is dependent on this particular definition of phases of forest dynamics, but this type of dependence is intrinsic to the perception of many ecological systems (O’Neill et al. 1986, Orloci and Orloci 1988).

We formulated four alternative hypotheses that might explain the apparent persistence of local populations of *Fagus grandifolia* under the natural sequence of closed- and open-canopy periods (see Table 1). In hypothesis 1 (resistance), we proposed that hurricane-related damage and mortality may be not severe enough to affect the projected stability of population size. The size of the population would tend to remain stable in both closed- and open-canopy periods. In hypothesis 2

TABLE 1. Population trends predicted by four hypotheses proposed to explain the long-term persistence of *Fagus grandifolia*.

Hypothesis	Open canopy	Closed canopy	Long-term alternation
Resistance	Stable	Stable	Stable
Recovery	Negative	Positive	Stable
Release	Positive	Negative	Stable
Complementation	Negative	Negative	Stable

Note: The open-canopy phase starts with a hurricane and includes the time when a large fraction of the forest is in multiple-treefall gaps. The closed-canopy phase occurs after the canopy has been restored from the most recent hurricane damage and a comparatively large fraction of the forest is under canopy or in single-treefall gaps.

(recovery), we proposed that the population may persist because intervals between hurricanes would be long enough to allow the population to recover during the closed-canopy period. The size of the population would tend to decline in the open-canopy period, but this trend would be balanced by an increasing trend after the canopy has been restored. In hypotheses 3 and 4, we postulated that persistence of *F. grandifolia* may be dependent upon recurrent disturbance (cf. Peters and Poulson 1994). In hypothesis 3 (release), we proposed that the size of the population would tend to increase over the open-canopy phase when understory trees and seedlings receive increased light. This trend would balance, over the long term, a negative trend that would occur in the closed-canopy phase. In hypothesis 4 (complementation), we proposed that the population would only persist if closed- and open-canopy periods alternated in time. This would happen if some critical life history process occurred at a sufficient rate only during one of the phases, while other such process only occurred at sufficient rates during the other phase. The long-term trend of population size would be declining if either the closed- or the open-canopy scenario were maintained indefinitely, but it would be stable if the two phases alternated in time (cf. Huenneke and Marks 1987, Moloney 1988).

In this study, we constructed size-classified matrix population models (Lefkovich 1965, Caswell 1989) based on observed patterns of recruitment, growth, and survival of *Fagus grandifolia* in Woodyard Hammock, an old-growth forest in northern Florida, over a 14-yr period that included Hurricane Kate in 1985. We used asymptotic population growth rates projected with our matrix models to evaluate the four hypotheses of population persistence. By denoting λ_o and λ_c , the asymptotic population growth rates for the open- and the closed-canopy phases, respectively, our hypotheses become: *H1* (resistance), $\lambda_o = \lambda_c = 1$; *H2* (recovery), $\lambda_o < 1 < \lambda_c$; *H3* (release), $\lambda_o > 1 > \lambda_c$; and *H4* (complementation), $\lambda_o < 1, \lambda_c < 1$. All these hypotheses were subjected to the assumption that the population is persistent under a natural long-term sequence of open- and closed-canopy phases. We tested this as-

sumption by simulating long-term sequences of open- and closed-canopy phases with sequences of transition matrices. From our demographic perspective, we analyzed trends in population size and structure, rather than in relative abundance in the community, and we did not discriminate between the interactions with abiotic factors and with co-occurring species.

METHODS

Study area

Woodyard Hammock is a 30-ha Southern mixed-hardwood forest located at Tall Timbers Research Station, 32 km north of Tallahassee, in Leon County, northern Florida, at 30°35' N and 84°20' W (Blaisdell et al. 1974, Hirsh 1981, Platt and Hermann 1986, Platt and Schwartz 1990). The forest is situated just inland from the northern shore of Lake Iamonia, at ~40 m above the sea level, on level terrain comprised of clay soils developed from marine deposits exposed during the Miocene (Platt and Schwartz 1990). According to records of two weather stations located near Woodyard Hammock (Quincy and Monticello, Florida), the mean annual temperature is 19°C, with a maximum monthly mean of 27°C in July and a minimum of 11°C in January, the mean annual rainfall is 1420 mm, and the driest months are October and November with a monthly mean of 70 mm (NOAA 1982). The growing season is ~273 d long, from March through November (Caham et al. 1990). According to NOAA records (Jarvinen et al. 1984), between 1886 and 1992, four storms with maximum sustained windspeeds >100 km/h passed within 100 km of Woodyard Hammock, in 1886, 1894, 1941, and 1985. The last of these storms, Hurricane Kate, passed within 30 km of Woodyard Hammock on 21 November 1985, following a period of heavy rainfall that had saturated the soil. Downbursts of wind up to 160 km/h were recorded in Leon County during the hurricane (Clark 1986) and tropical storm force winds lasted for ~8 h.

A 4.5-ha study plot was established in the middle of Woodyard Hammock in 1978 (Hirsh 1981, Platt and Hermann 1986). All trees in the plot with diameter at 1.5 m height (dbh) ≥ 2 cm were measured for dbh, classified as overstory (>15 m tall) or understory (≤ 15 m tall), mapped, and tagged. Censuses were repeated biennially to record diameter growth and recruitment of trees in the entire plot. Stems that grew into the dbh ≥ 2 cm size class were recorded as recruits. Mortality was recorded annually until 1985 and biennially starting in 1986.

Fagus grandifolia was one of the dominant overstory species in the plot. In 1978, density of this species was 124 trees/ha (dbh ≥ 2 cm) and basal area was 7.6 m²/ha. The number of live *F. grandifolia* individuals (dbh ≥ 2 cm) in the plot varied between 575 in 1978 and 546 in 1992. Our data base contains records for 641 trees of this species. Between 1978 and 1992, the pop-

ulation of *F. grandifolia* represented between 23 and 28% of all trees (dbh ≥ 2 cm) of overstory species in the plot. Other dominant overstory species were *Magnolia grandiflora* (density = 64 trees/ha, basal area = 24.7 m²/ha), *Liquidambar styraciflua* (124 trees/ha, 4.2 m²/ha), and *Pinus glabra* (40 trees/ha, 4.4 m²/ha). The three most abundant understory species were *Ostrya virginiana*, *Carpinus caroliniana*, and *Ilex opaca*. Gaps, defined as openings in the overstory, were mapped as polygons formed by connecting the bases of the bordering trees (i.e., expanded gaps of Runkle 1982). These expanded gaps occupied 31% of the plot before, and 62% after Hurricane Kate (Batista and Platt 1997). In 1992, the gap area remained high partly as a consequence of delayed mortality of damaged canopy trees.

Our analysis is based on the data obtained between 1978 and 1992. Consequently, the data set encompasses 7 yr preceding and 7 yr following Hurricane Kate. Climatograms (Walter 1971), constructed with data from weather stations located near Woodyard Hammock, revealed no striking differences between the patterns of monthly rainfall and mean temperature of these two 7-yr periods.

Analysis of demographic patterns

In the first part of our analysis we examined changes in the probability distribution of tree dbh, in the rate of recruitment, and in individual growth and mortality patterns of *Fagus grandifolia* associated with the occurrence of Hurricane Kate in 1985. The period between 1978 and 1984 was assumed to represent a closed canopy phase, and the period 1984–1992 an open-canopy phase of our conceptual model. Note that our use of the terms open and closed is relative, as the gap area was substantial before Hurricane Kate.

Probability distribution of tree size.—The Weibull distribution (Antle and Wain 1988) was fitted to each of the empirical dbh probability distributions obtained from the censuses. The parameters were estimated by maximum likelihood and the goodness of fit was assessed using the Kolmogorov-Smirnov one-sample test (Daniel 1990).

Recruitment.—The observed numbers of individuals reaching 2-cm dbh between two consecutive censuses were compiled from the data base. The hypothesis of equal recruitment (number of recruits) among the two-year intervals (“constant” recruitment rate) was tested with the Pearson chi-square statistic (Agresti 1990).

Growth.—A simple linear regression model of the form $d = a + bx + e$, where d is the increment, x is the initial dbh, a and b are regression parameters, and e is an error term, was fitted to individual dbh increments between 1978 and 1984 (closed canopy). For the increments between 1984 and 1992 (open canopy), a segmented regression model of the form $d = a + bx + e$, for $x < x_c$ and $d = z + e$, for $x \geq x_c$, was fitted, where z is a plateau attained by the expected increment

at the threshold dbh $x_i = (z - a)/b$. The parameters were estimated by least squares; for the segmented model the sum of squared errors was minimized by the Gauss-Newton method. To facilitate comparing between periods, after these analyses, we obtained mean annual growth rates by dividing the increments by the corresponding interval length. In addition, differences in mean annual growth rate between periods for selected dbh classes were examined with a t test calculated taking into account the covariance between growth in each period.

Mortality.—Logistic regression (Agresti 1990) was applied to model individual tree death as a Bernoulli variable $m(x)$ that takes the value one if the tree is dead at the end of the period considered, where x is the dbh. The probability of death $\pi(x)$ varied with dbh according to $\pi(x) = \exp\{p\{\ln(x)\}/[1 + \exp\{p\{\ln(x)\}]\}$, where $p\{\eta\}$ denotes a complete polynomial in η . We fitted models with quadratic polynomials for the interval 1978–1984 (closed canopy) and for the immediate mortality caused by Hurricane Kate, and with a cubic polynomial for the intervals 1984–1992 (open canopy) and 1986–1992 (strictly posthurricane mortality). A survival function was derived from these models as $s(x) = 1 - m(x)$, which takes the value one with probability $\sigma(x) = 1 - \pi(x) = \{1 + \exp[p\{\ln(x)\}]\}^{-1}$. For comparison, average annual mortalities were derived for the 1978–1984 and 1986–1992 intervals as $1 - \sigma(x)^{1/6}$.

Matrix models

In the second part of the analysis, we integrated the observed demographic patterns in size-classified matrix population models (Caswell 1989). We constructed separate transition matrices for the closed- and the open-canopy phases. Vital rates included in these matrices were estimated over the 1978–1984 and the 1984–1992 intervals respectively, so that the projection intervals were of 6 yr for the closed- and of 8 yr for the open-canopy models. We projected asymptotic population growth rates and stable size-frequency distributions for both phases, and we examined the sensitivity of asymptotic population growth to small changes in the vital rates. In addition, we manipulated the matrices to simulate the long-term dynamics of the population under various hurricane frequencies, as well as the effects of large changes in selected vital rates, and of isolating changes in vital rates that occurred simultaneously with other changes (e.g., changes in growth and in mortality). Transition probabilities in each of these models were not varied with density. For this reason, the results of the analyses are not predictions but projections that describe the population behavior over our observation periods (see Caswell 1989).

Estimation of the transition matrices.—We assumed that the only life-cycle transitions that could occur in one projection interval were death, survival in the same size class, survival and growth to the next size class,

and reproduction. Consequently, nonzero elements of the transition matrices were restricted to the diagonal, the first subdiagonal, and the first row. We denote $\mathbf{A} = \{a_{ij}\}$ a transition matrix, with diagonal elements $a_{ii} = P_i$ ($i = 1, \dots, k$), first subdiagonal elements $a_{i+1,i} = G_i$ ($i = 1, \dots, k - 1$), and first row elements $a_{1i} = F_i$ ($i = 2, \dots, k$), where k is the number of size classes. In what follows, we omit the subindices in P , G , and F whenever we refer to a generic size class with lower limit L and upper limit U . The true values of these parameters are

$$P = \text{Prob.}\{L \leq y < U \text{ and } s(x) = 1/L \leq x < U\},$$

$$G = \text{Prob.}\{U \leq y \text{ and } s(x) = 1/L \leq x < U\}, \text{ and}$$

$$F = E\{\text{number of recruits produced}/L \leq x < U\},$$

where x and y respectively denote the dbh at the beginning and at the end of the projection interval, and $s(x) = 1$ indicates survival. We estimated these vital rates based on the fitted size–probability distribution, growth and mortality curves, rather than on observed transition frequencies. The appeal of this approach is that the estimators change smoothly with changes in the size class boundaries. If the fitted models are correct, our estimators have the same essential large sample properties as those based on observed frequencies (Agresti 1990).

In our growth regression models $y = g(x) + e$, where $g(x) = x + E\{d\}$ and $E\{d\}$ is the expected increment. When the variance of e is small relative to the width of the size class, a good approximation of P , the probability of survival in the same class, is given by

$$P^* = \text{Prob.}\{L \leq g(x) < U \text{ and } s(x) = 1/L \leq x < U\}$$

$$= \left\{ \int_{(L,q)} f(x)\sigma(x) dx \right\} \div \left\{ \int_{(L,U)} f(x) dx \right\} \quad (1)$$

where $s(x)$ equals 1 with probability $\sigma(x)$, $q = \max[L, g^{-1}(U)]$ and $f(x)$ is the probability density function of the initial dbh. We estimated P by replacing q , $f(x)$, and $\sigma(x)$ in Eq. 1 by their estimates based on the growth, Weibull probability distribution, and mortality models, respectively. Similarly, we approximated G , the probability of survival and growth to the next class, with

$$G^* = \text{Prob.}\{U \leq g(x) \text{ and } s(x) = 1/L \leq x < U\}$$

$$= \left\{ \int_{(q,U)} f(x)\sigma(x) dx \right\} \div \left\{ \int_{(L,U)} f(x) dx \right\} \quad (2)$$

and constructed the estimate using the estimated growth, probability distribution, and mortality models. In other words, with $g^{-1}(U) > L$, our estimator of P was the predicted proportion of trees with initial size between L and $g^{-1}(U)$ that survive to the end of one projection interval, out of all trees with initial size between L and U ; and our estimator of G was the pre-

dicted proportion of surviving trees with initial size between $g^{-1}(U)$ and U , out of the same total (Note that if $q = L$ then $P^* = 0$). In addition, we calculated the estimators of $\Sigma_i = P_i + G_i$, the total survival rate of individuals in the i th class at the beginning of the projection interval, and of $\Gamma_i = G_i/(P_i + G_i)$, the conditional probability of growth to the next class for surviving individuals.

Estimation of fecundity was based on observed recruitment (as defined above), with the simplifying assumptions that only overstory individuals reproduce (cf. Harcombe et al. 1982), and that all overstory individuals have equal expected reproductive output (cf. Enright and Ogden 1979). Accordingly, our estimator of F was: $F^* = (n \div O)c$, where n is the number of recruits alive at the end of the period under consideration, O is the number of overstory individuals present at the beginning of this period, and c is the expected proportion of overstory individuals in the size class. This proportion was set to $c = 0$ for size classes below 16 cm, and to $c = \{\int_{(L,U)} f(x)h(x) dx\} \div \{\int_{(L,U)} f(x) dx\}$ otherwise, where $h(x)$ is the probability that an individual with dbh = x is in the overstory as estimated by a logistic regression model (Agresti 1990) on a linear function of x . Lacking actual fecundity data, we chose this crude approach because it involved few assumptions. The models, in turn, proved to be very robust to differences in estimated fecundities (cf. Harcombe 1987).

Definition of the size classes.—We delimited the size classes using a procedure designed to find a compromise between two types of error described by Vandermeer (1978) and Moloney (1986). The approximations of P and G from Eqs. 1 and 2 improve, for a given variance of e , as the width of the size class increases. The error in this approximation corresponds to Vandermeer's (1978) "error of estimation," which decreases as the size class width increases. A second type of error is introduced when using the transition matrix to project the size class distribution in time because all individuals in the same size class are implicitly assigned identical transition probabilities. This is Vandermeer's (1978) "error of distribution," which decreases as the size class width decreases below a finite value, provided the individual transition probabilities are continuous functions of size. The two errors are simultaneously introduced when estimates \tilde{P} of P , and \tilde{G} of G , are calculated from Eqs. 1 and 2, setting $f(x)$ to a uniform distribution function (i.e., $f(x) = 1/(U - L)$, $L \leq x < U$, and $f(x) = 0$ otherwise). We defined the global quadratic error as $\varepsilon = [(\tilde{P} - P)/P]^2 + [(\tilde{G} - G)/G]^2$, and estimated this error by replacing in the formula the true P and G with the corresponding observed transition probabilities.

The criterion used to set the size class boundaries was the sum of global quadratic errors estimated for the 1978–1984 and 1984–1992 intervals. We started with the smallest size class by setting $L = 2$ cm and

computing the sum of errors for increasing values of U . The upper limit of this class was set to the value of U for which the sum of errors appeared to have the absolute minimum in a graph (cf. Moloney 1986). This procedure was repeated for successive size classes by setting the lower limit to the value of the previous-class upper limit (all classes were defined by intervals closed to the left and open to the right). The resulting size classes were 2–4, 4–6, 6–11, 11–16, 16–28, 28–40, 40–52, 52–64, and >64 cm dbh. Beyond 64 cm dbh, observed transition probabilities became unreliable because the number of individuals was small.

Eigenanalysis and sensitivity analysis.—The dominant eigenvalue λ and the corresponding left eigenvector \mathbf{v} and right eigenvector \mathbf{w} of each transition matrix were obtained by the power method (Caswell 1989). These eigenvalues give the limit approached by the finite population growth rate if the transition frequencies remained constant. To compare between phases, these asymptotic growth rates were transformed to an annual basis by raising the λ s to the inverse of the corresponding projection interval in years (six for 1978–1984, and eight for 1984–1992). The stable size class distribution associated with each transition matrix was given by its first right eigenvector \mathbf{w} scaled so that its elements added to one.

Elasticities of λ with respect to the nonzero elements of the transition matrices were calculated as $\xi(a_{ij}) = \delta \ln(\lambda) / \delta \ln(a_{ij}) = a_{ij}v_iw_j / (\lambda \mathbf{v}'\mathbf{w})$, where v_i and w_j are respectively the i th and j th element of the eigenvectors \mathbf{v} and \mathbf{w} (Caswell 1989). These functions measure the proportional change in λ resulting from a small proportional change in a_{ij} when all other components of the model are fixed. de Kroon et al. (1986) noted that, since $\lambda = \mathbf{v}'A\mathbf{w}/\mathbf{v}'\mathbf{w} = \sum_{ij} a_{ij}v_iw_j/\mathbf{v}'\mathbf{w}$, each elasticity can be regarded as the relative contribution to λ of the corresponding matrix element. Sums of these contributions were computed for the diagonal, for the sub-diagonal, and for the fecundity elements of the transition matrices (cf. Enright and Watson 1991, Gotelli 1991). Each of these sums measures the proportional change in λ resulting from a small proportional change common to all the P_i , G_i , or F_i respectively, when the rest of the matrix is fixed. In addition, we computed the contribution to λ of Σ_i , the total survival rate of individuals in the i th size class. In our case, it is straightforward that $\xi(\Sigma_i) = \xi(P_i) + \xi(G_i)$, (by using Eqs. 4.60, 4.61, 6.49, and 6.38 from Caswell 1989).

Overall sensitivities of λ to small changes in the nonzero elements of the transition matrices were calculated as $S = \{\Sigma_i(\delta\lambda/\delta P_i)^2 + \Sigma_i(\delta\lambda/\delta G_i)^2 + \Sigma_i(\delta\lambda/\delta F_i)^2\}^{1/2}$, where the summations are taken over the transition-matrix elements not set to zero a priori. This measure is an upper bound to the change in λ produced by a given small perturbation of the transition matrix (Caswell 1978, 1989). In addition, sensitivities of λ to large departures from observed recruitment and mortality rates were examined numerically by recalculating

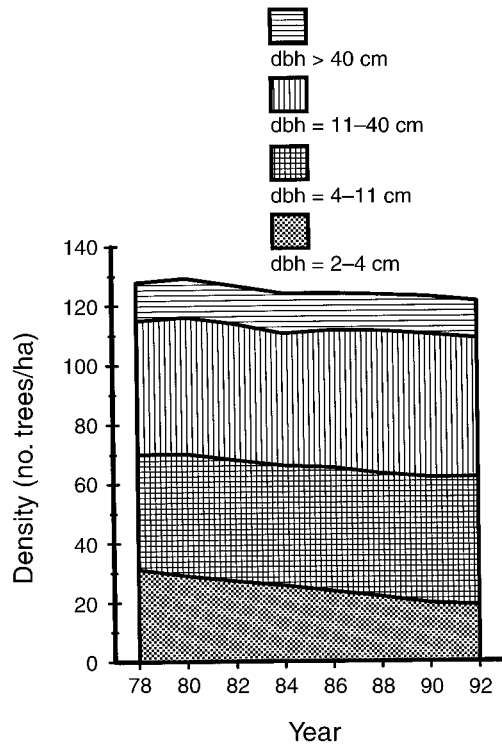


FIG. 1. Changes in *Fagus grandifolia* density between 1978 and 1992 in a 4.5-ha plot of Southern mixed hardwood forest in Woodyard Hammock, Florida.

λ after suitable alterations of the elements in the transition matrix.

Bootstrap comparisons.—We used a bootstrap procedure (Efron and Tibshirani 1993) to construct confidence intervals for estimated eigenvalues, eigenvectors, sensitivities, elasticities, and for the difference between annual finite population growth rates projected from the 1978–1984 and 1984–1992 intervals. We generated 1000 bootstrap samples by, each time, drawing randomly and with replacement 641 trees from our data base (cf. Meyer et al. 1986). The same analysis performed with the original data set (“all data”) was repeated for each bootstrap sample. This yielded new estimates for the parameters of the 1978 and 1984 Weibull distributions of dbh, and for the parameters of the growth and mortality regression models for the 1978–1984 and 1984–1992 intervals. These estimates were used to construct a transition matrix for each period in the same way as for all data. Eigenanalysis and sensitivity analysis of these two matrices were performed (leading eigenvectors were always written with non-negative elements), and the difference between population growth rates projected from them was computed after transformation to an annual basis. For each statistic, we defined the $1 - 2\alpha$ confidence interval as limited by the α and $1 - \alpha$ percentiles of the corresponding probability distribution generated by the 1000 bootstrap samples (i.e., the “percentile intervals,” Ef-

TABLE 2. Fitted Weibull distributions of tree dbh.

Year	<i>N</i>	α	γ	<i>D</i>	<i>P</i>
1978	575	0.142	0.782	0.044	>0.1
1984	558	0.121	0.823	0.057	>0.05
1986	555	0.126	0.815	0.038	>0.1
1992	546	0.120	0.816	0.043	>0.1

Note: *N* = number of trees; α and γ are parameters of the Weibull distribution with cumulative distribution function $F(x) = 1 - \exp\{-\alpha(x - 2)^\gamma\}$. *D* = Kolmogorov-Smirnov one-sample, two-sided test statistic and *P* = null probability of a larger *D*.

ron and Tibshirani 1993). As the original sample is not strictly random, we regard the results of this resampling procedure as our best approximation to the error of the estimates (see Caswell 1989: 185).

Software.—The *t* tests for comparing growth rate between periods and the χ^2 test of constant recruitment rate were calculated manually. All other statistical models were fitted using SAS: Proc LIFEREG for Weibull distributions, Proc REG and NLIN for growth models, and Proc LOGISTIC for mortality models (SAS Institute 1989b). The estimation and analysis of transition matrices were programmed in the SAS Interactive Matrix Language (SAS Institute 1989a). For the original data, and for the generation and analysis of bootstrap samples, this program was combined with SAS code for sorting the data and for fitting the statistical models using the SAS Macro Processing facility (SAS Institute 1990).

RESULTS

Observed demographic patterns

Density and size probability distribution.—Between 1978 and 1992 the density of *Fagus grandifolia* (dbh ≥ 2 cm) in the Woodyard Hammock plot remained between 128 and 121 individuals/ha (Fig. 1). The probability distribution of dbh (≥ 2 cm) was inverted-J shaped, and the largest observed dbh values were between 83.0 and 94.5 cm. The empirical distributions observed in 1978, 1984, 1986, and 1992 fit to Weibull distributions. Kolmogorov-Smirnov goodness-of-fit tests did not reject the hypothesis with $\alpha = 0.1$ for 1978, 1986, and 1992, and with $\alpha = 0.05$ for 1984 (Table 2). All trees < 16 cm dbh were in the understory (≤ 15 m tall), and all trees > 64 cm dbh were in the overstory (> 15 m tall).

Recruitment.—The number of recruits of *Fagus grandifolia* in the plot varied between 3 and 17 per 2-yr period. Although recruitment was quite variable among 2-yr periods (cv = 0.47), the hypothesis of constant recruitment rate over the 1978–1992 period was not rejected by a χ^2 test with $\alpha = 0.05$ ($\chi^2 = 12.5$, df = 6). Under this hypothesis the estimated recruitment rate was 1.06 trees·ha⁻¹·yr⁻¹. No trend in recruitment over time was noticeable.

Growth.—Diameter growth rate of *Fagus grandifolia*

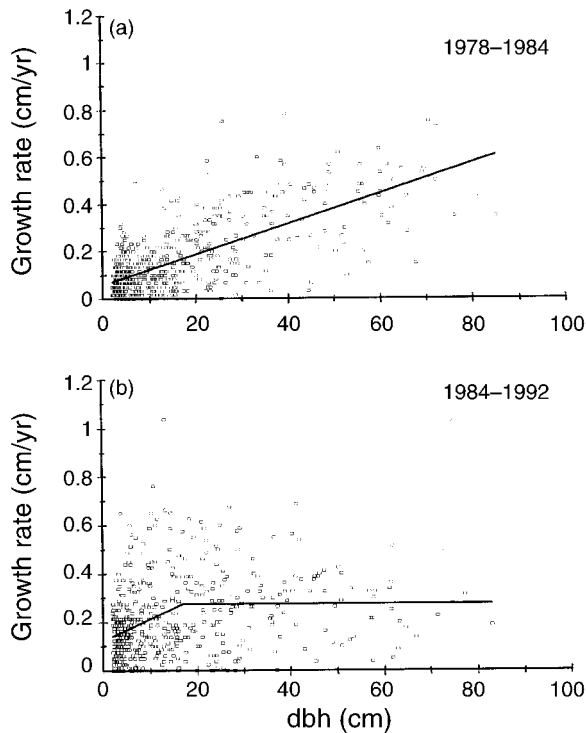


FIG. 2. Relationship between diameter growth of *Fagus grandifolia* and dbh in a 4.5-ha plot in Woodyard Hammock, Florida in (a) 1978–1984 and (b) 1984–1992.

folia increased with tree dbh. In the 1978–1984 interval (closed canopy), the increase in tree growth rate with dbh fit a linear model, varying from ~ 1 mm/yr for the smallest trees to ~ 6 mm/yr for the largest (Fig. 2a). Dispersion about the linear trend was substantial (standard error = 1.1 mm/yr), and growth of individual trees ranged from nondetectable over the whole period to ~ 8 mm/yr. In the 1984–1992 (open canopy) interval, the relation between tree growth and dbh was no longer linear, but fitted a segmented model predicting increased growth with tree dbh for trees < 17 cm dbh, but no trend for larger trees (Fig. 2b). Dispersion about this line (SE = 1.6 mm/yr) was larger than for the 1978–1984 period and growth of individual trees ranged from nondetectable over the whole period to ~ 10 mm/yr. The t tests ($\alpha = 0.05$) for comparing mean annual diameter growth in each size class between the 1978–1984 and 1984–1992 periods detected a significant increase in growth rate of small trees (size classes 2–4, 4–6, and 6–11, 11–16 cm dbh), a significant decrease in growth rate of trees 52–64 cm dbh, and no significant change in the remaining size classes.

Mortality.—In the 1978–1984 (closed canopy) interval, mortality of *Fagus grandifolia* exhibited a U-shaped pattern of association with log-diameter of trees. Mortality predicted by the logistic regression model was maximum for the smallest trees, decreased rapidly with increasing dbh for trees < 17 cm, and in-

creased slightly with dbh for larger trees, although the error of estimation of large-tree mortality was high (Fig. 3a). Immediate mortality caused by Hurricane Kate was very low; only 2 out of 490 trees < 40 cm dbh exposed to the disturbance were killed, while among larger trees 5 out of 61 were killed. However, mortality of large trees directly caused by the hurricane was significantly higher than their 1978–1984 average annual mortality (Fig. 3b). Following the hurricane the mortality of trees 2–4 cm dbh decreased significantly (Fig. 3c). As a result, the combined pattern for 1984–1992 (open-canopy period) was not U-shaped, with the mortality being significantly lower than in the closed-canopy period for the smallest trees (2–4 cm dbh), significantly higher for trees > 64 cm dbh, and not significantly different for medium-sized trees.

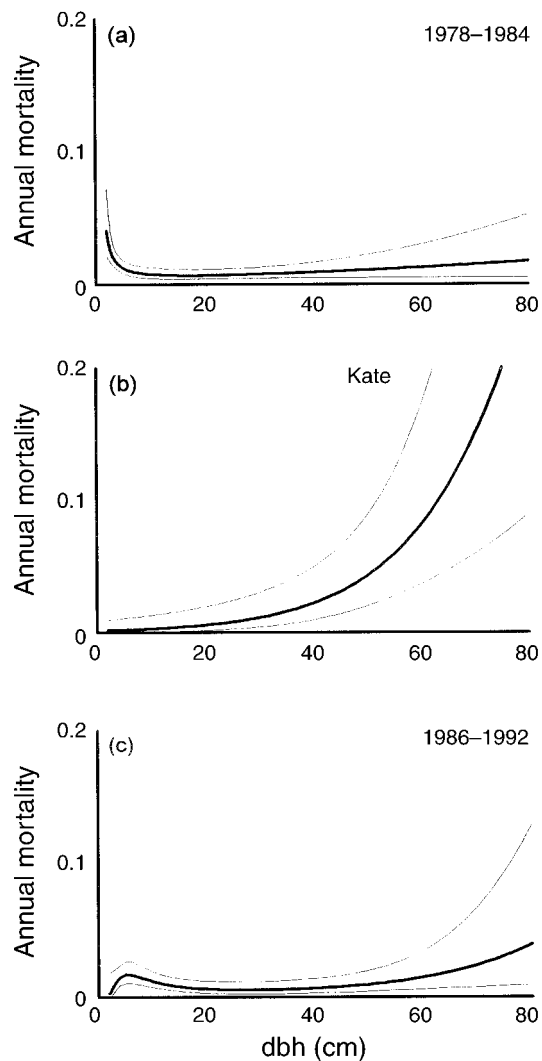


FIG. 3. Logistic regression curves of expected mortality of *Fagus grandifolia* as a function of tree dbh in (a) 1978–1984, (b) period 1985 (Hurricane Kate), and (c) 1986–1992; dotted lines enclose the 95% confidence intervals for the expected mortality.

TABLE 3. Transition matrices estimated for the *Fagus grandifolia* population in Woodyard Hammock in the closed (1978–1984) and open (1984–1992) canopy periods (dbh classes are in cm).

dbh (cm)	dbh (cm)								
	2–4	4–6	6–11	11–16	16–28	28–40	40–52	52–64	64+
1978–1984									
2–4	0.6955	0	0	0	0.0429	0.1488	0.2289	0.2471	0.2498
4–6	0.1575	0.6938	0	0	0	0	0	0	0
6–11	0	0.2321	0.8358	0	0	0	0	0	0
11–16	0	0	0.1139	0.8065	0	0	0	0	0
16–28	0	0	0	0.1526	0.8826	0	0	0	0
28–40	0	0	0	0	0.0768	0.8444	0	0	0
40–52	0	0	0	0	0	0.1085	0.8032	0	0
52–64	0	0	0	0	0	0	0.1396	0.7603	0
64+	0	0	0	0	0	0	0	0.1701	0.8878
Σ	0.8530	0.9259	0.9497	0.9591	0.9594	0.9529	0.9428	0.9304	0.8878
Γ	0.1847	0.2507	0.1200	0.1591	0.0801	0.1139	0.1480	0.1828	
1984–1992									
2–4	0.4739	0	0	0	0.0610	0.2265	0.3759	0.4158	0.4223
4–6	0.4341	0.3259	0	0	0	0	0	0	0
6–11	0	0.5399	0.6455	0	0	0	0	0	0
11–16	0	0	0.2550	0.6088	0	0	0	0	0
16–28	0	0	0	0.3311	0.8332	0	0	0	0
28–40	0	0	0	0	0.1234	0.8249	0	0	0
40–52	0	0	0	0	0	0.1266	0.7968	0	0
52–64	0	0	0	0	0	0	0.1233	0.7372	0
64+	0	0	0	0	0	0	0	0.1119	0.4929
Σ	0.9080	0.8658	0.9005	0.9399	0.9566	0.9515	0.9201	0.8491	0.4929
Γ	0.4781	0.6236	0.2831	0.3523	0.1290	0.1330	0.1340	0.1318	

Note: Σ values are the tree survival rates for each dbh class, and Γ values are probabilities of growth to the next class implicit in each transition matrix.

Matrix models

Closed-canopy phase.—Estimated probabilities along the diagonal of the 1978–1984 transition matrix were higher than along the subdiagonal (Table 3), reflecting the greater probabilities that surviving trees would remain in the same size class than grow into the next size class. Total survival rates (Σ) implicit in the transition matrix were compatible with the mortality patterns shown in Fig. 3a. The leading eigenvalue of this matrix (Table 4) was <1, projecting a slight decline in population size. However, as the value λ = 1 corresponded to percentile 84.2 of the bootstrap probability distribution, the hypothesis of λ = 1 or limiting population-size stability was not rejected (P = 0.316). The stable size-

frequency distribution for this period was monotonic decreasing, resembling the general pattern of the empirical distributions from 1978 and 1984 (Fig. 4). However, in a few of the size classes, the observed frequencies fell outside the 95% bootstrap confidence intervals for the equilibrium probabilities.

The overall sensitivity of λ to changes in the nonzero elements of the transition matrix was S = 0.574, with 95% confidence interval boundaries at 0.527 and 0.612. The elasticities of λ with respect to all diagonal elements P_i were significantly higher than the elasticities with respect to the corresponding subdiagonal elements G_i, and these were usually significantly higher than the elasticities with respect to the fecundity elements F_i

TABLE 4. Asymptotic population growth rates projected with the transition matrices estimated for the closed (1978–1984) and open canopy (1984–1992) phases.

Period	λ	Annual basis†	Elasticity analysis (contributions)		
			Survival	Growth	Fecundity
1978–1984	0.9834 (0.9595, 1.0123)	0.9972 (0.9931, 1.0020)	0.8328 (0.8216, 0.8906)	0.1440 (0.0957, 0.1525)	0.0232 (0.0133, 0.0263)
1984–1992	1.0073 (0.9785, 1.0350)	1.0009 (0.9973, 1.0043)	0.7067 (0.6847, 0.7320)	0.2492 (0.2281, 0.2672)	0.0441 (0.0396, 0.0482)

Notes: Values in parentheses are limits of the bootstrap 95% confidence intervals. Values of λ are scaled as the original projection intervals. Elasticity analysis gives the relative contributions to λ of all rates of survival in the same size class, rates of survival with growth to the next class, and fecundity rates.

† Asymptotic growth rates transformed, for comparison, to an annual basis as λ^{1/Δ}, where Δ is the projection interval in years.

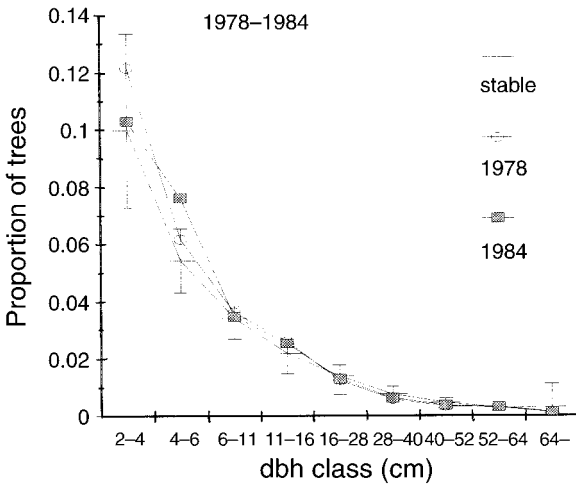


FIG. 4. Stable size class distribution of *Fagus grandifolia* projected for the 1978–1984 interval, and size class distributions observed in 1978 and 1984. Bars enclose the 0.95 bootstrap confidence intervals for the stable proportions in 1-cm size classes.

(Fig. 5). Consequently, the total relative contribution to λ of the rates of survival in the same size class was significantly higher than that of the rates of survival and growth to the next class, which was significantly higher than the total contribution of fecundities (Table 4). The elasticities of λ with respect to the total survival rates Σ_i , and the elasticities with respect to the diagonal elements P_i , increased from the smallest to the 16–28 cm dbh class, then decreased with dbh for larger classes. Estimation error of the elasticity of λ with respect to survival in the largest tree size class was very large (Fig. 5).

Open-canopy phase.—Compared to the 1978–1984 transition matrix, the 1984–1992 matrix had lower probabilities along the diagonal, higher probabilities along the subdiagonal, and slightly increased fecundities (Table 3). Although these differences result in part from the change in the projection interval, they also reflect changes in the patterns of average annual survival, growth, and recruitment. Total survival rates (Σ) changed for the small and for the large classes (increased in the 2–4 and decreased in the 4–16 cm and >40 cm dbh classes), but remained almost unchanged in the intermediate classes with respect to the 1978–1984 matrix. The growth parameters (Γ) were higher than in the 1978–1984 matrix for trees in smaller size classes, but lower for larger trees. These changes in Σ and Γ were compatible with the growth and mortality patterns depicted in Figs. 3 and 4.

The leading eigenvalue of the estimated 1984–1992 transition matrix exceeded 1, projecting a slight increase in population size (Table 4). However, as the value $\lambda = 1$ corresponded to percentile 30.3 of the bootstrap probability distribution, the hypothesis of $\lambda = 1$ or projected population-size stability was again

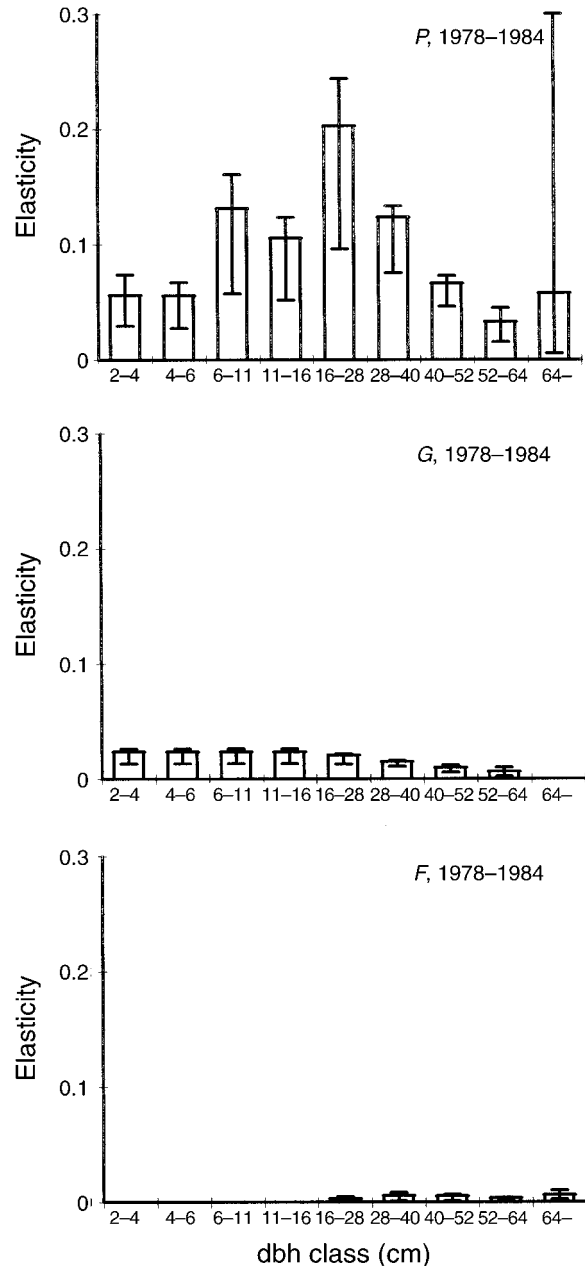


FIG. 5. Elasticities of the first eigenvalue of the 1978–1984 transition matrix (asymptotic finite population growth rate) with respect to: survival probabilities of trees in the same size class (P), probabilities of survival and growth to the next size class (G), and mean fecundity per tree in each size class (F). Bars enclose the 0.95 bootstrap confidence intervals.

not rejected ($P = 0.606$). The stable size-frequency distribution for this period was monotonic decreasing (Fig. 6). Although the empirical distributions from 1984 and 1992 showed the same general pattern, many of the observed frequencies fell outside the 95% bootstrap confidence intervals for the corresponding equilibrium probabilities.

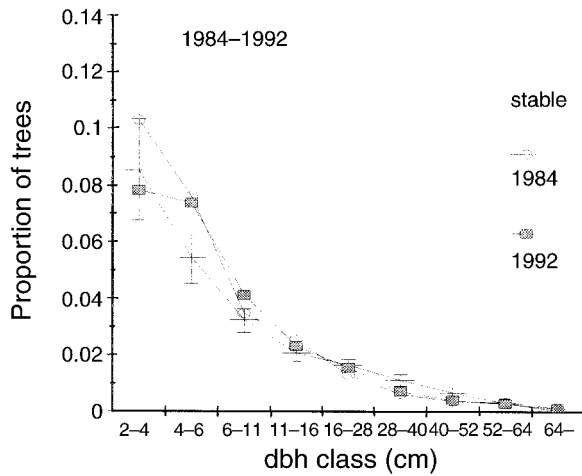


FIG. 6. Stable size class distribution of *Fagus grandifolia* projected for the 1984–1992 interval, and size class distributions observed in 1978 and in 1984. Bars enclose the 0.95 bootstrap confidence intervals for the stable proportions in 1-cm size classes.

The difference between asymptotic growth rates estimated for the open and closed-canopy phases, calculated after transforming the λ 's to an annual basis, had 95% bootstrap confidence boundaries at -0.0026 and 0.0088 . The value zero of this difference corresponded to percentile 14.7 of the bootstrap probability distribution. Therefore, the hypothesis of equal asymptotic population growth rate between the two phases was not rejected ($P = 0.294$). The stable size-frequency distributions projected from the 1978–1984 and 1984–1992 matrices had a similar monotonic decreasing general pattern, but differed significantly in some of the frequencies (Figs. 4 and 6).

The overall sensitivity of λ to changes in the 1984–1992 transition matrix was $S = 0.619$, with 95% bootstrap confidence interval boundaries at 0.592 and 0.642 . In this period, the elasticity of λ with respect to P_i was not significantly higher than with respect to G_i for the 2–4 cm dbh class, and significantly lower for the 4–6 cm dbh class. For classes of trees >6 cm dbh, the elasticities of λ with respect to P_i were significantly higher than those with respect to G_i and F_i (Fig. 7). As for the closed-canopy period, the total contribution to λ of the diagonal elements was larger than that of the subdiagonal elements, and the latter was larger than the total contribution of fecundities (Table 4). There was, however, a significant shift in contribution from the diagonal elements to the subdiagonal and fecundity elements between the 1978–1984 and 1984–1992 periods (Table 4). As in the closed-canopy period, the elasticities of λ with respect to the total survival rates Σ_i , and with respect to the diagonal elements P_i , increased from the smallest to the 16–28 cm dbh class, and decreased with dbh for larger classes. The vital rates with highest contribution to λ were the

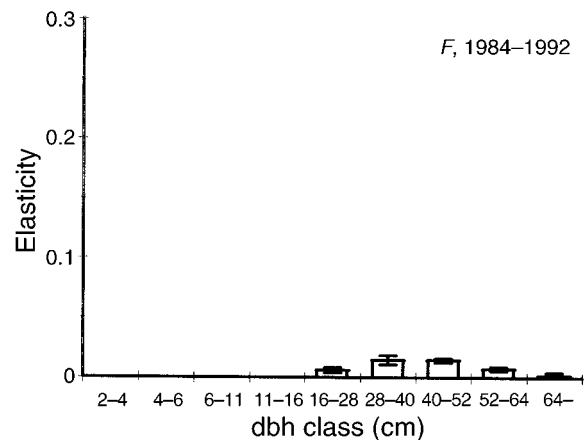
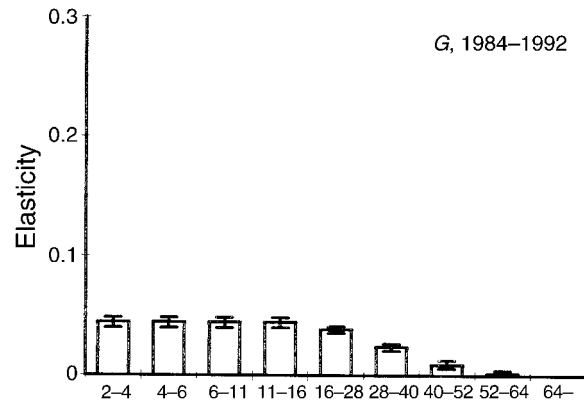
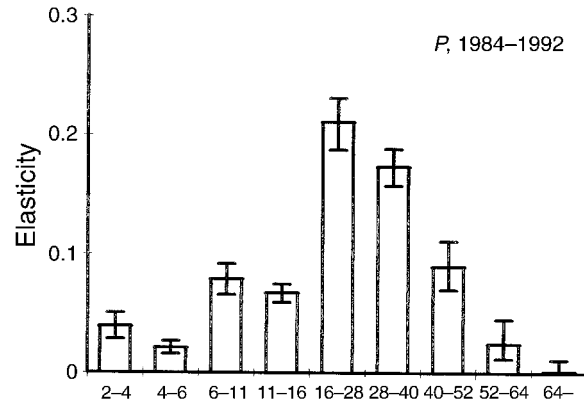


FIG. 7. Elasticities of the first eigenvalue of the 1984–1992 transition matrix (asymptotic finite population growth rate) with respect to: survival probabilities of trees in the same size class (P), probabilities of survival and growth to the next size class (G), and mean fecundity per tree in each size class (F). Bars enclose the 0.95 bootstrap confidence intervals.

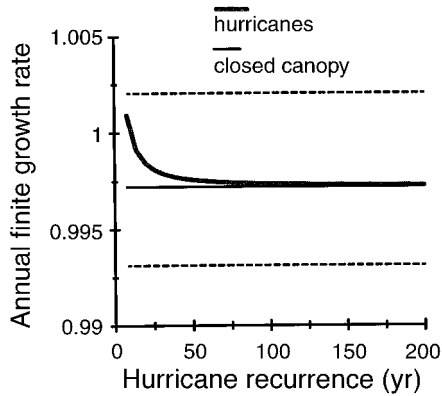


FIG. 8. Asymptotic population growth rate projected by matrix models simulating hurricane recurrence times between 8 and 200 yr (thick line). The horizontal thin line indicates the asymptotic growth rate projected from the closed-canopy period (1978–1984) and the dotted lines the corresponding 0.95 bootstrap confidence interval.

survival probabilities in the 16–28 and 28–40 cm dbh classes.

Simulation experiments.—We examined the long-term dynamics of the population under varying hurricane frequencies by constructing matrices $\mathbf{L}(n) = \mathbf{A}_c^n \mathbf{A}_o$, where \mathbf{A}_c and \mathbf{A}_o are the transition matrices estimated for the closed- and open-canopy periods respectively (cf. Silva et al. 1991). In these simulations, n was adjusted so that the hurricane recurrence $\rho = (8 + 6n)$ years, varied between 8 and 200 yr. Asymptotic population growth rates were obtained by eigenanalysis of each matrix $\mathbf{L}(n)$, and referred, for comparison, to an annual basis by raising each eigenvalue to the inverse of the corresponding ρ . In all simulations, the projected asymptotic growth rate was intermediate between the asymptotic growth rates projected for the 1978–1984 and the 1984–1992 transition matrices, approaching the closed-canopy growth rate as the time between hurricanes increased (Fig. 8). Since the hypotheses of population-size stability for these two periods, and the hypothesis of equal growth rate between periods were not rejected, this result suggested that the population size exhibits long-term stability under the simulated conditions. A drawback of these simulations was that the open-canopy period was always set at the beginning of the sequence. To check for any bias due to this deterministic approach, we simulated stochastic sequences of closed- and open-canopy periods (cf. Bierzychudek 1982, Silva et al. 1991, Åberg 1992). Each sequence had 3000 matrices randomly drawn from the set $\{\mathbf{A}_c, \mathbf{A}_o\}$, with constant probabilities (i.e., homogeneous, independent environments, Caswell 1989). In the sequences, the probabilities of \mathbf{A}_c and \mathbf{A}_o were adjusted to simulate expected hurricane recurrence times between 10 and 200 yr. Stochastic annual population growth rates were estimated as in Heyde and Cohen (1985) based on the last 2000 matrices of

each sequence. These estimates (not shown) closely overlapped those obtained with the deterministic approach, and fell within the 95% confidence interval for the asymptotic growth rate projected from the 1978–1984 matrix.

Responses to large departures from the recruitment rates observed in the closed-canopy phase were simulated by multiplying all F values in the 1978–1984 transition matrix by factors varying between 0.002 and 512. Asymptotic population growth rates projected from the perturbed matrices fell within the 95% bootstrap confidence interval for the original rate when the factor was between 0.3 and 3 (Fig. 9). Further increases or reductions of the F values produced significant changes in the growth rate. The largest simulated reduction ($0.002\times$) resulted in an annual growth rate of 0.9832, and the 512-fold increase in fecundity resulted in an annual growth rate of 1.0412.

The separate effects of changes in recruitment, survival, and growth patterns between the closed- and the open-canopy periods were isolated by altering selected elements of the 1978–1984 transition matrix. Survival and growth changes were introduced in this matrix using appropriate values of Σ and/or Γ derived from the 1984–1992 matrix to calculate new values for the corresponding P and G in the 1978–1984 matrix as $P = (1 - 0.75\Gamma)\Sigma^{0.75}$, and $G = 0.75\Gamma\Sigma^{0.75}$ (the constant 0.75 was used to adjust to a 6-yr interval). Recruitment rate differences were introduced by replacing the F 's with the corresponding values from the 1984–1992 matrix multiplied by 0.75 to adjust to a 6-yr interval. Both the changes in overall mortality, and in large tree growth and mortality, resulted in slightly decreased λ . The changes in overall growth and recruitment, as well as the changes in small tree growth and survival resulted in slightly increased λ (Table 5). However, all

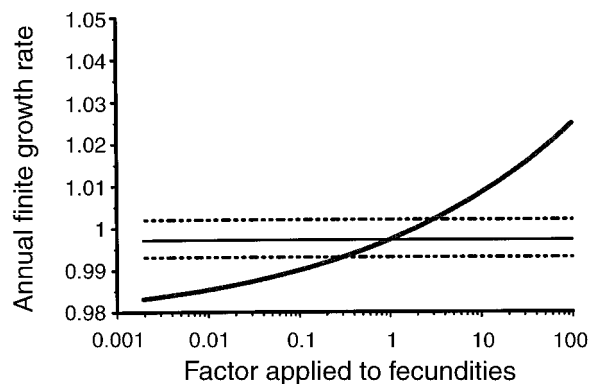


FIG. 9. Asymptotic population growth projected for simulated changes in the fecundity parameters F estimated for the closed-canopy period (1978–1984) (thick line). The horizontal thin line indicates the asymptotic growth rate projected from the closed-canopy period (1978–1984), and the dotted lines the corresponding 0.95 bootstrap confidence interval.

TABLE 5. Eigenvalues obtained in simulation experiments isolating changes in vital rates from the closed-canopy period to the open-canopy period.

Effect	λ
M3, G3	0.9794
M1, M2, M3	0.9810
None	0.9834
M2, G2	0.9849
F	0.9876
M1, G1	0.9944
G1, G2, G3	0.9987

Note: Effects are: M1, decreased mortality in the 2–4 cm dbh class; M2, increased mortality in the 4–16 cm dbh classes; M3, increased mortality in the dbh \geq 40 cm classes; G1, increased growth in the 2–4 cm dbh class; G2, increased growth in the 4–16 cm dbh classes; G3, decreased growth in the dbh \geq 40 cm classes; and F, increased recruitment rate.

of these simulations produced eigenvalues within the 95% bootstrap confidence interval of the original λ .

The effects of large increases in the mortality of the open-canopy period (in large part hurricane mortality) were simulated by replacing selected diagonal, and the corresponding subdiagonal elements of the 1984–1992 transition matrix by decreasing fractions of their original estimates. No decrease in the survival rates of trees >40 cm dbh was sufficient to move the simulated λ outside the 95% bootstrap confidence interval for the original λ . In contrast, the simulated λ fell below the lower limit of this confidence interval when the total survival rates in the 16–28 and 28–40 cm dbh classes were decreased by a factor of 0.85 or smaller, or when the survival rates of all trees >16 cm dbh were decreased by a factor of 0.89 or smaller.

DISCUSSION

Projections made from the observed demographic behavior of *Fagus grandifolia* in Woodyard Hammock indicate that, given the vital rates it exhibited during the 1978–1992 period, this species would be persistent. Observed size and structure of the population changed very little over this period, and the asymptotic population growth rates were very close to $\lambda = 1$ (stability). Transient departures from stability over the closed- or open-canopy periods are not likely to result in substantial changes in population size. At the asymptotic rate of population growth estimated for the closed-canopy phase, it would take 248 yr to halve the population; and at the rate estimated for the open-canopy phase, doubling the population would take 762 yr.

The evidence from this study supports the resistance hypothesis. Although growth and mortality schedules of *Fagus grandifolia* changed as a result of Hurricane Kate, the asymptotic population growth rate did not change significantly, and did not depart significantly from $\lambda = 1$ in either the closed- or the open-canopy periods. A pitfall in our result is that, while the resistance hypothesis is, in statistical terms, a null hypothesis, the power of the bootstrap tests we applied is

unknown. However, this conclusion was consistent with the results of the elasticity analysis. Those vital rates making the largest contribution to λ , the total survival of medium-sized trees, were very little affected by the hurricane. To some extent, release of small trees might have offset the effect of increased mortality and decreased growth of large trees, but this mechanism appears to have had minor importance relative to the endurance of large subcanopy trees (16–40 cm dbh). In our simulations, none of the individual changes in recruitment, growth, and mortality brought about by Hurricane Kate was sufficient to result in significant changes in the asymptotic population growth rate.

Even though Hurricane Kate did not affect the asymptotic stability of population size, it resulted in significant changes in the transient and the stable size class distributions. For this reason, although in both the closed- and the open-canopy phases the population size would remain stable given the respective stable size class distributions, under alternated closed and open canopy the transient behavior of the population might not result in persistence (cf. Caswell and Werner 1978). Our simulations, however, showed that the asymptotic population growth rate was very close to stability for all disturbance regimes. While persistence of the population would not be compromised, its structure would slightly fluctuate over time.

Our simulations suggest that recurrent disturbance by hurricanes more severe than Kate could compromise the local persistence of *Fagus grandifolia*. Despite increased tree recruitment and growth, slight simulated increases in mortality of trees 16–40 cm dbh in the open-canopy period resulted in a significant decrease in projected asymptotic population growth. If direct hurricane mortality were large, assessment of its demographic consequences would require an observation period longer than the one in this study, and possibly separate modeling of the strictly posthurricane dynamics. NOAA records (Jarvinen et al. 1984), however, indicate that while moderately intense storms like Kate are prevalent, high-intensity hurricanes are extremely infrequent in the northern Gulf of Mexico Coastal Plain. Only one high-intensity hurricane (Camille in 1969) has been recorded over more than a century in this region from northern Florida to eastern Texas. In contrast, in the Florida peninsula, where *Fagus grandifolia* is absent, high-intensity hurricanes with maximum sustained windspeeds >200 km/h have occurred frequently (Jarvinen et al. 1984).

Neither the recovery nor the complementation hypotheses were supported by our analysis. Estimated asymptotic population growth in the open-canopy phase was not <1 . A caveat is needed concerning the recovery hypothesis. As stated in our conceptual model, this hypothesis refers to a process that would result from increased population growth under closed-canopy conditions. In a less restrictive sense, however, because

the open-canopy phase starts with a pulse of increased mortality, some recovery must occur during this phase for the asymptotic population trend to be not declining. If our results are correct, population size of *Fagus grandifolia* is not controlled by recurrent hurricane disturbance (a density-independent factor), either directly, via damage and mortality, or indirectly, via increased competition with light-demanding tree species.

Although the observed patterns conform to the resistance hypothesis, our data leave some room for the release hypotheses. A mechanism involving release was proposed by Foster (1988) as an explanation for the presence of *Fagus grandifolia* and *Tsuga canadensis* in a hurricane-disturbed forest in New England. It is possible that our estimate of asymptotic population growth for the closed-canopy period might be influenced by long-term effects of previous hurricanes. Because our data excluded all individuals with dbh < 2 cm, our recruits come from seedlings that predate the beginning of the observations. As these recruits could have been exposed to open-canopy conditions created by the 1941 hurricane, our 1978–1984 data could overestimate the recruitment rate expected over a long period of closed canopy. In our simulations, however, λ was robust up to about threefold reductions in recruitment rate, and further reductions produced relatively small decreases in λ . This result, along with the known shade tolerance of *F. grandifolia*, suggests that a declining trend would be unlikely in the closed-canopy phase. Another problem is that the asymptotic population-size stability for the open-canopy period could be an artifact of the truncation of our sampling period. By 1992, most of the delayed hurricane mortality had already occurred, but many understory trees were still exhibiting increased growth because the canopy had not yet closed. However, in our simulations the effect of increased growth rate and decreased mortality of small trees was not enough to increase λ significantly, even when hurricane mortality was excluded. In addition, our data do not allow us to strictly rule out the possibility that the hurricane prompted a pulse of seedling recruitment, although no field observations suggested this possibility (W. J. Platt, *personal observation*).

Overall sensitivities of population growth to changes in the transition probabilities were lower for *Fagus grandifolia* in both the closed- ($S = 0.57$) and the open-canopy ($S = 0.62$) phases than for some equilibrium populations of tropical trees. Caswell (1989) calculated $S = 1.07$ for the population of *Pentaclethra macroloba* studied by Hartshorn (1975), and $S = 0.66 - 1.35$ for several populations of *Astrocaryum mexicanum* modelled by Piñero et al. (1984), and we obtained $S = 1.70$ for the model of *Araucaria cunninghami* presented by Enright and Watson (1991). This suggests that perturbations of the life cycle required to move a population away from equilibrium would be greater for *F. gran-*

difolia in Woodyard Hammock than for those tropical trees.

Changes in recruitment appeared, in our analysis, to have a minor influence on the population growth rate of *Fagus grandifolia*. This result supports the hypothesis of Harcombe et al. (1982) that in the short term successful regeneration is not likely to be critical for the local persistence of *F. grandifolia*. Marks (1975) suggested that *F. grandifolia* is “ill adapted to regenerate in the open.” Poulson and Platt (1989, 1995) suggested that, despite the ill adaptation, this species would persist even under high rates of gap formation because the light environment in the forest is heterogeneous enough to provide the necessary microsites for regeneration. These authors, and Canham (1988) suggested that population size would fluctuate with changes in the frequency of regeneration. In contrast, our results suggest that, for the fraction of the population ≥ 2 cm dbh, the effects of variation in regeneration are likely to be buffered by more influential vital rates. According to our results the vital rates most critical for the apparent persistence of *F. grandifolia* in Woodyard Hammock were the survivorships of large understory and of small overstory trees. Under the closed-canopy conditions survival in these size classes would be associated with shade tolerance. Poulson and Platt (1995) pointed out that survival and growth of these understory trees is related to their ability to project nearly horizontal branches towards canopy gaps. High survival of the hurricane might be related to a relatively large trunk diameter for a given height (Peters and Platt 1995), and to high branch elasticity reducing the risk a tree has of being pulled down or broken by falling neighbors (W. J. Platt, *personal observation*).

The same general pattern of life-cycle sensitivity we observed for *Fagus grandifolia* in Woodyard Hammock has been found in most matrix-model studies of tree demography. Population growth of forest trees appears to be most sensitive to survival, less sensitive to tree growth, and largely insensitive to fecundity (Harcombe 1987, Enright and Watson 1991, Silvertown et al. 1993). In fact, Gotelli (1991) suggested that this pattern of sensitivity may be characteristic of the wider class of organisms with long life-span, indeterminate growth, and reproduction restricted to the larger size classes. This generality suggests that conceptual models of forest dynamics (or other communities dominated by long-lived perennials) should not rely mainly on the regeneration niche concept (Grubb 1977), as survival rather than regeneration appears as critical for the persistence of many tree populations.

A large contribution to population growth of total survival rate in the intermediate size classes (the large prereproductives and small reproductives) appears to occur frequently among forest trees and herbs (Hartshorn 1975, Piñero et al. 1984, Burns and Ogden 1985, Caswell 1986, 1989, Enright and Watson 1991, Horvitz

and Schemske 1995). This suggests that traits associated with survival of large understory individuals would often be under high selection pressure (Caswell 1989). For the case of *Fagus grandifolia* in the Coastal Plain, these traits include those resulting in shade tolerance and in tolerance to canopy disruption by moderately intense hurricanes. Survival of these storms by understory individuals would be largely dependent on their ability to withstand the collapse of neighboring canopy trees. This capacity, in combination with shade tolerance, would also be advantageous in forests exposed to low rates of canopy disturbance by allowing large understory individuals to succeed fallen canopy trees in single treefall gaps. Thus, traits conferring *F. grandifolia* its shade tolerance and its resistance to canopy disruption might have remained linked during confinement of this species to the southern Coastal Plain during Pleistocene glaciations (Delcourt and Delcourt 1987), and its subsequent northward expansion.

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