

Dynamics of an Old-Growth Longleaf Pine Population

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ABSTRACT

Concepts regarding longleaf pine (*Pinus palustris* Mill.) and its ecological role in southeastern habitats have changed over the past decade as a result of studies of population dynamics within the old-growth stand on the Wade Tract in southern Georgia. In this paper we characterize the old-growth longleaf pine stand on the Wade Tract using data from an eight year period of study (1979-1987). We then address two aspects of the population dynamics. First, we investigate patch dynamics in the absence of large-scale disturbance, focusing on intraspecific interactions occurring within and among even-aged/sized patches of trees that comprise this old-growth population. We develop models for prediction of the influence of neighbors on recruitment, growth, and mortality of trees within patches. Predictions of these models indicate a negative relationship between adults and juveniles, but also suggest that open space is not the only factor limiting recruitment. Growth and mortality of juveniles in patches is predicted by our models to be most sensitive to the presence of other patches containing large trees, and the impact of intraspecific competition is predicted to diminish as trees increase in size. Second, we describe the effects of a large-scale disturbance, Hurricane Kate, on the demography and resultant patch dynamics of the old-growth population. The hurricane transiently reversed size-specific patterns of mortality; the increased mortality of large trees appeared to be random, however, with respect to most aspects of the ages and sizes of these trees. While the pre-Kate size-class distribution did not closely resemble that expected on the basis of size-specific growth and mortality of trees over the eight year period of study, the hurricane shifted the size-class distribution even farther from that stable size-class distribution, accentuating the nonequilibrium nature of the population dynamics.

Results of our eight-year study demonstrated that transient occurrences of elevated mortality as a result of large-scale disturbances such as hurricanes can result in rapid changes in certain components of the old-growth population. Demographic characteristics do not change rapidly, however, following disturbances; changes occurring during intervals between disturbances do so very slowly as a result of infrequent recruitment, slow growth, and low mortality. While longleaf pine stands are likely to appear static over short time intervals as a result of demographic inertia, in reality they are changing continually, but slowly, as a result of past large-scale disturbances and current patch dynamics. Variation in frequency and intensity of large-scale disturbances can interact with the patch structure and stand dynamics to produce very wide ranges of states characterizing stands of this species. Nonetheless, longevity of adults and their spatial distribution in the population (in the vicinity of opening patches), and likelihoods of regeneration that are increased by facilitation of frequent low-intensity fires buffer the population, decreasing the chances of declines to very low densities and preventing replacement by other tree species.

INTRODUCTION

"The (longleaf pine) forests are also characterized by frequent transitions in the ages and in the density of growth, so that the effect is often that of a succession of large and small groves, either gradually merging into one another or changing abruptly from young and dense to mature and opener growth, or to a mixture of variable sizes and age." G.F. Schwarz (1907)

Ecological Paradigms for Longleaf Pine Savannas

Habitats in which longleaf pine (*Pinus palustris* Mill.) was the dominant tree once were widespread in uplands of the southeastern coastal plain of the United States. Although there are some general descriptions of longleaf populations from the early 1900s (e.g., Schwarz 1907; Chapman 1909; Forbes 1930; Penfound and Watkins 1937; Harper 1943; Wahlenberg 1946), widespread decimation of old-growth stands around the turn of the century has left almost no undisturbed habitats (see Simberloff, this volume). Moreover, second-growth longleaf pine stands, now very rare in this landscape (Noss 1988, 1989), have been variously altered by subsequent anthropogenic impacts and do not resemble old-growth stands (Means and Grow 1985). It is no surprise, therefore, that studies of longleaf pine in the twentieth century have been primarily silvicultural in nature, oriented around timber production (e.g., Mattoon 1922; Wahlenberg 1946; Croker 1968; Croker and Boyer 1975).

Perhaps more importantly, the focus on succession in plant ecology over the past 50 years and on hardwood forests as the "climax" vegetation in the southeastern coastal plain of the United States has resulted in longleaf pine being characterized as essentially an upland loblolly pine. Ecologically, *Pinus palustris* has been regarded as a secondary successional species typical of xeric sites and maintained by frequent fires, the origin of which was often assumed to be man (Wells 1928, 1942; Wells and Shunk 1931; Braun 1950; Quarterman and Keever 1962; Monk 1967, 1968; Veno 1976; Vankat 1979; Quarterman 1981). Rare dissents to this concept (see Chapman 1932; Harper 1943) went unheeded. Until recently, there have been no critical attempts to examine this succession paradigm or the role of longleaf pine as a seral species maintained by recurrent fires.

In 1978, we initiated a long-term study of the population ecology of the old-growth stand of longleaf pine on the Wade Tract in southern Georgia. Results of this work (Platt et al. 1988) suggest that longleaf pine is a long-lived conifer that occurs in uneven aged/sized stands. Old-growth populations appear to have been comprised of small patches of trees. Within patches, trees were likely to be even aged/sized, while patches were likely to contain trees of variable ages/sizes, ranging from recent recruits to trees several centuries in age. In addition, patches without any pines were likely to be present in old-growth populations (Platt et al. 1988). Approximately 70% of points thrown at random on the Wade Tract do not land beneath crowns of longleaf pine. While the extent to which longleaf pine habitats resembled open savannas or closed-canopy forests was likely to vary over space and time, any given patch potentially might have remained open (i.e., without pines) for periods of time ranging from decades to centuries (Platt et al. 1988). Consequently, invasion of hardwoods might be expected, except for the frequent occurrence of fire (Platt et al. 1991; Rebertus et al. this volume).

Platt et al. (1988), building on ideas of Mutch (1970) and Williamson and Black (1981), suggest that pyrogenicity of longleaf pine tends to block replacement of pine by hardwoods, thereby short-circuiting succession. Large longleaf pines (both alive and standing dead) are frequently struck by lightning on the Wade Tract; similar observations were made by Harper (1943) about half a century earlier. These lightning strikes provide a mechanism for converting a localized disturbance into a widespread ground fire. The spread of fire is promoted by needles that are incendiary when dry (Williamson and Black 1981; Platt et al. 1991). By facilitating frequent low-intensity fires that prevent invasion of open sites by competitors and that maintain sites in states suitable for regeneration, longleaf pine appears to be a key species influential in maintaining the open, savanna-like aspect of many upland southeastern coastal plain habitats (Platt et al. 1991). The concept of a long evolutionary relationship between fire and longleaf pine (as well as associated plant species; Rebertus et al. this volume; Streng et al. this volume), that results in a persistent community over time is, therefore, very different from concepts involved in successional models that dominated earlier in the century.

This evolutionary paradigm does not predict any stable equilibrium containing both longleaf pine and hardwood species in southeastern pine savannas. Longleaf pine is predicted to increase in

abundance within patches in the landscape at the expense of hardwoods as long as fires occur frequently enough to reduce hardwood densities and promote conditions (open space and herbaceous ground cover) favoring pine regeneration (Rebertus et al. 1989). Such conditions can result from small or large areas burning when lightning strikes occur frequently (such in the Gulf coastal plain and peninsular Florida; Maier et al. 1979), or from large areas burning during drought periods, even in areas where lightning strikes occur less frequently (see Harper 1943). Although longleaf pine savannas are likely to contain relatively few hardwoods when fires occur frequently (especially if they occur in the early part of the growing season), hardwoods may be present, especially in larger openings, as a result of inherent spatial variation in fire intensity (see Rebertus et al. this volume).

Scope of the Current Study

In this paper, we address two aspects of the population dynamics of the old-growth longleaf pine stand on the Wade Tract. First, we investigate patch dynamics in the absence of large-scale disturbance, focusing on intraspecific interactions occurring within and among even-aged/sized patches of trees that comprise this old-growth population. Using the data from an eight year period of study (1979-1987), we examine the hypotheses of Platt et al. (1988) regarding how recruitment, growth, and mortality of trees within patches are likely to be influenced by their neighbors. Second, we describe the effects of a large-scale disturbance, a hurricane, on the demography and resultant patch dynamics of the old-growth population. We develop hypotheses regarding long-term impacts of such disturbances on longleaf pine populations. These studies enable us to explore concepts inherent in the pyrogenicity paradigm summarized above.

CHARACTERISTICS OF THE WADE TRACT POPULATION

Population Composition

Initial description of the old-growth population on the Wade Tract was based on study of a mapped, tagged, 42.1 ha stand that was conducted from 1979-1983. Details of the methods involved are presented in Platt et al. (1988). These data have

been supplemented by annual mortality censuses conducted each fall over the next four years (1984-1987), by growth measurements (diameter at breast height; hereafter dbh) in 1987, and by mapping of additional recruits (trees < 1.5 m tall in 1983, but \geq 1.5 m tall in 1987) in 1987. For analysis of growth and mortality, trees were grouped into 10 cm intervals (e.g., 0-9.9, 10.0-19.9, ..., 80-89.9) that hereafter are expressed as 0-10, 10-20, ..., 80-90 cm size classes. In some analyses, trees in the largest size classes were combined because of small sample sizes.

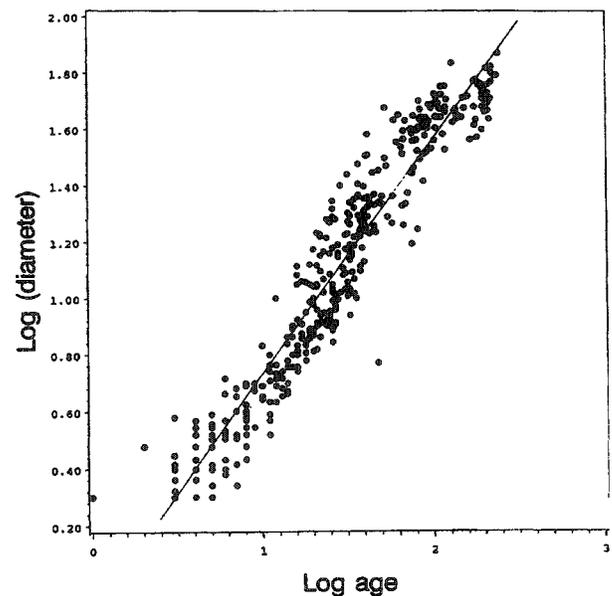


Figure 1. Relationship between log age and log diameter at breast height of 399 longleaf pines randomly selected from the mapped population on the Wade Tract. The straight line is the best fit least squares regression (see text for details).

The data obtained by Platt et al. (1988) indicated that the population was uneven-aged and sized, containing many cohorts of trees. Over the past several centuries, new cohorts have entered the population frequently, at least once per decade. Also, trees in the stand ranged from recent recruits in the grass stage to trees several centuries old. The age distribution was somewhat J-shaped, with about 2/3 less than 50 years and 1/3 ranging in age from 50-250 years. Older trees, 3-5 centuries in age, were present in the stand as scattered individuals.

As the ages of longleaf pine increase, their diameters (at breast height) also increase, but at a rate less than directly proportional to tree age (Platt et al. 1988). The relationship is illustrated in Fig. 1 as a plot of the log size versus log age, obtained from a random sample of 399 trees (5% of the population) used by Platt et al. (1988). The result-

ing relationship can be described by the least-squares regression equation:

$$\log(\text{size}) = 0.83121 \log(\text{age}) - 0.09942 \quad (1)$$

The value of R^2 (0.913) indicates a strong relationship between ages and sizes of trees in the old-growth stand. A residual plot (not shown) further indicates the adequacy of this model. The relationship is nonlinear; doubling the ages of trees results in an approximately 1.78-fold increase in dbh. For example, doubling the age of a tree from 20 to 40 years will result, on the average, an increase from 9.6 to 17.1 cm. On the average, doubling the age of a 40 year old tree to 80 years results in an increase of 17.1 to 30.4 cm, and doubling of an 80 year old tree to 160 years results in an increase to 54.0 cm. The doubling of the age of a 160 year old tree would result in an expected average dbh of 96.1 cm for trees 320 years old.

Age-size relationships for longleaf pine on other sites might not necessarily resemble those for longleaf pines on the Wade Tract. Greater growth might be expected, for example, in the clay soils of the Tallahassee Red Hills region than in xeric sandhills or seasonally flooded flatwoods. Mesic sites with good soils might be expected to produce even greater annual growth. The slope of the age-size relationship also would be expected to vary with the density of trees; removal of larger trees might release small trees, resulting in faster growth. Hence, age-size relationships in second-growth stands should not necessarily reflect age-size relationships of the old-growth stands from which they were derived. Nonetheless, if age-size relationships in populations on other sites are as strong as those on the Wade Tract, sizes of trees once present on those sites might be reconstructed using remnant trees in second-growth stands.

Spatial Patterns

Results of initial analyses of the spatial patterns of trees on the Wade Tract indicated that recruitment into the smallest size class (≥ 1.5 m tall) tended to occur in openings located away from large trees (Platt et al. 1988). We examined average patch size for the entire mapped plot using variogram estimates. The variogram (designated as 2γ ; see Cressie 1991) is defined as:

$$2\gamma(r) = \text{variance} \{ \text{dbh}(\mathbf{s}) - \text{dbh}(\mathbf{u}) \} \quad (2)$$

where $\text{dbh}(\mathbf{s})$ and $\text{dbh}(\mathbf{u})$ are the diameters of trees at locations \mathbf{s} and \mathbf{u} , respectively, and $r = \|\mathbf{s} - \mathbf{u}\|$, the distance between locations \mathbf{s} and \mathbf{u} . Let \mathbf{s}_i and \mathbf{s}_j denote the locations of the i -th and j -th trees in the stand. The variogram is estimated from data by:

$$2\hat{\gamma}(r) = \frac{1}{N_r} \sum_{i < j} \{ \text{dbh}(\mathbf{s}_i) - \text{dbh}(\mathbf{s}_j) \}^2 I\{r - 0.5 \leq \|\mathbf{s}_i - \mathbf{s}_j\| \leq r + 0.5\}, \quad (3)$$

where

$$N_r = \sum_{i < j} I\{r - 0.5 \leq \|\mathbf{s}_i - \mathbf{s}_j\| \leq r + 0.5\} \quad (4)$$

and

$$I\{r - 0.5 \leq \|\mathbf{s}_i - \mathbf{s}_j\| \leq r + 0.5\}$$

equals one if

$$\|\mathbf{s}_i - \mathbf{s}_j\|$$

the distance between trees i and j lies between $r - 0.5$ m and $r + 0.5$ m, and equals zero otherwise. N_r is the number of such pairs located between $r - 0.5$ and $r + 0.5$ m. Fig. 2 shows a plot of the empirical variogram against distance r . The variogram initially increases very rapidly with increasing distance, until a value of 507 cm^2 is attained at a distance $r = 28$ m, suggesting an average patch diameter of 28 m. At that patch diameter, approximately 16 such patches would be expected per hectare. Hence, large numbers of small patches characterize the Wade Tract population. The gradual increase in the variogram as distances increase beyond 28 m indicates large-scale spatial heterogeneity in tree diameters.

The descriptions available for other old-growth populations of longleaf pine reveal a similarity to the Wade Tract in that all are uneven-aged and/or sized, containing a wide variety of age/size classes (see Platt et al. 1988). A general characteristic of old-growth stands appears to be that they are comprised of many cohorts of very different ages and sizes, with each cohort divided among small patches scattered throughout the stands. While smaller trees are very abundant on the Wade Tract, in some stands there is a tendency for large areas to contain mostly large trees, with the smaller size classes being underrepresented (Schwarz 1907; Chapman 1909; Wahlenberg 1946).

SPATIO-TEMPORAL POPULATION DYNAMICS IN THE ABSENCE OF LARGE-SCALE DISTURBANCES

Models of Population Processes

The spatio-temporal dynamics of the Wade Tract population were explored by decomposing the population dynamics into recruitment, size-specific growth, and size-specific mortality processes and modeling each individual component separately. Because fitting spatio-temporal models to data is computationally intensive, models were fit to data from a 200 x 200 m subplot of the mapped plot (Fig. 3). This region was chosen because it has a relatively gentle topography, an absence of severe human disturbances, and many different size classes of trees. To avoid edge-effects, trees located outside this 4 ha region, but within 50 m of its border, were used in model fitting. The salvage of dead timber prior to 1979 has resulted in disturbance of the ground cover, especially where logs were dragged out of the forest. Field observations indicated that recruitment of longleaf pines was positively associated with these disturbance paths, which were mapped and subsequently digitized. Fig. 3 includes the locations of these disturbance paths.

Spatial patterns of recruitment, growth, and mortality of conifers have often been hypothesized to be influenced by interactions among trees (Meyer 1938; Cooper 1960, 1961; Pielou 1962; Laessle 1965; Mohler et al. 1978; Weiner 1984; White 1985; Platt et al. 1988). Statistical analysis of the effects of such interactions requires the definition of

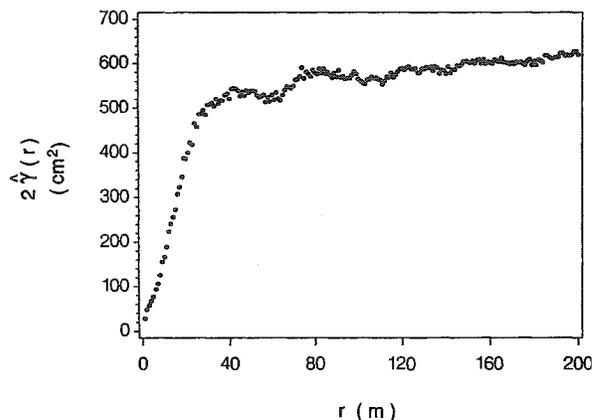


Figure 2. Empirical variograms $[2(r)]$ for differences in tree diameters (at breast height) at different distances (r) separating pairs of trees. The variograms are in cm^2 , and distances are in m. The shift in slope, which indicates the diameter of patches containing similar sized trees, occurs at a distance of 28 m.

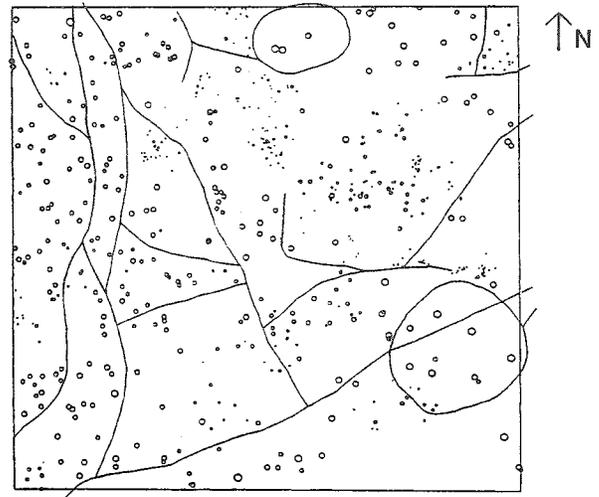


Figure 3. Map of all longleaf pine ≥ 1.5 m tall and disturbance paths in the 200 x 200 m subplot in 1979. The map is drawn at a scale of one inch equals 40m. Circle diameters are proportional to the dbh of trees. North is at the top of the page. Region B is in the upper left of the subplot.

some measure of the influence of trees in the neighborhood of a given tree or a given point in space. A number of such measures have been considered by ecologists. Frequently, an arbitrary radius has been defined, and the number of plants within that radius considered (e.g., Mack and Harper 1977, Waller 1981, Pacala and Silander 1985). Rebertus et al. (1989) used distances to and sizes of nearest neighbors. Mead (1966), Mithen et al. (1984), and Matlack and Harper (1986) used Thiessen polygons to define the "available area" to an individual plant. Because the locations and sizes of trees within a neighborhood of a given plant may be important in defining an index of their competitive influence, measures based on numbers of plants within a given distance of that plant, nearest neighbors, or Thiessen polygons are unlikely to be adequate. We follow the approach of Weiner (1984), who has advocated additive functions of distances and diameters of trees within a neighborhood of a given individual.

Because longleaf pines on the Wade Tract occur in small patches containing single-aged cohorts, individual trees should be influenced by interactions occurring within and among adjacent cohorts (Platt et al. 1988). Moreover, different size classes of trees may respond differently to competitive interactions. To assess the relative importance of interactions within and among size classes, longleaf pines were divided into three size classes: juveniles (< 10 cm dbh), subadults (between 10 and 30 cm dbh), and adults (≥ 30 cm dbh). Each size class was analyzed separately. The effects of competitive interactions were assumed to be an additive function

of the distance and diameter of neighboring trees located within a radius of 50m from each tree. For any tree in the j th size class located at coordinates $s = (x,y)$, the intensity of interactions with neighbors belonging to the k -th sizeclass (W_k) was assessed by

$$W_k(s) = \sum_i (\text{dbh}_{ik})^m / (r_{ik})^n \quad (5)$$

where dbh_{ik} and r_{ik} are the diameter of and the distance to the i -th neighboring tree in the k -th size class, respectively, and the sum is over all neighbors in size class k , where $k = j, \dots, 3$. The powers m and n are chosen to obtain the best fitting model. Note that equation (5) is general and thus can be used to express the intensity of interactions potentially influencing any of the components of the demographic processes.

Recruitment. Between 1979 and 1987, 66 trees were recruited (i.e., entered the smallest size class of tagged trees) in the subplot. Most recruits (89%) occurred in a 120 x 150 m region in the northwest corner of the subplot. Locations of recruits in this region, hereafter denoted as B , were used to model the recruitment process. The locations of recruits in region B $\{s_1, s_2, \dots, s_n\}$ form a spatial point pattern. The spatial point pattern of recruits can be modeled through the intensity function $\lambda(s)$, which can be interpreted as the density of recruits at the location s . We will model recruit locations as a function of the locations of subadult and adult trees, and disturbance paths. In particular, assume that these locations are generated from a modulated Poisson process (Cox 1972) with intensity function

$$\lambda(s) = \exp\{\beta_0 + \beta_1 d_r(s) + \beta_2 [W_2(s) + W_3(s)]\} \quad (6)$$

where β_0 , β_1 , and β_2 are unknown parameters to be estimated, and $d_r(s)$ is the distance between the location s and the closest disturbance path. The intensity of competitive interactions with trees in size class k at location s is modeled as

$$W_k(s) = \sum_i 1/r_{ik} \quad (7)$$

where r_{ik} is the distance between s and the i -th tree in the k -th size class, and the sum is over trees within 30 m of location s . Note that equation (7) is a special case of equation (5) where $m=0$ and $n=1$. Under a

modulated Poisson process, the number of recruits in B is Poisson distributed with mean $\mu = \int_B \lambda(s) ds$. Conditional on that number, recruit locations are a random sample from a probability density proportional to the intensity function $\lambda(s)$. Thus, regions of high intensity will tend to contain large numbers of recruits, while regions of low intensity will tend to contain few recruits. The parameter β_0 is an intercept term. A value of $\beta_1 = 0$ indicates that recruitment is independent of disturbance paths, $\beta_1 > 0$ indicates positive dependence, and $\beta_1 < 0$ indicates negative dependence between recruitment and disturbance paths. Similarly, $\beta_2 = 0$ indicates independence between recruits and large trees, $\beta_2 < 0$ indicates negative dependence, and $\beta_2 > 0$ indicates positive dependence between recruits and large trees. Maximum likelihood estimates of the parameters of this spatial recruitment process model were obtained using methods described in Rathbun (1990).

The goodness-of-fit of the recruitment-process model was assessed by comparing empirical K -functions (Ripley 1977), calculated from the data, to K -functions calculated from simulated realizations of the model. The function $K_{ij}(r)$ is defined to be the expected number of trees in size class j within distance r of a randomly selected tree of size class i divided by the density of trees in size class j . Ripley's (1977) estimator of the K -function is estimated by

$$\hat{K}_{ij}(r) = |B| \sum_{k=1}^{n_i} \sum_{l=1}^{n_j} W_{kl}^{-1} I(r_{kl}) / (n_i n_j), \quad (8)$$

where n_i is the number of trees in size class i in the region B , $|B|$ is the area of B , r_{kl} is the distance between trees k and l , $I(r_{kl})$ is an indicator function [$I(r_{kl}) = 1$ if $r_{kl} \leq r$ and 0 otherwise], and the summation is over all distinct pairs of trees in the two size classes. The weight function w_{kl} is equal to the proportion of the circumference of a circle centered at s_k and passing through s_l which is inside the region B . Lewis and Shedler's (1979) rejection-sampling algorithm was used to simulate the recruitment-process model. The transformation

$$\hat{L}_{ij}(r) = [K_{ij}(r)/\pi]^{1/2} - r \quad (9)$$

was used to linearize the K function under assumptions of complete spatial randomness and independence (Besag 1983).

Growth. The change in dbh between 1979 and 1987 was used to model growth of longleaf pines

that survived to 1987. Because different size classes of trees might respond differently to intraspecific competition, growth increments of each size class were analyzed separately. Interactions between trees in a given size class with trees in smaller size classes were assumed to be negligible [i.e., asymmetric interactions: see Weiner and Thomas (1986); Schmitt et al. (1987); Weiner 1990], but interactions with smaller trees within size classes were not assumed to be negligible. For the j -th size class, a multiple linear regression was performed on square-root growth increment against tree diameter (in 1979) and $W_k(s)$;

$$W_k(s) = \sum_i (\text{dbh}_{ik} / r_{ik}) \quad (10)$$

where dbh_{ik} and r_{ik} are the diameter of and the distance to the i -th neighbor in the k -th size class, and the sum is over all neighbors in size class k , where $k = j, \dots, 3$. The square-root transformation was applied to normalize the growth increments. Note that equation (10) is a special case of equation (5) in which $m = n = 1$.

Mortality. A space-time logistic regression model (Rathbun and Cressie 1993) was fit to annual mortality data over the period from 1979-1987 using the CATMOD procedure in SAS. Annual mortality data can be considered as binary random variables. Let $Y_{ij}(s) = 0$ if the tree in size class j at the point s is dead at time t ($t = 1980, \dots, 1987$), and let $Y_{ij}(s) = 1$ if that tree is alive. Provided that the tree is alive at time $t-1$, the probability that the tree is dead at time t is assumed to be equal to

$$P\{Y_{ij} = s\} = 1 / [1 + \exp\{\alpha_0 + \alpha_1 \text{dbh}(s) + \sum_{k=j}^3 \beta_k W_{ik}(s)\}], \quad (11)$$

where α_0 is an intercept term, α_1 models the effect of tree diameter, and the β_k models the interactions with trees in the k -th size class. Each size class was analyzed separately. For trees in the j -th size class, the predictor variables are the tree's diameter in 1979, and a distance function (see equation 5),

$$W_{tk}(s) = \sum_k (1/r_{ik}) ; k=j \dots 3 \quad (12)$$

where r_{ik} is the distance to the i -th tree in the k -th size class, and the sum is over all living neighbors in size class k , where $k = j, \dots, 3$, at time $t-1$. Interactions with trees in smaller size classes are assumed to be negligible.

Patch Dynamics

Recruitment. Recruitment of new individuals into the Wade Tract population is not limited by restricted seed dispersal. Observations during the 1987 and 1990 mast years indicate that germination of at least some seeds occurred over almost all of the Wade Tract. Recruitment into the smallest size class, however, appears to be influenced by the location of juveniles relative to locations of disturbance paths and other longleaf pines (Platt et al. 1988). The fitted recruitment-process model [see equation (6)] yields the estimated intensity function:

$$\hat{\lambda}(s) = \exp\{-0.013 - 0.192d_R(s) - 1.68W(s)\}. \quad (13)$$

The intensity of recruitment tends to increase with decreasing distance to the closest disturbance path and with increasing distances from neighboring large trees. Consequently, recruitment tends to be clustered in openings in the ground cover that are located away from established trees in the stand. The expression above indicates that, all else being equal, the intensity of recruitment at a point u , which is located at a distance $d_R(u) = \log(0.05)/b_1 = 15.6$ m from a disturbance path is reduced to 5% of that at a location s , which is on the disturbance path. Likewise, the presence of an adult or subadult tree at a distance $b_2/\log(0.95) = 32.8$ m away from a given location v reduces the intensity of recruitment at v by 5% of that expected in the absence of that large tree. Thus, we expect the zone of influence of subadult and adult trees, although weak at large distances, potentially to extend to distances over 30 m from the trees.

Diagnostic plots assessing the goodness-of-fit of the recruitment-process model are presented in Fig. 4. Fig. 4a, which deals with the predicted and realized relationships between larger size classes of trees and recruits, contains the empirical function $\hat{\Lambda}_{01}(r)$ computed from the data and simulation envelopes obtained from 99 realizations of the fitted recruitment-process model. The function $\hat{\Lambda}_{01}(r)$ falls within the simulation envelopes except at some smaller distances, where it falls below the lower envelope. Thus the model mimics the main features of the empirical $\hat{\Lambda}_{01}(r)$ curve reasonably well, suggesting that the recruitment-process model adequately describes a negative association between large trees and recruits.

Fig. 4b, which deals with predicted and realized relationships among recruits, contains the em-

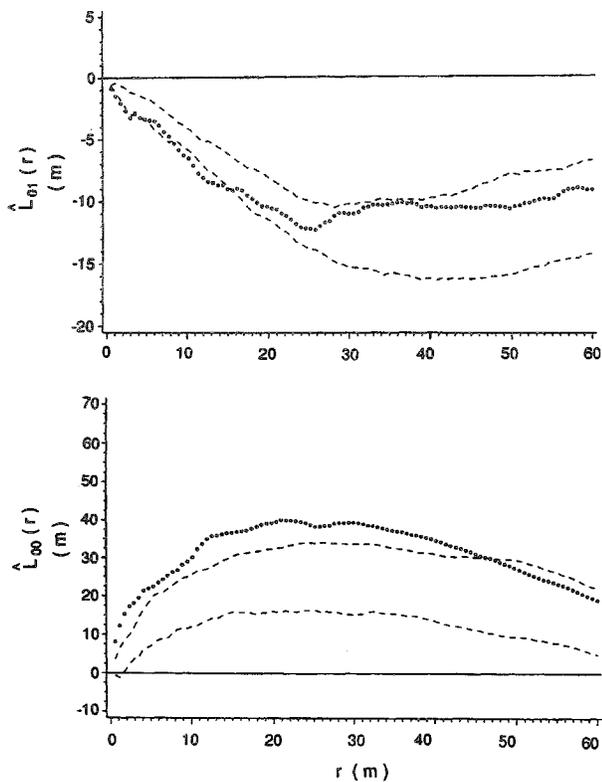


Figure 4. Diagnostic plots for determining the goodness-of-fit of the recruitment-process model. The empirical functions (dotted lines) are graphed as a function of the distances (r) between juveniles and larger trees [$\hat{L}_{01}(r)$; upper] and between juveniles and other juveniles [$\hat{L}_{00}(r)$; lower]. The upper and lower simulation envelopes (dashed lines) for the fitted recruitment-process model are indicated by dashed lines.

empirical function $\hat{L}_{00}(r)$ and simulation envelopes obtained from 99 realizations of the fitted recruitment-process model. Model predictions fail to predict the $\hat{L}_{00}(r)$ curve, except at the largest scales of pattern. While the simulation envelopes indicate that recruits should show clustering, the model failed to show as strong a clustered pattern as actually occurs in the population. Evidently, the model predicts clusters of recruits in openings where no recruits were actually present. We suggest that such a pattern might occur if open space were not the only factor limiting recruitment into the population.

Growth. Data on growth of trees in patches, presented in Fig. 5, reinforce and amplify patterns described by Platt et al. (1988). Mean diameter growth initially increases rapidly as size increases, until a maximum average growth of about 4-4.5 mm/year is attained when trees are about 20-25 cm dbh. The variance in growth rates increases faster than the mean when trees are small, reflecting an inequality in growth increments within clumps of juveniles (Fig. 5). As slow-growing trees die, the variance decreases, so that for trees above 35 cm, the variance in growth rates is minimal. Skewness

of growth increment also reflects these patterns, with growth rates being highly skewed (towards higher growth) when trees are small. Most trees do not grow rapidly, and over time, these trees die. At the same time, among larger trees, progressively fewer grow at rates much faster than others of the same size. Thus, skewness decreases as size increases.

Above diameters of about 20-25 cm, growth of trees slows rapidly with increasing size (Fig. 5). In particular, trees above 30-35 cm dbh exhibit slow, but consistent annual diameter increases (< 2.5 mm/year) over the remainder of the life cycle. Among larger trees, increments in dbh are correlated with increments in tree rings, indicating that our measurements reflect actual increases in diameter of these slowly-growing trees. Data on annual ring increments of cross-dated cores collected in 1987 from 31 haphazardly-selected large trees 49-76 cm dbh on the Wade Tract were provided by D. West and T. Doyle. The dbh increments over the

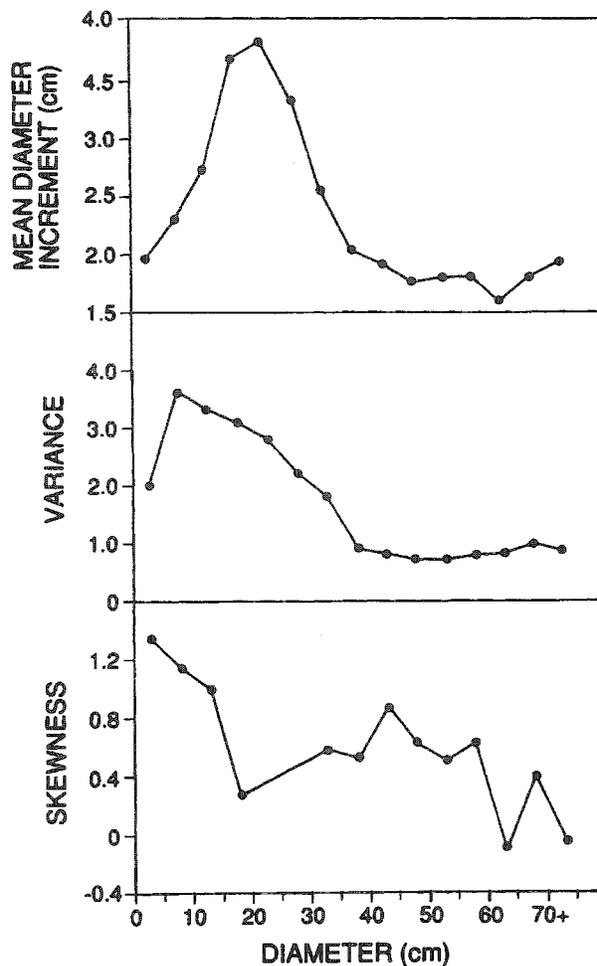


Figure 5. Size-specific growth of Wade Tract longleaf pine, measured as increments in the diameter at breast height of trees in 5-cm size classes over an eight year period. The mean (upper), variance (middle), and skewness (lower) are presented for trees measured in 1979 and surviving until 1987.

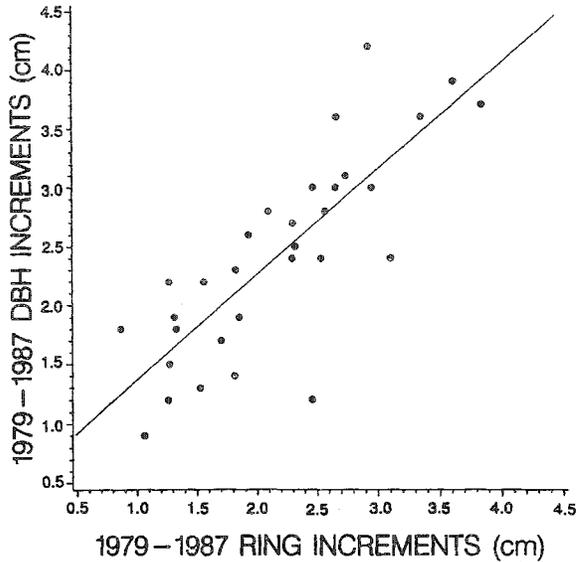


Figure 6. The relationship between dbh increments (cm) and ring increments (cm) of 31 large longleaf pine on the Wade Tract over the period from 1979-1987.

eight year period of study are plotted against eight year ring increments for these 31 trees in Fig. 6. The two measurements are correlated; $r^2 = 0.6502$. The slope of the least squares best-fit regression equation [eight year dbh increment = 0.8925 (eight year ring increment) + 0.4724] was not significantly different from a value of 1.0 ($t_{1,28} = 0.88$; $P > 0.1$).

Growth rates are influenced by interactions both within and among size classes (Table 1). Trees growing in the proximity of large numbers of conspecifics tend to grow more slowly than isolated trees. Scatterplots of growth increments (square-root transformed) are plotted against interaction indices [$W_j(s)$, where j = size class; see (1)] for each size class in Fig. 7. In this figure, the steepness of the slopes indicate relative intensities of interactions among juveniles, subadults, and adults. For

example, growth rates of juveniles are more strongly affected by interactions with subadults or adults than by interactions among juveniles. The term for interactions among juveniles was not statistically significant, suggesting that such interactions may have little impact on juvenile growth. Interactions with adults more strongly influence subadult growth rates than interactions among subadults. Based upon comparisons of slopes, interactions involving adults more strongly influence juvenile growth rates than subadult or adult growth rates.

Although the models explain roughly half of the variation in square-root growth increment of juveniles and subadults, only 18% of the variation was explained for adults (Table 1). This result suggests that the growth of trees in small size classes is more strongly influenced by competitive interactions than growth of trees in large size classes

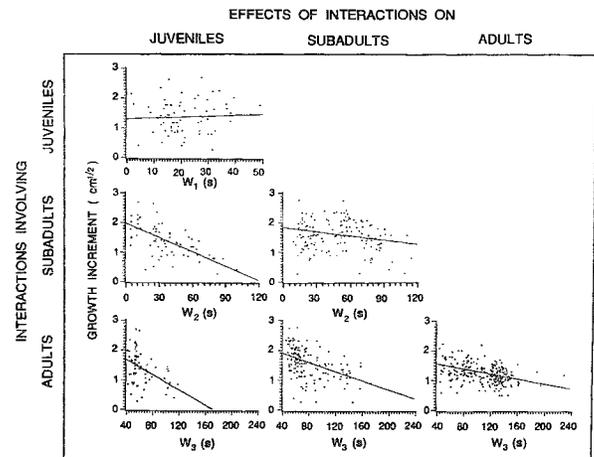


Figure 7. Scatterplots showing the relationship between growth increments ($cm^{1/2}$) of juveniles, subadults, and adults and interaction indices [$W_j(s)$] involving trees in the same or a larger size class. Solid lines are the best fit regression equations.

Table 1. Multiple linear regression analyses (intercepts and regression coefficients) of the effects of dbh and interaction indices (involving trees in the same or larger size classes) on eight year diameter growth increments ($cm^{1/2}$) of juveniles, subadults, and adults. Standard errors are in parentheses.

Size class affected	Intercept	dbh	Interactions with:			R^2
			juveniles	subadults	adults	
juveniles	3.12 (0.23)	0.0690 (0.0254)	-0.0107 (0.0049)	-0.0198 (0.0023)	-0.0178 (0.0029)	0.62
subadults	2.55 (0.20)	0.0259 (0.0061)	—	-0.0094 (0.0014)	-0.0122 (0.0012)	0.47
adults	2.04 (0.14)	-0.0063 (0.0024)	—	—	-0.0046 (0.0006)	0.18

[but see Thomas and Weiner (1989) for a caveat regarding use of neighborhood analysis to assess the importance of competition]. Adult trees tend to be relatively isolated from other trees (Platt et al. 1988), so interactions might be expected to be less intense than among smaller trees, which tend to be located in closer proximity. Furthermore, smaller trees also tend to have fewer resources to draw on (because of smaller root systems and leaf areas), and so may be more sensitive to competitive influences. Other factors not considered in the present analyses may also be important in determining growth. These may include the genetic makeup of individual trees, or localized microenvironmental variation. Accidents during the lifetimes of individual trees may also influence growth. For example, scarring by fire, wind damage, or infection by pathogens may adversely affect tree growth. As a consequence of such unique historical events, especially if they act locally, much higher percentages of variation may not be explained by population-level statistical analyses.

Mortality. Annual mortality is depicted as a function of tree size in Fig. 8. When mortality of trees directly and indirectly killed by Hurricane Kate is excluded, average annual mortality is low for all size classes. The smallest size class has the highest average annual mortality (3.2-11.6% annually); thinning of clumps of juveniles is responsible for most of the mortality. Mortality decreases to very low levels (0.0-1.0% annually) for trees 10-40 cm dbh. For trees above 40 cm there is a pattern of slowly increasing mortality with increasing tree size. Among trees ≥ 70 cm dbh, mortality is highly variable, ranging from 0 to 25% annually.

Excluding trees killed by Hurricane Kate, 126 trees ≥ 30 cm dbh died over the eight year period. More than 95% of this mortality was attributable to three sources. Lightning strikes, which accounted for 52% of the mortality, varied considerably from year to year. Most of the strikes kill single trees, but cluster strikes of 2-12 trees were recorded during the 8 years of study. The number of windthrows (34% of the mortality) also varied from year to year. The largest numbers of windthrows occurred in 1985, when a tornado-like storm struck part of the Wade Tract. Fires burning through scars on trees, causing snapoffs, accounted for 10% of the mortality. A number of these scars probably dated from the early 1800s, at which time cuts similar to those on the Wade Tract were commonly made on large trees to obtain resins for individual use (E.V. Komarek, Sr., pers. comm.).

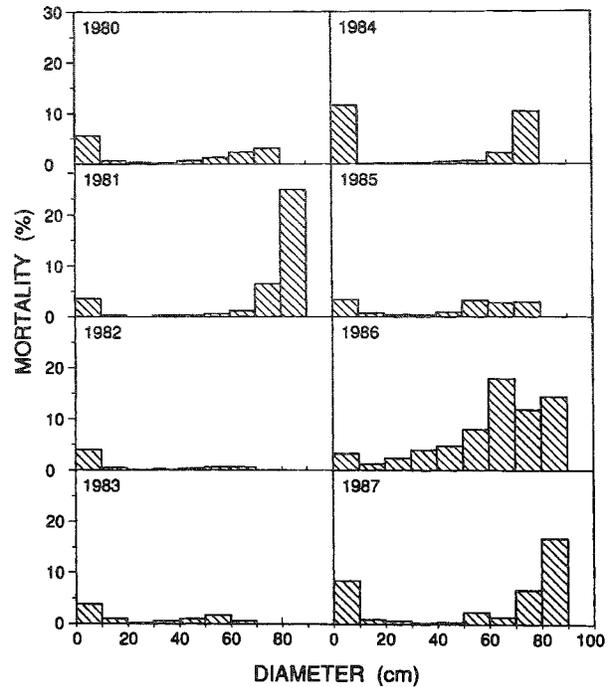


Figure 8. Size specific mortality, expressed as the percentage of trees in 10-cm size classes that died during intervals between annual censuses of the mapped longleaf pine population on the Wade Tract between 1979 and 1987.

Although interactions both within and among size classes reduce tree growth, such interactions have little influence on survivorship (except in the smallest size class). Interactions within size classes do not significantly influence mortality within any size class, nor do interactions among size classes significantly influence subadult or adult mortality. For juveniles, the best fitting model [see equation (11)] yields an estimated annual probability of mortality equal to

$$P\{Y_{ij}=(s)\} = \frac{1}{1 + \exp\{1.87 + 0.249\text{dbh} - 0.263W_{i2}(s)\}}, \quad (14)$$

where $W_{i2}(s)$ is the interaction index for subadults [$k = 2$; see equation (12)]. Fig. 9 shows a plot of estimated annual juvenile mortality rates against juvenile diameter and the interaction index for subadults. This figure suggests that juveniles growing in the proximity of large numbers of subadults would be expected to have higher annual mortality rates than isolated juveniles. Patches containing both juveniles and subadults occur when older and/or faster growing juveniles enter the subadult size class, while more suppressed trees remain in the juvenile size class. At this time, mortality rates of the smaller trees are expected to be increased.

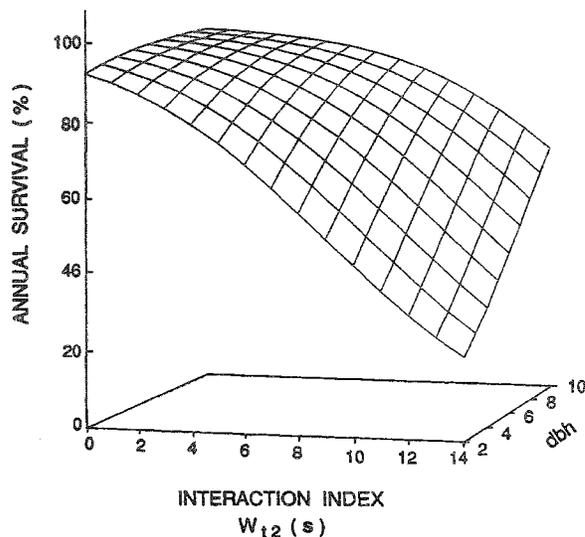


Figure 9. The relationship between the interaction index, dbh, and annual survivorship of juveniles in the 200 x 200 m subplot on the Wade Tract. The response surface shifts from about 90% survival when dbh is large and the interaction index is low (few and small neighbors located far away from juveniles) to about 20% survival when the dbh is small and the interaction index is high (many and large neighbors located close to juveniles).

THE IMPACT OF A LARGE-SCALE DISTURBANCE: HURRICANE KATE

Mortality Attributable to Hurricane Kate

On November 21, 1985, the eye of Hurricane Kate passed very close to the Wade Tract. Downbursts of wind up to 160 km/hr were estimated for Leon County, Florida, just south of Thomas County, Georgia (Clark 1986). Heavy rains, both from Kate and two previous tropical storms that passed through the area, in combination with high winds from Kate, resulted in tip-ups and snap-offs of large trees, some of which were cavity trees of red-cockaded woodpeckers (Engstrom and Evans 1990). A special census to describe hurricane impact was conducted several months after the hurricane (Platt et al. 1993).

Hurricane Kate directly resulted in the deaths of 137 trees, including 81 tip-ups and 49 snap-offs. Increased mortality is reflected in the size-specific mortality for 1986 in Fig. 8; the 1985 census had been completed only a few weeks prior to the hurricane. Mortality from Kate increased with tree size; almost 20% of trees from some larger size classes were removed by the hurricane.

The direct impact of Hurricane Kate on trees ≥ 30 cm dbh was assessed by comparing a sample

of 57 randomly selected trees from the pool of trees tipped-up (17) or snapped-off (40) during the hurricane with the random sample of 111 trees ≥ 30 cm dbh in the random sample taken from the population in 1981 to describe age-size relationships (Fig. 2). For the former sample, a section as close to breast height as possible was taken from the trunk of each tree. Each section was sanded, and the number of annual rings was counted (only trees with sound centers were included in the sample). Ages of trees in this random sample ranged from 69 to 318 years. Average ages and diameters of trees in the three random samples were as follows: tip-ups 145 years, 48.1 cm; snap-offs 187 years, 50.5 cm; and 1981 live trees 115 years, 45.1 cm.

The impact of the hurricane on large trees appeared random with respect to most aspects of the age-size relationship (Fig. 10). An analysis of covariance (log age used as a covariate) indicated that slopes describing the relationship between log dbh

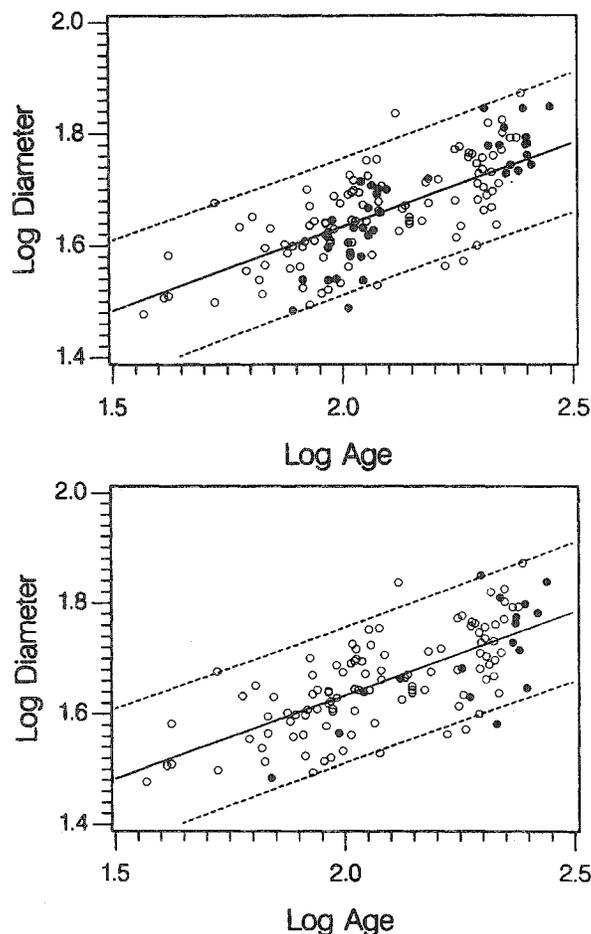


Figure 10. Relationships between log age and log diameter at breast height for large trees snapped-off (upper) and tipped-up (lower) during Hurricane Kate in 1985. Closed circles represent trees felled during the hurricane. The solid line is the least squares best fit regression equation and dotted lines the 95% limits for the 1981 random sample of live trees ≥ 30 cm dbh (open circles) from the mapped plot.

and log age differed significantly among the three groups ($F [2,162 \text{ df}] = 7.98; P = 0.005$). Slopes of regression equations for the age-size relationships were: tip-ups, 0.5274; snap-offs, 0.4515; and 1981 live trees $\geq 30 \text{ cm dbh}$, 0.3009. The only significant difference among pairs of slopes, however, was between tip-ups and the 1981 random sample ($F [1,147] = 15.45; P < 0.001$). Inspection of the data (Fig. 10) indicated that trees snapped-off during Kate were similar in age and size to those in the 1981 sample, but that trees tipped-up during the hurricane tended to be smaller than 1981 live trees of the same age.

Hurricane Kate has had lingering effects on the Wade Tract. Mortality indirectly attributable to Kate has continued to occur. In the 1987 census, for example, mortality of large trees is higher than in any other census except 1986. This increased mortality resulted from deaths of large trees damaged, but not immediately killed by Hurricane Kate. In addition, large trees located next to boles or within crowns of large trees that fell during Kate were often killed by heat produced at their bases when logs or tree crowns burned. A total of 232 (227 of the trees initially tagged in 1979, 5 in the 1983 cohort) trees were directly or indirectly killed by Kate; more large trees were killed by Kate than by all other causes combined over the 8 year period of study. Data from annual mortality censuses since 1987 indicate that fire-related mortality of large trees ultimately attributable to Kate has continued for at least five years post-hurricane, further accentuating the impact of the hurricane (W.J. Platt and S.L. Rathbun, unpublished data).

The Impact on Population Dynamics

To evaluate the impact of large-scale disturbance, we calculated transition probabilities for the eight year period from 1979-1987, given conditions of the occurrence of a hurricane (Kate) or no hurricane (no-Kate). In the former, all trees on the mapped plot were included in calculations of size-specific growth and survival probabilities (Table 2; Part A). In the latter, trees killed by Hurricane Kate (both directly and indirectly) were excluded from all calculations (Table 2, Part B). In each matrix, probabilities of mortality are listed in the bottom row. Probabilities of remaining in the same size class between 1979 and 1987 form the upper diagonal, and probabilities of growth into the next size class form the lower diagonal. All trees growing to a larger size class entered the next class; none skipped a size class over the eight year period of

study. Estimates of recruitment into the smallest size class were not included in the transition matrix, since we did not know the relative contribution of each adult size class to that recruitment.

We compared the observed 1979 Kate and no-Kate size class distributions to stable size class distributions expected if observed size-specific probabilities of mortality and growth into larger size classes (Table 2) remained constant over time (Lefkovitch 1965; Hartshorn 1975; Werner and Caswell 1977; Hughes 1984). Using an iterative procedure, we determined the population growth rate for the projected stable distribution that most closely resembled the 1979 size class distribution. Similarity between observed and projected stable size class distributions was measured with the likelihood-ratio test statistic G (Sokal and Rohlf 1969). Given a particular population growth rate, pseudo-stable size class distributions were calculated using methods described in the Appendix of Platt et al. (1988).

We bootstrapped (Efron 1979; Efron and Gong 1983) the effect of stochastic variation in the estimated transition probabilities on the shape of the projected stable size class distribution. Our approach resembled that of Meyer et al. (1986), except that in addition to pseudo-rates of population growth, we calculated pseudo-stable size class distributions. We also relaxed assumptions made by Platt et al. (1988). Instead of conditioning on observed numbers of individuals in each size class, we bootstrapped the population unconditionally. For each bootstrap replication we randomly sampled individuals with replacement from the population as a whole. A pseudo-rate of population growth was then calculated by finding that rate for which the pseudo-stable size class distribution best fit the bootstrapped size class distribution.

Similarity of the best fitting pseudo-stable size class distribution to the bootstrap size class distribution was measured using the likelihood ratio statistic G . The distribution of G values was then used to test the hypothesis that sampling variation alone accounts for differences between observed and stable size class distributions projected from estimated transition probabilities. For each size class, we also ranked the simulated frequencies by increasing size and plotted "90% confidence intervals" bounded by the 51st and 950th frequencies. Because frequencies of trees in different size classes were not independent, the family-wide error rate for these intervals is unknown.

Table 2. Size class transition matrices for Wade Tract longleaf pines ≥ 1.5 m tall: 1979-1987.**Part A: Including Effects of Hurricane Kate**

1987 dbh class	1979 dbh class							
	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70+
0-10	0.517							
10-20	0.165	0.677						
20-30		0.269	0.694					
30-40			0.260	0.702				
40-50				0.242	0.773			
50-60					0.131	0.728		
60-70						0.099	0.611	
70+							0.078	0.694
Deaths	0.317	0.054	0.046	0.055	0.095	0.173	0.311	0.306
N (1979)	2662	1456	719	631	746	475	167	36

Part B: Excluding Effects of Hurricane Kate

1987 dbh class	1979 dbh class							
	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70+
0-10	0.755							
10-20	0.083	0.833						
20-30		0.140	0.866					
30-40			0.128	0.829				
40-50				0.158	0.891			
50-60					0.085	0.871		
60-70						0.082	0.851	
70+							0.090	0.871
Deaths	0.162	0.026	0.006	0.013	0.024	0.047	0.060	0.129
N (1979)	2625	1435	696	607	705	428	134	31

NOTE.—The proportions of trees present in 10-cm size classes in 1979 that remained in that size class in 1987 (upper diagonal), entered the next larger size class (lower diagonal), or died (bottom row) sum to 1.0.

The observed (1979) and expected (based on transition matrices) size class distributions are compared for Kate and no-Kate conditions in Fig. 11. In neither case is the Wade Tract longleaf pine population close to equilibrium (see Platt et al. 1988). The 1979 size-class distribution with Kate most closely resembled a stable size class distribution projected for an increasing population with $\lambda = 1.017$ (Fig. 11). The 95% bootstrap confidence limits for λ (1.005, 1.029) indicate a significant departure from unity. Differences between the 1979 and the best-fitting stable size class distributions ($G = 294.9$) were larger ($P < 0.001$) than those for all 1000 projections generated by bootstrapping the transition matrix. The observed 1979 size class distribution contained more individuals than expected in the 10-20, 50-60, and 60-70 cm size classes, and fewer than expected in the 20-30 and 30-40 cm size classes.

When the effects of Hurricane Kate were removed, the 1979 size-class distribution most closely resembled the stable size class distribution projected from an increasing population with $\lambda = 1.063$ (Fig. 11, right). The 95% confidence limits for λ (1.054, 1.072) indicate a significant increase over the value of λ when effects of Kate were included in the analysis. Differences between the 1979 size class distribution and the best fitting stable size class distribution ($G = 145.7$) were larger than all but 3 of 1000 ($P = 0.003$) projections generated by bootstrapping the transition matrix. When the effects of Kate were removed, the 1979 distribution also more closely resembled the expected stable size class distribution. Nonetheless, the observed 1979 distribution still contained more than the expected numbers of trees in the 10-20 and 50-60 cm size classes and fewer than expected in the 20-30 and 30-40 cm size classes.

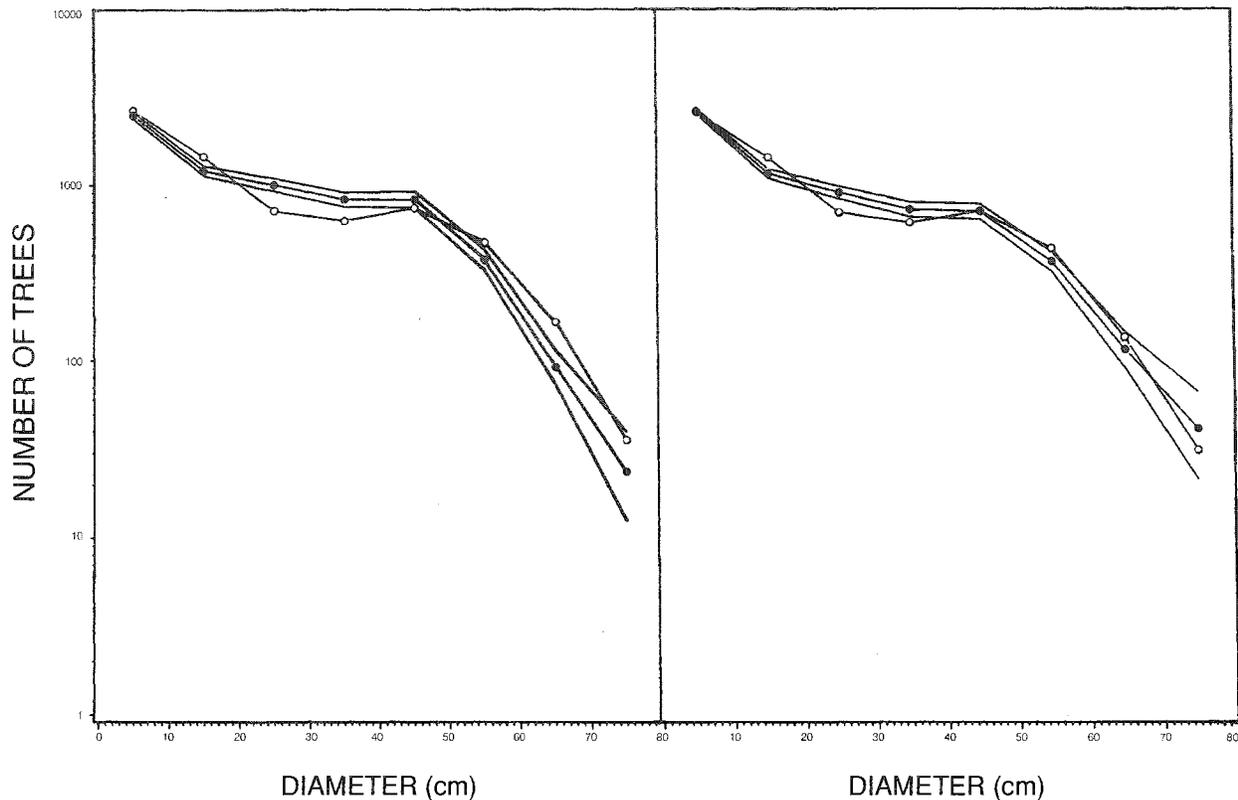


Figure 11. Observed (open circles) and predicted (solid circles) stable size class distributions for Wade Tract longleaf pine populations with (left) and without (right) Hurricane Kate. The growth rates are $\lambda = 1.017$ (left) and 1.063 (right). Solid lines denote 90% confidence limits around the best fitting stable size class distributions.

DISCUSSION

Large-Scale Disturbances and Transient Elevations of Mortality

In seven out of eight years, mortality of longleaf pine on the Wade Tract was highest in the smallest size classes, and then decreased to very low levels among adult trees (also see Platt et al. 1988). Similar patterns have been recorded for other tree species (see review of Harcombe 1987). The mortality of adult trees was so low that trees entering adult size classes would be expected to live many centuries, producing turnover rates on the order of millenia. However, we also recorded very slight increases in mortality among the very largest trees. Although year-to-year variation in this mortality was large, averages of the annual mortality produced, over the eight year period, a U-shaped pattern similar to that postulated originally by Goff and West (1975). Sources of adult tree mortality (which occurred before senescence) were abiotic, primarily lightning and windthrows (cf. Harcombe and Marks 1983). Increased mortality of the largest longleaf pines on the Wade Tract probably was associated with their tendency to be somewhat isolated, located away from other trees.

Hurricane Kate transiently altered the "typical" size-specific patterns of mortality, resulting in more mortality of large trees in one day than in all other seven years of the study. Such ephemeral increases in mortality of largest trees in plant populations would not be readily detected by short-term studies, and thus would contribute to the weakness of the evidence for increased mortality of large trees in most studies (see Harcombe 1987). Size-related patterns of mortality similar to those caused by Hurricane Kate have resulted from other hurricanes (Basnet et al. 1992; Boucher et al. 1990; Foster 1988a,b; Gresham et al. 1991; Reilly 1991). Total mortality from Hurricane Kate was less than mortality in nearby old-growth hardwood forests also impacted by Kate, suggesting that savanna pines may be more resistant to hurricane damage than hardwood trees or forest pines (Platt et al. 1993; also see Bromley 1939).

In coastal regions, periodic large-scale disturbances might constitute one major source of mortality of large trees in longleaf pine populations. The most recent two previous hurricanes to impact Thomas County occurred in 1929 and 1941, suggesting a return time of approximately 30 years. If other hurricanes had impacts similar to Kate, then

about 20-25% of the total mortality of large trees might be expected to result from hurricanes. Over such a 30 year period in which one hurricane occurred that had an impact similar to Kate, mortality from wind damage would likely exceed lightning as the major source of mortality of large trees.

Although larger trees were more likely to be killed as a result of the hurricanes, mortality of large trees appeared to be random with respect to most age and size characteristics. Mortality from Kate was nonrandom, however, with respect to red-cockaded woodpecker nest cavities (Engstrom and Evans 1991). Although red-cockaded woodpeckers select large trees with redheart (*Phellinus pini*) for construction of nest cavities (Jackson 1977; Conner and Locke 1982; Hooper 1988), nest cavity construction apparently caused structural damage, creating weak points in trunks that increased the chances of severe hurricane damage. The increased likelihood that longleaf trees containing red-cockaded woodpecker cavities would be damaged by Hurricane Kate resembles the increased likelihood, documented by Putz and Sharitz (1991), that trees with prior damage in the Congaree Swamp were more likely to have been redamaged during Hurricane Hugo. The occurrence of one event (a nest cavity or damage in one storm) may have no overt effect until some later time during the life cycle.

The spatial locations of longleaf pines damaged and killed by Hurricane Kate also deviated from a random pattern of mortality on the Wade Tract. Most large trees severely damaged or killed were located in low areas, and almost all tip-ups occurred in two localized low flatwoods. In these flatwood sites, deep tap roots are not present; the deepest roots extended only to the hardpan just below the surface of the soil. Trees in these wet flatwoods, which have water seeping from the soil in the winter and spring, grow more slowly than trees randomly sampled from the Wade Tract as a whole (Platt and Rathbun, unpublished data). Hence, a greater likelihood of tip-ups in areas where growth is slower than average could have caused the age-size slope of tip-ups to differ from that of trees randomly selected from the entire Wade Tract.

Differential hurricane-related mortality of large trees in different areas of the Wade Tract indicates that turnover rates are likely to vary spatially within the population. Flatwoods stands of longleaf pine may, as a result of trees not having tap roots anchored deeply in the soil, be more im-

pacted by large-scale disturbances than stands located on more well drained soils. Hence, the intervals between recurrent openings by large-scale disturbances such as hurricanes may be shorter in flatwoods than in other stands. Because large-scale blowdowns would occur more frequently, flatwoods stands also may be more likely to contain large patches of dense, even-aged trees (i.e., the "harricans" reported by Sherrard 1903; Schwarz 1907; Forbes 1921, 1930; Wahlenberg 1946) in an otherwise open landscape.

Patch Formation and Recruitment

Rates of formation of open patches without longleaf pine on the Wade Tract are spatially and temporally variable. In the absence of large-scale disturbances, patch formation would occur slowly, requiring many centuries as larger trees were removed from the population by lightning and windthrows. Occasional large-scale events (e.g., hurricanes) would result in pulses of mortality, thereby quickly opening patches of variable size. As a result, localized areas within a population may rapidly change states at irregular intervals determined by patterns of large-scale disturbance.

Patches that open on the Wade Tract, either rapidly or slowly, are not colonized quickly (Platt et al. 1988). There is some minimum size of openings, suggested by spatial analyses to be areas with diameters about 30 m, that results from the negative relationships between the spatial distribution of adults and juveniles. Large trees, those most likely to produce large numbers of cones (and also most likely to have large negative effects on recruitment), tend to be isolated from other trees (Platt et al. 1988) and thus closest to open patches that reach this minimum size. This tendency for large trees to be located in the vicinity of opening patches on the Wade Tract buffers changes in population density, because patches suitable for colonization are likely to be within dispersal range of (but not too close to) cone-producing adults. Consequently, only catastrophic mortality of all adults within large areas would tend to remove the buffering resulting from these patterns to the spatial distribution of trees. If high mortality of large trees were to occur in some area during a large-scale disturbance, however, recruitment into the open patch produced might be delayed for some time, perhaps generations, accentuating the nonequilibrium dynamics and open, savanna-like aspect of the stand.

Patches remain open for variable periods of time that reflect, in part, patterns of longleaf pine

reproduction. Longleaf pine has long been recognized as a species that masts, exhibiting large variation in cone production from year-to-year (Ashe 1894; Forbes 1930; Maki 1952; Mattoon 1922; Schwarz 1907; Wahlenberg 1946). Recent mast years on the Wade Tract have occurred in 1978, 1987, 1990, and 1991, on the average slightly more than once every 3 years, but with a highly variable interval between successive mast years. Cone production on the Wade Tract occurs almost exclusively by trees ≥ 30 cm dbh, and the numbers of cones produced increase with tree size (Platt et al. 1988). Trees ≥ 60 cm dbh produce cones most consistently from year to year and also produce very large cone crops (as much as 90% of the total cone production) during mast years (W.J. Platt, J.L. Hamrick and M.L. Hiss, in prep.). Hence, not all patches (or all parts of any given patch) may have large trees, those that produce most cones during mast years, within dispersal range (approximately twice the height of trees; see Boyer 1958, 1963), which could result in variable intervals of time between reaching the minimum size for colonization and actual recruitment into that opening.

Successful recruitment of a patch depends not only on patch size, the spatial distribution of adult trees, and intervals between mast years, but also on site conditions within patches (see review in Platt et al. 1988). In addition, the natural occurrence of multiple fires per decade (see Platt et al. 1991) would have increased the chances of concurrent timing of masting and bare mineral soil (Chapman 1932). Recruitment has occurred at least once a decade over the past 250 years on the Wade Tract, suggesting that this has not been a major demographic bottleneck in the population. We note that this does not mean that patches are colonized as soon as they reach some minimum size; rather only that some patches are colonized at least once a decade. Indeed, our model predictions strongly suggest that site conditions play an important role in determining patterns of recruitment into the population and may be important in creating the open, savanna aspect of the Wade Tract landscape.

The number of trees in entering cohorts on the Wade Tract is highly variable. Our recruitment-process model is based on numbers of trees entering open patches being Poisson distributed; hence, the variance in numbers of recruits should be equal to the mean number of recruits in patches. Examination of observed patterns of recruitment reveals that the variance in numbers of recruits in open patches is greater than the mean. We have found no evidence that interactions among juveniles affect either growth or mortality of juveniles. Con-

sequently, it appears unlikely that density-dependent mechanisms will regulate the intensity of recruitment into an open patch beyond those effects resulting from interactions with larger size classes (i.e., interactions that determine patch size and whether an opening is large enough for successful colonization). Natural variation in numbers of trees entering patches could result in such variation being maintained as the cohorts age, producing variable numbers of adults per patch formed in the stand.

Patch Dynamics

In those periods of time between large-scale disturbances, our models predict that intraspecific interactions will be important in structuring the population. Growth and mortality of longleaf pine on the Wade Tract, however, appear much less strongly influenced by trees of similar size than by trees of larger sizes in the population. In addition, depressant effects are predicted to occur over progressively larger areas as tree size increases. Thus, given the small patch sizes on the Wade Tract, interactions among patches (especially where size differentials are great, such as large adults and new recruits) are likely to be more important than within-patch interactions in structuring growth and mortality of trees in a patch. The single exception to this generalization might be during the times of maximum growth, when trees of very different sizes might be present in the same patch.

Furthermore, the spatial arrangement of patches within a population is likely to influence the magnitude of depressant effects occurring as a result of intraspecific competition. Because adult trees have greater depressant effects than subadults on juveniles, progressively slower growth and higher mortality are predicted in patches of juveniles surrounded by increasing numbers of patches containing very large trees. Mortality that is high among small trees, but declines with increasing size, is a common pattern among tree species (see Harcombe 1987). This pattern also occurs within the longleaf pine stand on the Wade Tract as a thinning of recruits in patches. However, most mortality appears to result from the presence of larger trees in the vicinity rather than from competition among recruits for resources. Field observations indicate that slow growth of small trees close to larger trees results from the absence of sufficient bark to protect the small trees from damaging fires. In addition, as the distances between such small and large trees decrease, small trees are increasing

likely to be exposed to high fire temperatures resulting from the pyrogenic shed needles (Platt et al. 1991).

The importance of intraspecific competition diminishes greatly with increases in size. Thus largest trees in the population become independent of the patch structure. It is these trees that are the most highly fecund on the Wade Tract (Platt and Hamrick, unpublished data). The ability to obtain and allocate resources to reproduction is likely to be associated with reduced depressant effects exerted by surrounding larger trees. We predict that the onset and magnitude of reproduction in any given longleaf pine is strongly influenced by the density and sizes of larger trees in the vicinity of that tree.

Most studies and models of intraspecific competition in populations of conifers have focused on asymmetric interactions occurring among different sized trees present at variable densities (see Weiner 1990). Such interactions are clearly important in non-spatially structured populations (i.e., where entire stands consist of a single "patch" containing a narrow range of ages and sizes of trees that are replaced following some catastrophic large-scale disturbance such as fire; e.g., Laessle 1965; Weiner 1984; Weiner and Thomas 1986; Thomas and Weiner 1989). Many conifers, however, occurred naturally (at least in old-growth stands) as monospecific stands containing small patches of trees of variable ages and sizes. A number of studies of such species have focused on within-patch intraspecific competition as the cause for thinning of recruits during the early stages of the life cycle (e.g., Meyer 1938; Cooper 1960, 1961; Pielou 1962; Mohler et al. 1978; White 1985). Our study indicates that within-patch interactions, especially those involving juveniles, are likely to be swamped by among-patch interactions in such spatially structured populations (given a wide range of tree sizes). Differences in spatial structure thus could produce quite different asymmetries of competitive interactions among trees within stands, changing selection pressures (see Hamrick et al. this volume), and producing different responses over time (see Weiner 1990).

Population Dynamics

Results of our eight-year study demonstrated that transient occurrences of elevated mortality (which is size-dependent and spatially arrayed) as a result of large-scale disturbances (hurricanes) resulted in rapid changes in certain components of

the old-growth longleaf pine population on the Wade Tract. Nonetheless, size-class distributions based on tree diameters in 1979, 1983, and 1987 (Fig. 12) are very similar, differing in only subtle ways. In each of the three years, the largest numbers of trees were in the smallest size class, and frequencies of trees tended to decrease with increasing size. The slowing of growth and reduction of mortality as trees reached middle sizes resulted in an accumulation of such sizes in the population, producing size-class distributions that resemble rotated sigmoids (see Goff and West 1975). These patterns indicate that populations of longleaf pine do not change rapidly in response to large-scale disturbances.

Very slow changes in the composition of the old-growth longleaf pine population result from demographic inertia. Demographic characteristics do not tend to change following disturbances, so any changes in longleaf pine populations that occur during intervals between disturbances will do so very slowly as a result of infrequent recruitment, slow growth, and low mortality. Centuries are required to replace large trees, removed from a patch,

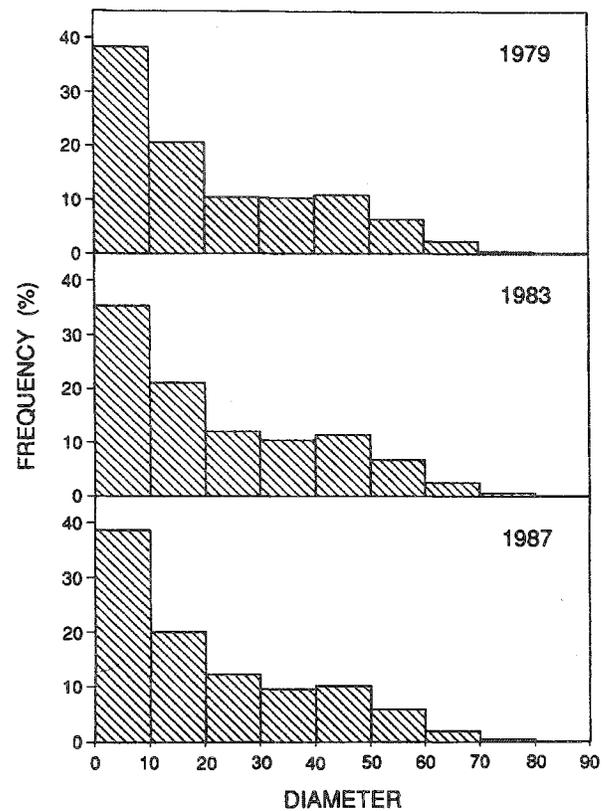


Figure 12. The frequency (measured as percent of total numbers of longleaf pine in the mapped plot on the Wade Tract) of trees in 10-cm size classes in 1979, 1983, and 1987.

by trees of comparable size. In addition, patches contain trees for only part of the time; at other times, patches remain treeless. In some longleaf pine habitats, turnover times may be quite long, possibly even millenia.

Any shift away from some equilibrium (as caused by Hurricane Kate), is not likely to be followed by a rapid shift back towards that equilibrium. Delayed recovery, especially following recurrent large-scale disturbances, might result in reduced densities of trees in such areas. The lower limit to densities at which the population will persist will increase as the frequency of recruitment decreases (and hence the population becomes more even aged and sized). However, the tendency for recruitment to occur in open areas buffers changes in population density (at a very slow rate) because adult mortality is associated with eventual entry of new individuals into the population. Platt et al. (1988) suggest that longleaf pine stands will become more savanna-like (with more open space in the population) as the frequency of large-scale disturbances increases.

Large-scale disturbances are likely to occur frequently; in southeastern coastal regions hurricanes alone are likely to occur more than once a century (Neuman et al. 1981; Simpson and Riehl 1981). As a result, longleaf pine populations in coastal regions are likely to exist in non-equilibrium states almost continually. While longleaf pine populations may appear relatively static over short time intervals as a result of demographic inertia, in reality they are likely to be changing continually as a result of past large-scale disturbances.

While the pre-Kate size-class distribution did not closely resemble that expected on the basis of size-specific growth and mortality of trees (see Platt et al. 1988), the hurricane shifted the size-class distribution even farther from a stable size-class distribution. Nonetheless, the density of trees increased between 1979 and 1987. A total of 1379 trees (recruits derived from the 1978 mast year) entered the 0-10 cm size class between 1979 and 1987. This exceeded the 1207 trees that died during the same interval, resulting in a 2.5% increase over eight years. Changes in numbers, however, were not consistent among size classes. The smallest size class increased by 3.5%, while adult trees (those ≥ 30 cm dbh) declined by 3.1%. The decrease in adults resulted primarily from Hurricane Kate; when these trees were removed from the data, mortality rates were more than halved in most large size classes and the total number of adult trees increased by 3.1% over the eight year period.

Densities would normally be expected to increase in plant populations following transient disruptions by large-scale disturbances if mortality of older, larger plants opened patches in which recruitment of many juveniles can occur. However, as predicted by our models, recruitment of longleaf pine does not depend solely on the opening of space, and hence occurs only when certain other conditions are met. Thus, recruitment may be spread out over long periods of time ranging from decades to perhaps centuries. In addition, following recruitment into a patch, which most often occurs synchronously, thinning of trees within patches occurs slowly, and so patches decline in density over decades-centuries. As a result of recruitment being spread over long periods of time coupled with low rates of decline in the density of recruits to predisturbance levels (i.e., one or a few trees), longleaf pine stands may be more likely to exist in states where the density of trees is increasing than decreasing.

Open space suitable for recruitment might decrease and become limiting if the density of large trees were to increase to levels sufficient to depress growth and survival of recruits in open areas. Because hurricane intensity decreases following landfall (Anthes 1982), such conditions might be likely at all times in locations away from the Atlantic or Gulf coasts. Decreased recruitment, coupled with very slow growth and low mortality of large trees, could have produced the underrepresentation of small trees and open aspect of the inland old-growth longleaf pine barrens described by early travelers in the southeast (e.g., Bartram 1766; Williams 1827, 1837). In such populations, there would be fewer patches of grass-stage juveniles and young trees in height growth than on the Wade Tract. The patch structure of these pine barrens probably would have been less evident to travelers than on the Wade Tract because the patches merge into a background of larger, essentially randomly spaced trees as they reach larger sizes (see Platt et al. 1988). Nonetheless, patch structure was recognized by at least some naturalists (i.e., Schwarz 1907).

Changes in longleaf pine stands might occur in all regions if hurricanes were to increase or decrease in frequency and intensity over periods of time ranging from decades to centuries. Fluctuations in hurricane frequency have been documented and related to variation in global climate patterns (e.g., Gray 1990). Because hurricane intensity appears to be related to sea surface temperatures in tropical regions (see Emanuel 1988a,b), changes in global climate patterns also would likely

produce changes in the intensity (and perhaps also in the frequency) of hurricanes impacting longleaf stands in coastal regions (Emanuel 1987). Thus longleaf stands over coastal and more interior regions might change in response to patterns of change in the most prominent large-scale disturbance impacting the coastal plain of the southeastern United States.

The concept of longleaf pine stand dynamics that emerges from our study is that these populations change rapidly and in variable ways as a result of periodic large-scale disturbances, but change very slowly in the intervals between disturbances. As a result the population is predicted almost always to be changing and not close to equilibrium. Such a population potentially could be displaced by other species more capable of responding to post-disturbance conditions and, hence, increasing more rapidly in density during the intervals between disturbances (i.e., ruderal species of Grime 1977, 1979). However, nutrients (especially phosphates) are extremely limiting in longleaf pine savannas (see Christensen 1977), and thus rapid growth and maturation might not be possible following large-scale disturbances such as hurricanes. Species in highly and chronically stressful environments are predicted to be characterized by selection for traits that enhance survival of adverse conditions (Greenslade 1983). Consequences of such selection include slow growth, delayed maturation, and reduced reproduction. Such predicted adaptations resemble those exhibited by longleaf pine, suggesting that one consequence of continual low nutrient availability might be selection for traits that result in demographic inertia and thus

an inability to respond rapidly to changes in the environment.

Nutrients may be available in the vegetation, however. Species capable of obtaining those nutrients might be capable of more rapid growth and reproduction than otherwise would be possible. Is it possible that via pyrogenicity, longleaf pine shifts limited nutrients to a state where they are transiently available, especially to offspring, thereby stimulating growth through vulnerable stages (see Grelen 1975) of the life cycle and removing potential competitors at the same time?

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