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Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA

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Summary

1 Using 18 years of permanent-plot data from a 4-ha stand, we investigated whether stand dynamics is predictable, i.e. driven by competition (inferred from species shade tolerances), or unpredictable (driven by frequent exogenous disturbance or other factors). We also considered whether small disturbance might accelerate or retard succession. The study involved dynamics of stems ≥ 4.5 cm diameter at breast height (d.b.h.) for 10 important species in a southern mixed hardwood forest 80 years after selective removal of *Pinus taeda.*

2 Shade-tolerant species (*Ilex opaca*, *Fagus grandifolia*, *Magnolia grandiflora*, *Acer rubrum*, *Nyssa sylvatica*) increased in small d.b.h. classes, whereas intermediate (*Quercus alba*) and shade-intolerant species (*Q. nigra*, *Q. hemisphaerica*, *Liquidambar styraciflua*, *Pinus taeda*) did not.

3 Per-capita ingrowth was higher for shade-tolerant species (0.016–0.024) than for intermediate and shade-intolerant species (0–0.006), whereas mortality was lower ((0.006–0.015 vs. 0.019–0.035).

4 Over 18 years, ingrowth exceeded mortality loss slightly, resulting in an increase in number of stems of about 1%, from 995 to 1029 stems ha^{-1}; average live basal area (BA; 35.9 m^2 ha^{-1}) varied by less than 2% over eight surveys spanning 18 years. Basal area increased substantially for three species (*Ilex opaca*, *Pinus taeda*, *Acer rubrum*), and declined strongly for three others (*Quercus nigra*, *Q. hemisphaerica* and *Fagus grandifolia*).

5 The stand d.b.h. distribution had a rotated sigmoid form which became flatter over time. Species d.b.h. distributions were mostly bell-shaped for intolerant species, and irregular-to-monotonic declining for shade-tolerant species. Over time, bell-shaped distributions moved to the right and irregular distributions remained irregular.

6 A hurricane in 1986 caused loss of 4.5% of standing BA. Compositional change was most rapid during the hurricane interval and ingrowth was highest in the two intervals following the hurricane. Effects on species trends in density, basal area, mortality or recruitment were minor.

7 Temporal trends in species abundances mostly supported the hypothesis of predictable successional change related to competition for light. However, d.b.h. distributions of shade-tolerant species and rapid declines in BA of *Quercus nigra* and *Fagus* indicated that other processes are also important and will limit predictability of change.

Key-words: disturbance, forest succession, shade tolerance, stand dynamics, tree mortality

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Introduction

In many forests of the world, composition and structure are a product of internal processes, such as competition for light, playing out in the context of exogenous disturbance. For example, observations based on space-for-time substitution, stand reconstructions (e.g. Glitzenstein *et al.* 1986; Bergeron 2000) and longitudinal studies (e.g. Cain & Shelton 1995; Arevalo *et al.* 2000) show successional replacement of shade-intolerant species by shade-tolerant species during recovery from major disturbance. In addition, gap dynamic models based largely on competition for light produce plausible results (cf. Shugart 1984; Pacala *et al.* 1996). Thus, change is often predictable, at least to a degree.

However, in some systems forest change may be more chaotic and less predictable because of disturbance, of which one widespread form is wind (Foster & Boose 1992; Matlack *et al.* 1993; Everham 1995; Pontailler *et al.* 1997; Boose *et al.* 2001). Windstorm effects may span the full range from large, infrequent, high-intensity disturbance to small, frequent, low-intensity disturbance. Likewise, vegetation responses can vary widely, depending on both the nature of the disturbance and initial stand condition (see Everham & Brokaw 1996; Myers & van Lear 1998). Whilst disturbance may promote persistence of shade-intolerant species by creating light gaps (Putz 1983; Myers & van Lear 1998), it may also accelerate succession (e.g. Glitzenstein & Harcombe 1988; Arevalo *et al.* 2000; Webb & Scagna 2001; also see Abrams & Nowacki 1992; Battaglia *et al.* 1999) if there is abundant advance regeneration of shade-tolerant species present under a shade-intolerant canopy.

Other influences on forest dynamics may include weak competition (Hubbell 1997, 2001; Hubbell *et al.* 1999), which results in a sort of drift in species composition, as well as recruitment limitation (Clark & Ji 1995; Clark *et al.* 1998; Hubbell *et al.* 1999), historical contingency (e.g. Connell & Slatyer 1977; Henry & Swan 1974) or climate change (e.g. Iverson & Prasad 1998). All these would reduce the role of light competition in determining vegetation change, and thereby reduce the predictability of change.

Mesic forests of the Coastal Plain region of the south-eastern United States of America (USA) are particularly interesting with regard to the roles of internal processes and external events. Episodes of exogenous canopy disturbance are common (Glitzenstein *et al.* 1986; Platt & Schwartz 1990; Batista & Platt 1997) and hurricanes, in particular, are frequent (Runkle 1990; Gresham *et al.* 1991; Sheffield & Thompson 1992; Myers & van Lear 1998). These may damage canopy trees (Putz & Sharitz 1991), open gaps, provide opportunities for new regeneration, increase the number of seedling regeneration niches, favour tree species tolerant of strong winds, or disrupt tendencies towards competitive exclusion of shade-intolerant species (Myers & van Lear 1998). With respect to competitive exclusion, Coastal Plain forests are distinguished by an unusually high diversity of woody plants (Marks & Harcombe 1975; Christensen 1988). One explanation for the diversity is interruption of the competitive exclusion process by hurricane disturbance (Doyle 1981; Glitzenstein *et al.* 1986). In some situations, hurricane disturbance may be so frequent and variable that changes in species composition become essentially unpredictable because different suites of species will be favoured after different hurricanes because of differences in disturbance (Platt & Schwartz 1990; Batista & Platt 1997).

Our own work on tree populations (Harcombe & Marks 1983) and stand reconstructions (Glitzenstein *et al.* 1986) in southern forests has, however, suggested more predictable successional change driven by interspecific interactions. This suggestion is supported by measured differences among species in response to light limitation (Lin *et al.* 2001, 2002) that are consistent with their inferred differences in shade tolerance (cf. Burns & Honkala 1990). Our work helps to explain observations that two shade tolerant species (*Fagus grandifolia* and *Magnolia grandiflora*) are important dominants in late-successional stands on mesic sites across the south-eastern USA (Gano 1917; Kurz 1944; Blaisdell *et al.* 1973; Christensen 1988; Harcombe *et al.* 1993). The work is all based on inference from short-term or cross-sectional studies or stand reconstructions.

Progress in understanding the combined actions of initial conditions, external events and internal processes can be made using cross-sectional studies and inferential methods. However, longitudinal studies are necessary to identify which of many possible disturbance scenarios might explain observed structure and dynamics (Bakker *et al.* 1996; Sheil 1999). Unfortunately, direct observations of long-term forest change are rare (but see Woods 2000a,b). Our study of Weir Woods was initiated in 1980 to address the roles of external and internal processes in determining dynamics in a stand in which *Fagus* and *Magnolia* were among the leading dominants. The stand had been selectively logged early in the 20th century; the post-logging forest was a mixture of residual populations of hardwoods and a cohort of *Pinus taeda* that had invaded logging gaps (Glitzenstein *et al.* 1986). In addition to a hurricane passing over the site in 1986, there is also evidence of earlier episodes of major natural disturbance in the 19th century (Glitzenstein *et al.* 1986). The purpose of the present paper is to investigate forest changes during the period from 1980 to 1998 to see whether variation at this stage of development (60–80 years after the major human disturbance) is better understood in terms of successional recovery driven by competition for light or by other factors.

We address the following specific questions: (i) Is the understorey becoming enriched in shade-tolerant tree species? (ii) Are populations of shade-intolerant species declining? (iii) Are the changes in population structures consistent with species' shade tolerances and the hypothesized direction of successional change? (iv) Did the 1986 hurricane alter succession?

Study site

Mesic forests, dominated by a diverse mixture of broad-leaved deciduous trees (mostly *Quercus* spp., *Fagus grandifolia*), broad-leaved evergreens (*Magnolia grandifolia*) and conifers (*Pinus* spp.), occur on the south-eastern coastal plain of the United States from southern Virginia to eastern Texas (Christensen 1988; Platt & Schwartz 1990; Harcombe *et al*. 1993; Ware *et al*. 1993). Such forests are also recorded in studies of pre-settlement vegetation(Delcourt & Delcourt 1974, 1977; Schafale & Harcombe 1983), although they apparently occupied a relatively small proportion of the landscape (cf, Schwartz 1994). Stands dominated by beech and magnolia were interpreted as the 'potential vegetation' or the regional climatic climax by many early workers (e.g. Gano 1917; Pessin 1933; Kurz 1944; Blaisdell *et al*. 1973; Delcourt & Delcourt 1974), but not by Quarterman & Keever (1962).

Wier Woods, the study site, is located in Hardin County, Texas (30–16′ N, 94–12′ W) approximately 16 km north of Beaumont. It is part of the Big Thicket (Marks & Harcombe 1981), a region in Texas of about 2500 km^2, mostly in the drainage of the Neches River and located 50–100 km inland from the Gulf of Mexico and 75–125 km west of the Louisiana border. Stand dominants include *Pinus taeda*, *Magnolia grandiflora*, *Quercus alba*, *Fagus grandifolia* and *Q. nigra* (nomenclature follows Correll & Johnston 1970). The sub-dominants are *Ilex opaca*, *Q. hemisphaerica* (= *Q. laurifolia* of our previous reports), *Liquidambar styraciflua*, *Nyssa sylvatica* and *Acer rubrum*. Of these, *Ilex* and *Acer* are mostly restricted to the midstorey. Other common woody plants of the midstorey and understorey include *Ilex vomitoria*, *Cornus florida*, *Symplocos tinctoria* and *Ostrya virginiana*. The stand was selectively logged for *Pinus* in about 1917 (F. Wier, personal communication; Glitzenstein *et al*. 1986). Tree-ring analyses indicated earlier episodes of canopy opening in 1810 and 1855, as well as, to a lesser extent, in the mid 1960s (Glitzenstein *et al*. 1986).

The vegetation is assignable to a type variously called Southern Mixed Hardwood (Quarterman & Keever 1962), Beech-Magnolia-Holly (Delcourt & Delcourt 1977), Lower Slope Hardwood Pine (Marks & Harcombe 1981), or the *Fagus grandifolia–Magnolia grandiflora* Forest Alliance (Weakley *et al*. 1998). The soil is a fine-loamy, siliceous, thermic Typic Glossaqualf of the Waller Series. It is a seasonally saturated soil with argillic horizons formed from illuvial clay. The climate is humid subtropical, with a long growing season (approx. 240 days) and an even distribution of precipitation throughout the year (144 cm). Average monthly maximum temperature in August is 33.1 °C; average monthly minimum temperature in January is 5.8 °C (Port Arthur, TX, approximately 40 km SSE of Wier Woods; National Climatic Data Center 1994). In the spring and fall, strong frontal systems with steep temperature gradients move through the area, often accompanied by high winds or tornadoes. In addition, the Big Thicket area is frequented by summer thunderstorms, tropical storms and hurricanes. Between 1871 and 1991, 20 hurricanes made landfall within 120 km of the site (see Neumann *et al*. 1993).

On 26 June 1986, Hurricane Bonnie passed over Wier Woods with wind velocities that reached approximately 120 km h^{-1} (33 m s^{-1}; Neumann *et al*. 1993). The eye passed just west of the site (Harcombe, personal observation) travelling in a NNW direction at a velocity of approximately 30 km h^{-1} (Neumann *et al*. 1993). Hurricane simulations based on National Weather Service records indicate that this was the largest hurricane to affect the site over the previous 100 years (Harcombe & Boose, unpublished data). The Port Arthur weather station reported a maximum wind velocity of 165 km h^{-1} and a minimum barometric pressure of 98.8 kPa.

Methods

To monitor forest change, we set up a permanent study plot of approximately 4 ha divided into 101 contiguous 20 × 20 m plots. All live stems ≥ 4.5 cm d.b.h. were measured in 1980 and tagged shortly thereafter. In 1982, 1985, 1987, 1989, 1992, 1995 and 1998 all tagged trees were re-measured and any stems that had reached 4.5 cm d.b.h. since the last measurement (ingrowth) were tagged. Before data were analysed, trees with missing or seriously anomalous values were assigned an interpolated d.b.h., and trees that had been missed in earlier surveys were assigned d.b.h. values by back projection based on calculated mean growth rates for the appropriate time period, species and size class. In addition to the periodic measurements, mortality surveys were conducted each May, during complete cruises by a crew of two to three observers. Trees were considered dead only if the crown was fully dead.

We chose to analyse data by 20 × 20 m plot; measurement units roughly this size have proven useful in stand dynamics models because this coincides roughly with the area of influence of a large canopy tree. This scale of observation thus appears appropriate for predicting some elements of forest dynamics, especially tree growth (Fulton & Harcombe 2002). Rates of mortality, ingrowth and change were calculated for each 2–3-year interval, and adjusted to an annual basis by dividing by the number of years. We report basal area mortality in addition to stem mortality because basal area mortality is an indicator of the amount of new physical space (or resource) that is available for exploitation by other individuals in the population. Also, it is relatively insensitive to the minimum d.b.h. limit for measurement (Runkle 2000).

As part of the answer to the question of whether the hurricane altered succession, we also analysed multivariate trends in species composition (Philippi *et al*. 1998). Changes in species composition may be considered as vectors in a space defined by the importance of

Table 1 Mortality and ingrowth (fractional change per year and stems ha^{-1} year^{-1}) for major tree species at Wier Woods for all individuals ≥ 4.5 cm d.b.h. Annual values were calculated separately for each measurement period and then averaged over the eight measurement periods. Tolerance designations follow Burns & Honkala (1990)

	Fractional annual rates			Absolute annual number	
Species	Basal area mortality	Stem mortality	Ingrowth	Stem death	Ingrowth
Pinus taeda (intolerant)	0.004	0.008	0	0.54	0
Liquidambar styraciflua (intolerant)	0.009	0.019	0.006	1.67	0.50
Quercus nigra (intolerant)	0.047	0.059	0	1.64	0
Quercus hemisphaerica (intolerant?)	0.027	0.035	0.002	0.68	0.08
Quecus alba (intermediate)	0.021	0.032	0	1.89	0
Acer rubrum (tolerant)	0.019	0.017	0.016	1.49	1.43
Nyssa sylvatica (tolerant)	0.008	0.011	0.015	0.76	1.01
Magnolia grandiflora (tolerant)	0.010	0.010	0.022	0.74	1.71
Fagus grandifolia (very tolerant)	0.033	0.015	0.026	0.63	1.08
Ilex opaca (very tolerant)	0.007	0.006	0.024	1.85	7.55

individual species; these vectors may be compared by their magnitude and direction (McCune 1992). We used basal area as the species importance metric and chose a city-block representation of multivariate space because it is less sensitive to outliers than a euclidean representation (McCune 1992; Legendre & Legendre 1998). Magnitudes of compositional change vectors were calculated at both the site level and the 20 × 20 m plot level for all 2–3-year survey intervals as the city-block (Manhattan) distance between beginnings and ends of the vectors, adjusting to annual rates of change by dividing by the number of years. We compared the directions of pairs of vectors representing successive survey intervals by calculating the distance between the vector ends after the vectors were placed at a common origin and standardized to unit length (McCune 1992). This distance will vary from zero for two parallel vectors to a maximum of 2.0 for two orthogonal or opposite vectors. Our expectation was that an effect of the hurricane on the direction of succession would be indicated in a substantially higher change in direction between the hurricane interval and the one preceding or following it, as compared with changes in direction between the other interval pairs.

Shade tolerance categories follow Burns & Honkala (1990), except for *Quercus hemisphaerica*, which has not been classified. Because of its ecological similarity to *Q. nigra*, we consider it intolerant or intermediate. Analysis of light-dependent growth and mortality of saplings supports the published categorizations for the species we have investigated (Lin *et al*. 2001, 2002).

Results

SHADE TOLERANTS VS. SHADE-INTOLERANTS (QUESTIONS 1 AND 2)

The shade-tolerant species (*Ilex*, *Fagus*, *Magnolia*, *Acer*, *Nyssa*) had low annual per-capita mortality (0.006–0.017). Most of the less-tolerant species had higher mortality (0.019–0.059) (*Quercus alba*, *Q. nigra*, *Q. hemisphaerica*, *Liquidambar*; Table 1), except that *Pinus* had a very low death rate (0.008) because it had no small individuals. Ingrowth was likewise skewed in favour of the shade-tolerant species (Table 1), and the ranges did not overlap (0.015–0.024 for shade tolerants vs. 0–0.006 for shade-intolerants). *Ilex opaca*, which occurs mainly in multistemmed clumps and shows strong propensity for clonal sprouting, had the most ingrowth in absolute terms. It contributed 42% of all new stems, 24% of which involved clonal addition to existing clumps. The other shade-tolerant tree species (*Fagus*, *Magnolia*, *Acer*, *Nyssa*) accounted for 29% of the ingrowth. Shrub species (*Ilex vomitoria*, *Symplocos tinctoria*) and minor tree species (mostly *Cornus florida*) accounted for about 26%, and *Liquidambar*, a shade-intolerant tree species contributed 3%. The three species of *Quercus* collectively recruited only one new stem over the 18 years, and the final shade-intolerant species, *Pinus*, recruited none. The net effect of differences in death and ingrowth rates was enrichment of the understorey in stems of shade-tolerant species (Fig. 1). As shade-tolerant species became more important in the understorey, overall stem mortality declined from about 25 stems ha^{-1} year^{-1} to about 12 stems ha^{-1} year^{-1} over the period of the survey.

The status of the important tree populations was summarized by plotting average annual ingrowth rate vs. average annual mortality rate (Fig. 2). Species to the left of the 1 : 1 line increased, and species to the right decreased in stem numbers (Table 2); many of the changes were substantial but gradual (Appendix 1). The increasers are all shade-tolerant; the decreasers are all shade-intolerant or intermediate (*sensu* Burns & Honkala 1990; see also Lin *et al*. 2001, 2002).

D.B.H. DISTRIBUTIONS (QUESTION 3)

According to Goff & West (1975), mature stands are expected to have a rotated sigmoid form for the overall

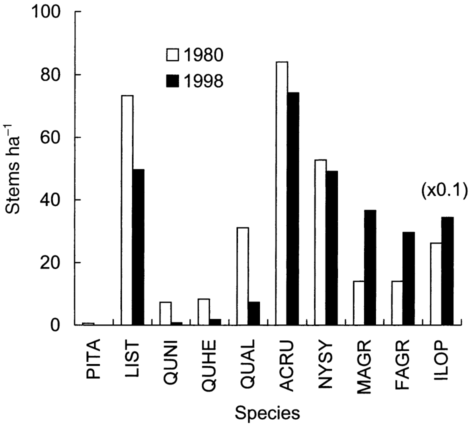

Fig. 1 Comparisons between 1980 and 1998 of density (stems ha^{-1}) of 4.5–15 cm d.b.h. stems by species. Species are arranged in order of increasing shade tolerance. PITA = *Pinus taeda*, LIST = *Liquidambar styraciflua*, QUNI = *Quercus nigra*, QUHE = *Q. hemisphaerica*, QUAL = *Quercus alba*, ACRU = *Acer rubrum*, NYSY = *Nyssa sylvatica*, MAGR = *Magnolia grandiflora*, FAGR = *Fagus grandifolia*, ILOP = *Ilex opaca*.

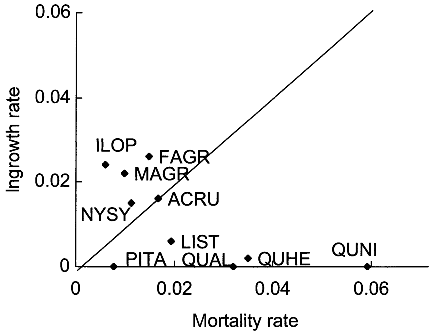

Fig. 2 Scattergram comparing species by their ingrowth and mortality rates. Rates are averages of the annualized period rates (Table 1). Species codes are given in the legend for Figure 1.

d.b.h. distribution owing to concentration of mortality in stems of intermediate d.b.h. (because of shading by larger trees) and in stems of large d.b.h. (because large stems that emerge above the canopy are susceptible to blowdown). For individual species, we expect shade-intolerants to have a roughly bell-shaped distribution because of ingrowth suppression and high mortality for small understorey stems. Shade-tolerant species should have broader distributions because of lower mortality of small individuals in the shade. Irregularities in d.b.h. distributions suggest temporal variation in ingrowth. While d.b.h. distributions must be interpreted cautiously (cf. Harcombe & Marks 1983; Harcombe 1987), we feel justified in doing so in this case because repeated observations at short intervals allowed us to identify the separate contributions of growth and mortality to the changes.

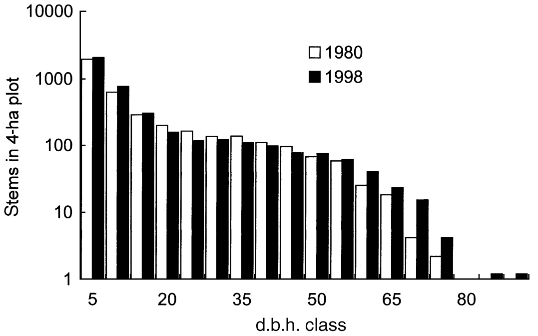

Fig. 3 Whole-stand d.b.h. distributions for 1980 and 1998. *X*-axis values are lower class limits; classes are each 5 cm wide. *Y*-axis values are total numbers of stems in the 4-ha study area (log scale).

The whole-stand d.b.h. distribution had a rotated sigmoid form (Fig. 3), which became slightly more pronounced over the years in accordance with expectation. The increases in small stems (< 10 cm d.b.h.) would not necessarily have been predicted; inspection of d.b.h. distributions by species (Fig. 4) indicates that they were caused by substantial ingrowth of *Ilex*, *Magnolia* and *Fagus*. These increases masked substantial declines in small stems of *Acer*, *Liquidambar* and *Quercus alba* owing to low ingrowth and high death rates.

Table 2 Species-level stocks in absolute basal area (m^2 ha^{-1}), absolute density (stems ha^{-1}), relative basal area (fraction of total), relative density (fraction of total) and net change over 18 years at Wier Woods for stems ≥ 4.5 cm d.b.h.

	Absolute values				Relative values				Net change over 18 years	
	Basal area		Density		Basal area		Density			
Species	1980	1998	1980	1998	1980	1998	1980	1998	Basal area	Density
Pinus taeda (intolerant)	10.50	12.64	73	64	0.30	0.35	0.07	0.06	0.20	–0.12
Liquidambar styraciflua (intolerant)	1.37	1.59	95	73	0.04	0.04	0.10	0.07	0.15	–0.23
Quercus nigra (intolerant)	3.69	2.04	40	14	0.11	0.06	0.04	0.01	–0.45	–0.65
Quercus hemisphaerica (intolerant?)	1.60	1.40	25	14	0.05	0.04	0.03	0.01	–0.13	–0.44
Quecus alba (intermediate)	4.13	3.67	72	41	0.12	0.10	0.07	0.04	–0.11	–0.43
Acer rubrum (tolerant)	0.69	0.85	91	87	0.02	0.02	0.09	0.08	0.23	–0.04
Nyssa sylvatica (tolerant)	1.20	1.41	66	65	0.03	0.04	0.07	0.06	0.18	–0.02
Magnolia grandiflora (tolerant)	4.59	5.31	73	91	0.13	0.15	0.07	0.09	0.16	0.25
Fagus grandifolia (very tolerant)	4.00	2.74	38	47	0.12	0.08	0.04	0.05	–0.31	0.24
Ilex opaca (very tolerant)	1.57	2.71	274	371	0.05	0.08	0.28	0.36	0.72	0.35

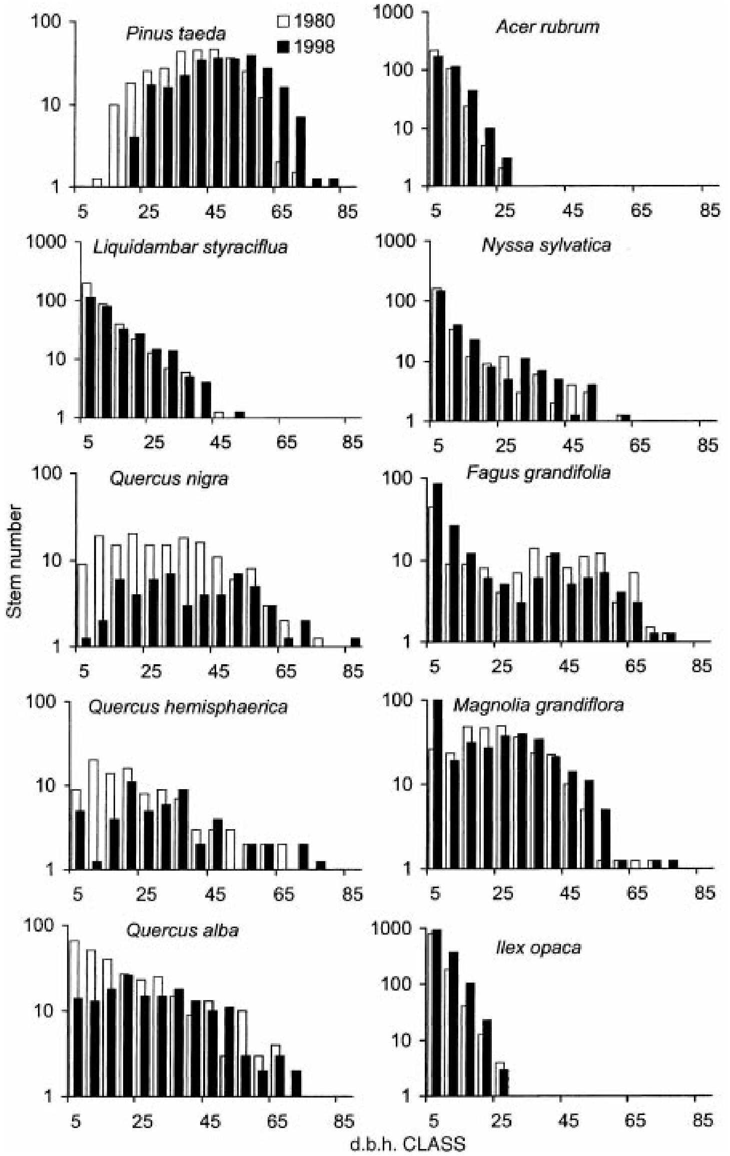

Fig. 4 Species d.b.h. distributions for 1980 (light bars) and 1998 (dark bars). *X*-axis values are lower class limits; classes are each 5 cm wide. *Y*-axis values are total numbers of stems in the 4-ha study area (log scale); note different scales for different species. Species are arranged in order of shade tolerance from top left (intolerant) to bottom right (very tolerant).

For stems 15–30 cm d.b.h., there was a net decline of 18.3 stems ha^{-1}. The decline was unevenly distributed, with a single species, *Magnolia*, contributing most of it. *Magnolia* is a shade-tolerant species and the effect was the result of high outgrowth from the 15–30 cm d.b.h. class and low ingrowth of individuals from the < 15 cm d.b.h. class, rather than thinning mortality. The low ingrowth of *Magnolia* from the < 15 cm d.b.h. class suggests a past period of low recruitment or high sapling mortality. The four additional species most responsible for the decline in the 15–30 cm d.b.h. class were *Quercus nigra*, *Q. hemisphaerica*, *Q. alba* and *Pinus taeda*, all intermediate or intolerant species with high death rates and mostly low ingrowth rates.

The d.b.h. distributions of individual species (Fig. 4) were mostly consistent with expectation. Of the shade-intolerant species, three had broadly bell-shaped distributions (*Pinus*, *Quercus nigra*, *Q. hemisphaerica*). The fourth, *Liquidambar*, was an exception; it was close to the monotonic-declining form usually associated with shade-tolerant species. *Quercus alba*, a species of intermediate shade tolerance, had a flat-irregular distribution, as did the two overstorey dominants (*Magnolia*, *Fagus*); d.b.h. distributions for the three other shade-tolerant tree species (*Ilex*, *Acer*, *Nyssa*) were monotonic declining.

Changes in d.b.h. distributions from 1980 to 1998 were also roughly consistent with shade tolerance. In the shade intolerant-intermediate group, the smaller d.b.h. classes declined. Two of the species (*Pinus*, *Liquidambar*) showed modest rightward shifts in their distributions. The shade-tolerant species showed either increases in the smallest d.b.h. class (*Magnolia*, *Fagus*, *Ilex*) or modest decreases (*Nyssa*, *Acer*). There was also a large decline in *Fagus* in the canopy (> 30 cm d.b.h.), which was most noticeable as a drop in species basal

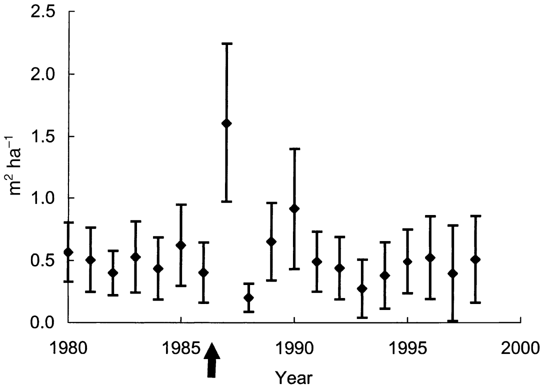

Fig. 5 Basal area (m^2 ha^{-1}) of stems found dead in each year between 1980 and 1998 in the 4-ha study plot. Values are averages over 101 plots; bars are indicators of variability calculated using the formula for 95% confidence interval. Arrow marks hurricane year.

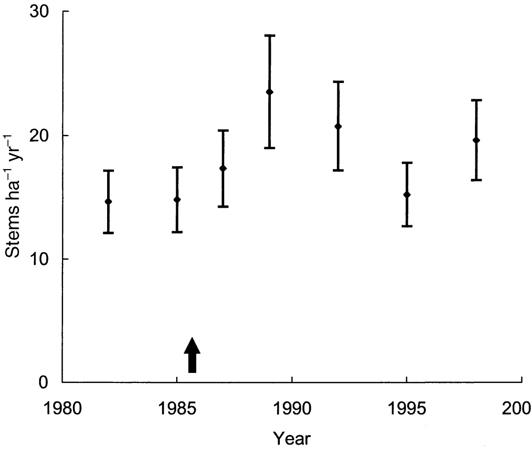

Fig. 6 Overall ingrowth (stems ha^{-1} year^{-1}) by survey interval. Values are averages over 101 plots; bars are indicators of variability calculated using the formula for 95% confidence interval. Arrow marks hurricane year.

area from 1989 to 1998 (Appendix 2); this is unexpected for a shade-tolerant canopy dominant.

The changes in d.b.h. distributions resulted in large increases in species basal area for *Pinus*, *Magnolia* and *Ilex*, a modest increase for *Acer* and substantial declines for *Quercus nigra*, *Q. hemisphaerica*, *Q. alba* and *Fagus* (Table 2; Appendix 2). The intolerant species did not all decrease in basal area and the tolerant species did not all increase.

HURRICANE EFFECTS (QUESTION 4)

In 1987, the survey year including the small hurricane, basal area loss was almost three times the average (Fig. 5), amounting to 4.5% of stand live basal area. Basal area loss was slightly higher in the second and third years following the hurricane, though nearly indistinguishable from the natural range of variation over the rest of the period. More plots experienced loss in the hurricane (60% of the plots vs. 40% for non-hurricane years) and four plots experienced loss higher than the per-plot maximum for non-hurricane years.

Ingrowth was highest in the two intervals after the hurricane (Fig. 6; 14.6–23.5 stems ha^{-1} year^{-1}). Temporal variation was significant (repeated-measures ANOVA; $P < 0.05$). We found no relationship between hurricane mortality and subsequent ingrowth in scattergrams of post-hurricane ingrowth vs. 1985 live basal area and change in basal area between 1985 and 1987 (not shown). Also, we found no relationship between cumulative ingrowth per plot and initial stem density or cumulative tree mortality.

The rate of compositional change, as indicated by the magnitudes of the change vectors, was noticeably higher during the interval with the hurricane (Table 3) at both the whole site and plot levels. However, the hurricane does not appear to have affected the direction of change at the stand level: between the hurricane interval and the preceding interval the change in direction was somewhat smaller and between the hurricane interval and the following interval the change in direction was in the range of values for other pairs of survey intervals (Table 3).

Over the 18 years of this study, basal area loss did not vary greatly from year to year (except for the hurricane year; Fig. 5, Table 4), and neither did mortality (14.8 stems ha^{-1} year^{-1}, SD = 1.64) or ingrowth (18.0 stems ha^{-1} year^{-1}, SD = 8.4). Consequently, stand basal area and overall density showed little change (Table 3), even though some individual species changed substantially (Table 2, Appendices 1 and 2).

Discussion

SHADE TOLERANTS VS. INTOLERANTS

Over 18 years without major disturbance, the understorey tree stratum became enriched in shade-tolerant species relative to shade-intolerant and intermediate species because of lower death rates and higher

Table 3 Changes in stand species composition in multivariate species-space calculated using analysis of change vectors (see text). Magnitude indicates overall amount of change in a survey interval. Direction change is the difference in angle of the change vector between one interval and the previous interval (a value of zero indicates no change in direction; a value of two would indicate movement in species space in an opposite or an orthogonal direction)

Interval	Magnitude of change		Direction change
	Site level	Plot level	
80–82	0.44	1.11	
82–85	0.59	0.93	0.82
85–87	0.90	1.55	0.40
87–89	0.48	0.95	0.74
89–92	0.48	1.13	0.92
92–95	0.36	0.79	0.62
95–98	0.60	1.13	0.59

Table 4 Stand-level stocks (m^2 ha^{-1} or stems ha^{-1}) and fluxes (annual rates) at Wier Woods for all stems > 4.5 cm d.b.h.

	1980	1988	Min	Max	Average	SD	Range*	Death	Overall net change
Basal area	34.4	35.5	34.4	35.6	35.9	9.72	±1.67%	1.50%	3.20%
Density	995	1029	967	1029	992	236	±3.13%	1.60%	3.42%

*(1/2(max stock-min stock))/average stock.

ingrowth rates; these differences translated into absolute numerical growth of the populations of tolerant species and decreases in the populations of intolerant species. The results support the view that trends in composition have a predictable component, even long after disturbance, and that the predictability is related to competition for light. While this is not a new finding, few studies have actually documented such changes over time (but see Arevalo *et al.* 2000; Woods 2000a,b), especially in the context of known year-to-year variation in tree death.

Although light competition can account for the major trends, there are interesting anomalies in d.b.h. distributions that are not explained by competition for light. First is the under-representation in some of the d.b.h. classes between 10 and 30 cm for two of the shade-tolerant species (*Fagus*, *Magnolia*), but not for the others (*Ilex*, *Acer* and *Nyssa*). Although recruitment variation has previously been proposed as an explanation for such under-representation (Harcombe & Marks 1978, 1983), causes and magnitudes of such variation have not yet been identified. We have no explanation for why the *Liquidambar* d.b.h. distribution was much more like a shade-tolerant than a shade-intolerant species or why the number of small *Acer*, which might have been expected to increase, as did small individuals of the other shade-tolerant species, actually declined. Finally, a more problematic anomaly is the rapidity of the declines in dominance of *Q. nigra*, which lost 45% of its basal area (and 65% of stems over a wide range of d.b.h. classes) in less than a decade, and *Fagus*, which lost 31% of its basal area (especially from the larger d.b.h. classes). The shade-intolerant *Q. nigra* was expected to decline, albeit more slowly, but the shade-tolerant *Fagus* would be expected to continue increasing. One possible explanation is climate change, to which *Fagus* at this site may be particularly vulnerable, because it responds negatively to elevated summer temperatures (Cook *et al.* 2001). Also, it is close to the south-western limit of its range (Little 1971); this limit is predicted to shift northward in response to global climate change (Iverson & Prasad 1998). Similar negative responses to climatic change have been predicted for *Fagus sylvatica* in Europe (see Pontailler *et al.* 1997).

HURRICANE EFFECTS

The hurricane-related spike in mortality (roughly 5% of stand basal area) was about three times the year-to-year average for the undisturbed condition. The low level of damage is consistent with that reported for a somewhat larger hurricane in a comparable stand in Florida by Batista *et al.* (1998). The low post-hurricane rise in numbers of new stems > 4.5 cm d.b.h. is consistent with the low level of basal area loss. Our analysis of vectors of compositional change suggests that the somewhat larger magnitude, without a correspondingly significant degree of change in direction, implies a modest acceleration in successional change. The limited response is not surprising, considering that the hurricane was of low intensity (maximum wind speeds of 120 km h^{-1}) and relatively fast-moving, so the duration of tree exposure to high winds was low. The results reinforce the point that hurricanes come in a wide variety of forms (Myers & van Lear 1998). Reports of major hurricane damage are common in the literature (e.g. Spurr 1956; Foster 1988a,b; Gresham *et al.* 1991), but most storms are small and have modest effects (Batista *et al.* 1998; Myers & van Lear 1998; Burslem *et al.* 2000).

Whether a hurricane accelerates or reverses succession depends both on the magnitude of the disturbance and the condition of the stand. With the passage of time since the last major event that permitted recruitment of shade-intolerant species, a stand understorey would become progressively enriched in shade-tolerant species, as we have shown. At some point, the stand might reach a threshold, above which shade-tolerant species would be important enough in the understorey that they would capture the major proportion of any light resources made available by small hurricanes. The net effect of the hurricane would then depend upon the state of the overstorey. If intermediate or intolerant species were important, acceleration of succession would result. If the transition was already well along and the disturbance small, then the net effect on succession would be neutral. If, on the other hand, the disturbance was large, succession could be re-initiated by recruitment of shade-intolerant species. Our results are most consistent with acceleration by a small disturbance, as previously hypothesized (Glitzenstein *et al.* 1986).

The large decline that we observed in the *Quercus* species over a relatively short period suggests that these species could disappear from this stand unless disturbance were to initiate a pulse of recruitment. This is indirect support for the hypothesis that disturbance is important to maintain woody plant species richness in southern forests (Glitzenstein *et al.* 1986; Platt & Schwartz 1990), although our data suggest that a small hurricane was insufficient to promote such a response. There are many examples suggesting that more intense disturbances are common (cf. Runkle 1990; Putz & Sharitz 1991; Pontailler *et al*. 1997; Szwagrzyk & Szewczyk 2001), and can be sufficient to stimulate regeneration of intermediate and intolerant species like *Quercus* and *Pinus.* Stand-replacing disturbances (Dunn *et al*. 1983; Foster 1988a,b; Peterson & Pickett 1995; Arevalo *et al*. 2000) would, of course, also initiate regeneration of intolerant species.

PREDICTABILITY AND STAND DYNAMICS

Overall, population and stand dynamics at Wier Woods show several distinctive elements that are consistent with the hypothesis that competition for light is important, and is resulting in predictable change. However, competition for light does not explain the large, rapid declines in dominance of *Fagus* and *Quercus nigra*, the irregular d.b.h. distributions of two shade-tolerant canopy species (*Fagus*, *Magnolia*), or the fact that *Acer*, a shade-tolerant species, declined in numbers. Thus, change is not simply successional recovery from a past major disturbance episode, nor is it strongly controlled by small disturbances. Indeed, recruitment limitations, climatic variation, or other factors must be constraining our current ability to predict stand-level change.

A theoretical framework for forest dynamics that can accommodate the patterns we observed, along with the anomalies, is one that incorporates both predictable and unpredictable elements. Forests are neither strongly ordered deterministic systems, nor are they necessarily chaotic, stochastic or unpredictable. Because species are long-lived, it takes a long time for successional dynamics to play out (cf. Woods 2000a,b). The directionality related to competition for light confers a degree of predictability on population changes over time; site conditions constrain and channel those changes; external forces (disturbance, disease, climatic anomalies, human intervention) may change rates or directions of the changes, sometimes in ways that would not have been predicted. Detailed studies of change like the one described in this paper help put empirical bounds on the complexity and uncertainty (Peterson & Pickett 1995), and thereby promote the development of a satisfactory and robust synthetic theory of forest dynamics.

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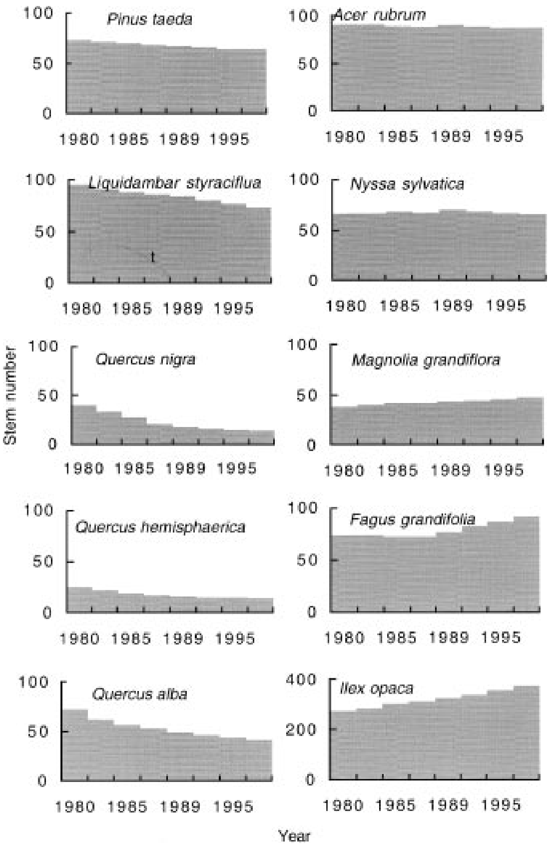
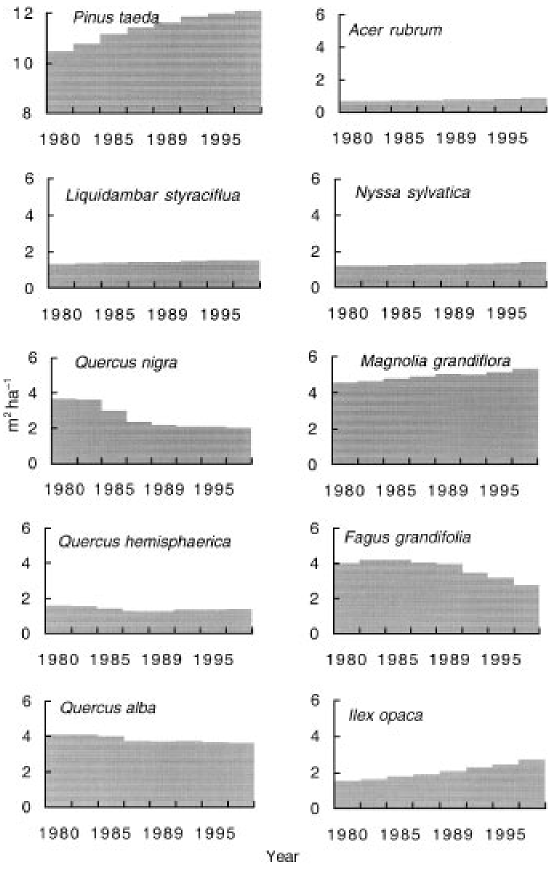


Appendix 1 Density (stems ha^{-1}) by survey year (1980, 1982, 1985, 1987, 1989, 1992, 1995, 1998) for the 10 most important species in the stand (linear scale). Species are arranged in order of shade tolerance from top to bottom and left to right. Note different scale for *Ilex opaca.*



Appendix 2 Basal area (m^2 ha^{-1}) by survey year (1980, 1982, 1985, 1987, 1989, 1992, 1995, 1998) for the 10 most important species in the stand. Species are arranged in order of shade tolerance from top to bottom and left to right. Note different scale for *Pinus taeda.*