Springer

Structure and Pattern in Temperate Seasonal Forests

Author(s): Martin F. Quigley and William J. Platt

Source: *Vegetatio*, Apr., 1996, Vol. 123, No. 2 (Apr., 1996), pp. 117-138

Published by: Springer

Stable URL: https://www.jstor.org/stable/20048662

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms

Springer is collaborating with JSTOR to digitize, preserve and extend access to *Vegetatio*

JSTOR

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Vegetatio **123:** 117–138, 1996.
© 1996 *Kluwer Academic Publishers. Printed in Belgium.*

Structure and pattern in temperate seasonal forests

Martin F. Quigley[1] & William J. Platt
Department of Plant Biology, Louisiana State University, Baton Rouge, LA 70803, USA; [1] *Present address: Department of Botany, Eastern Illinois University, Charleston, IL 61920, USA*

Received 7 March 1994; accepted in revised form 10 October 1995

Key words: Deciduous forests, Disturbance, Gap/phase dynamics, Stratification, Understory pattern

Abstract

Demography, spatial pattern, and diversity of canopy and subcanopy trees, shrubs, and lianas were compared in two cool and two warm temperate North American forests, paired at 30° and 40° north latitudes. All woody stems ≥1 cm dbh in 16 randomly located, non-contiguous plots totalling 1 ha at each of the four sites were measured, mapped, and identified. Basal area and overall density did not differ between latitudes. Demographic and spatial analyses revealed remarkable similarity in spatial dispersion, irrespective of density or species composition. At all sites, dispersion of canopy trees was random but all understory stems were uniformly distributed relative to all canopy trees. Species diversity and vertical structure differed between the warm and cool temperate sites, especially in species composition of individual strata. Associations of understory species relative to canopy species were more random at 30° than at 40° north, where a higher degree of association between canopy and understory species' patterns, coupled with their size class distributions, suggested more lengthy regeneration cycles and an alternation of species assemblages. The forests at 30°, those subject to periodic canopy disturbance by hurricanes, had more vertical mixing of species (i.e., canopy species represented in all size classes), more tree saplings, and significantly more shrub and liana species.

Introduction

Mixed species, seasonal hardwood forests occur from 26° N to 47° N in eastern North America (Braun 1950; Delcourt and Delcourt 1987; Monk 1968; Vankat 1990). These forests, in which dominant tree species lose their leaves at least transiently each year in the winter, are characterized by co-dominant canopy species and a variable, stratified understory containing juveniles of the canopy species as well as shrubs and subcanopy trees (Braun 1950; Harcombe & Marks; Martin 1992; Runkle 1985; Terborgh 1985).

The American hardwood forests may be broadly divided into cool- and warm-temperate based on differences in climate and species composition. Cool-temperate hardwood forests are variously dominated by *Fagus, Acer, Quercus*, and a variety of less widespread species; *Tsuga canadensis*, an evergreen gymnosperm, may be locally abundant in more northern forests (Braun 1950; Delcourt & Delcourt 1987; Runkle 1982). Warm-temperate hardwood forests south of the Appalachians are characterized by a mixture of deciduous trees (e.g., *Fagus, Quercus, Liquidambar*) and broadleaf evergreens, in which *Magnolia, Ilex*, and subtropical understory species become increasingly common as latitude decreases (Axelrod 1966; Monk 1968; Platt & Schwartz 1991).

In recent years, the paradigm that has dominated study of the hardwood forests of eastern North America is the intermediate disturbance theory (Connell 1978), supplanting the concept of competitive succession to a climax equilibrium state (e.g., Monk 1968; Whittaker 1975). Gap dynamics, usually in conjunction with much rarer larger-scale disturbance, are postulated to be the primary determinant of temporal and spatial scale of species regeneration (Canham 1989; Canham & marks 1985; Glitzenstein *et al.* 1986; Harcombe & Marks 1977; Lorimer 1981; Platt & Strong 1989; Poulson & Platt 1989; White 1979). Despite evidence of periodic catastrophic damage to forest canopies con-

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

siderably north of 40° (Bormann & Likens 1979; Dunn *et al.* 1983; Foster 1988; Henry & Swan 1974), studies in northern forests have tended to focus on gap-phase dynamics (e.g., Poulson & Platt 1989; Runkle 1979; Williamson 1975). In contrast, recent studies of southeastern forests, especially those in the coastal plain, have focussed more on the effects of larger-scale canopy disturbance, and specifically hurricane damage (e.g., Glitzenstein *et al.* 1986; Harcome & Marks 1983; Platt & Schwartz 1990; but see Ware *et al.* 1993).

Guilds of species form relatively discrete but transitory strata (defined here as shrubs, subcanopy, canopy, and lianas) in temperate hardwood forests (Terborgh 1985). While vertical strata cannot be unambiguously defined (Harcombe & Marks 1977), a combined assessment of growth form, current size class, and species' potential stature can be used to categorize the plants of these seasonal forests (Smith 1973; Terborgh 1985). Species populations may be loosely aggregated across forests (Platt & Hermann 1986; Platt & Schwartz 1990), just as relative stratification among species may be consistent (Harcombe & Marks 1977; Terborgh 1985). Studies of interactions among species assemblages and between the canopy and understory have suggested that understory dynamics may influence canopy composition. Survival and growth of these juveniles trees in gaps has been postulated as the proximate and ultimate cause of spatial pattern of canopy trees (Platt & Schwartz 1990; Poulson & Platt 1989; Williamson 1975). However, the patterns of dispersion and vertical stratification of species in warm- versus cool-temperate forests have not been explicitly compared.

To explore the idea of differential subcanopy pattern and diversity in response to canopy disturbance, we compared the demography, composition, vertical structure and spatial dispersion of woody understory plants in relation to the canopy trees in four temperate forests. At each site, one aggregate hectare was sampled in 16 replicates of randomly located non-contiguous plots of 25 by 25 m. The variables measured and analyzed, for all woody plants $\geq$1 cm dbh, included size, stratum category, spatial location, and species. Diversity within and among the strata, basal area, density and dispersion were analyzed, with sites treated as replicates within latitude. The analyses were focused on latitudinal differences between warm and cool temperate forests in three areas of specific interest: 1) demographics of four vertical stratum categories; 2) species diversity both within plots and among sites; and 3) pattern of spatial dispersion of the understory (both shrub layer plants and subcanopy trees) and lianas relative to the canopy trees.

Methods

Study sites

Four forest sites were selected, two each located at approximately 40° and 30° north, on either side of the Appalachian divide that bisects the eastern US (Fig. 1) (See Braun 1950). The sites are: Hueston Woods, Preble County, Ohio; Black Rock Forest, Orange County, New York: Tunica Hills, West Feliciana Parish, Louisiana; and Titi Hammock, Thomas County, Georgia. All sites are mixed-species eastern deciduous forests, with *Fagus grandifolia* a dominant canopy species. The southern forest sites are not recent hardwood "disclimax" forests that, with fire suppression, have replaced pine savanna in much of the southeast (see Ware *et al.* 1993). All four sites have more or less sloping terrain and variable soil moisture gradients. While no American forest can be said to have been completely unaffected by human incursion, all four sites have long-term protected status. Each forest has been the site of previous studies: Vankat *et al.* (1975), Canham *et al.* (1990) (Hueston Woods); Raup (1938, 1964), Lorimer (1980, 1985) (Black Rock); Delcourt & Delcourt (1974) (Tunica Hills); Blaisdell *et al.* (1974), Platt & Schwartz (1990) (Titi Hammock).

Climatic conditions are similar for the paired sites at each latitude. Average monthly precipitation does not vary markedly at any site; however, annual rainfall is greater at 30° than at 40° N (Fig. 2). Frost-free periods at 30°, about 9 months, are 50% longer than those at the northern sites (NESC 1992, and see Runkle 1985; Fig. 2). Periodic canopy disturbance by hurricanes or other windstorms affect all four sites, but with widely differing estimated return times. These are on the order of many decades to centuries at 40° N (Bormann & Likens 1979; Foster 1988; Henry & Swan 1974; Simpson & Lawrence 1971), and two decades or less at 30° along the Gulf Coast (Neumann *et al.* 1987; Simpson & Lawrence 1971).

Hueston Woods

This forest is a remnant of the once extensive beech-maple-oak forests of southern Ohio (see Braun 1950), now reduced to scattered islands of mixed hardwoods separated by vast agricultural clearings (Table 1). Pri-

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

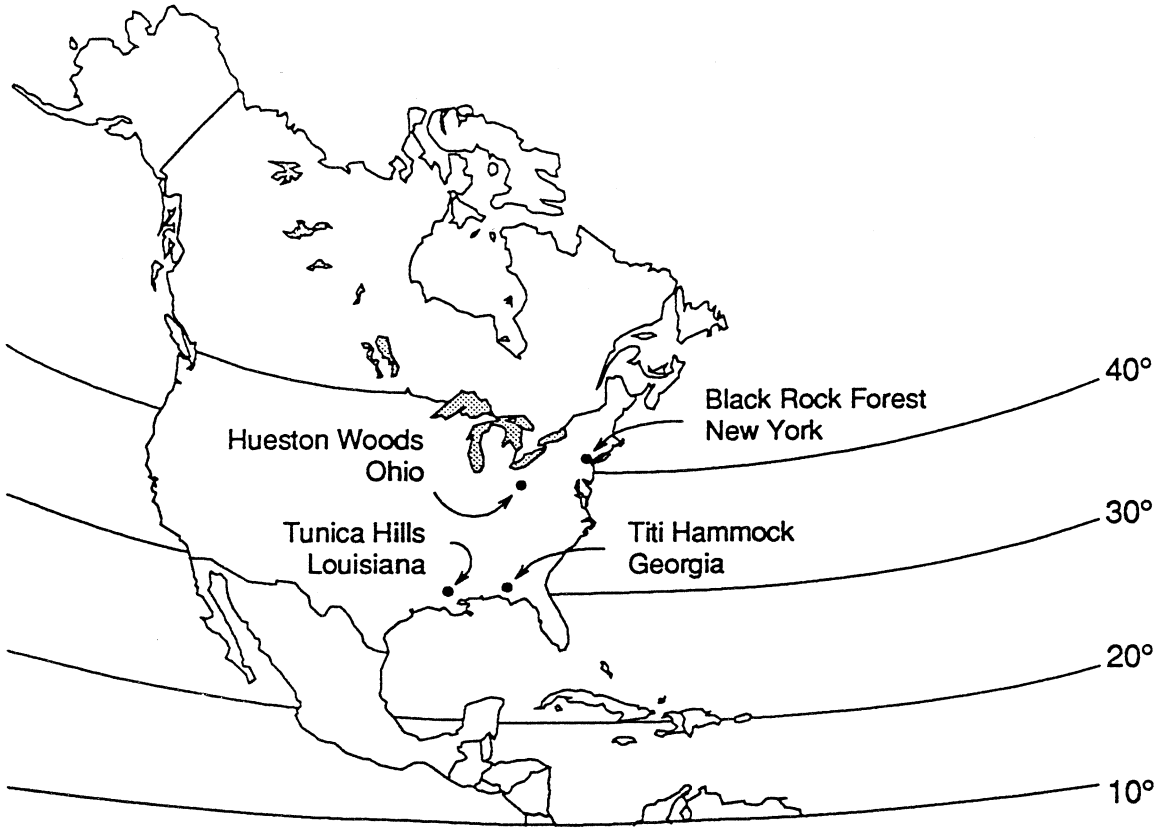

Fig. 1. Study site locations at 30° and 40° north latitude, in eastern North America.

vately held from 1797 until 1941, when it became a state park, Hueston Woods has had only limited selective cutting that ended in the 1920s (Vankat *et al.* 1975; J. Udstuen, pers. comm.). Organic soil overlies clay on flat-topped ridges that are separated by moderately steep-sided (angles to 60%) ravines that slope toward the impoundment of Acton Lake; rapid erosion and small landslides are common in the ravines (Vankat *et al.* 1975). Annual rainfall is 900 mm yr^{-1} and somewhat heavier in the growing season than in the winter months (NESC, Cincinnati station, 1992) (Fig. 2.2). No specific data were available for periodicity of cyclonic windstorms, or for occurrence of natural fire.

The forest has an irregularly closed canopy dominated by *Fagus grandifolia, Quercus velutina, Q. rubra, Acer saccharum* and *A. nigrum* (Vankat *et al.* 1975). The dense understory is comprised mostly of juveniles of canopy species, but includes rosaceous shrubs and sub-canopy trees such as *Cornus florida* and *Asimina triloba*; less abundant species (e.g., *Platanus occidentalis* and *Maclura pomifera*) occur along drainages.

Black Rock Forest

The forest is located on upper slopes and valleys of glaciated granitic hills on the west side of the Hudson River, just north of West Point, New York (Table 1). These Hudson Highlands are an extension of the Appalachian ridge of northern New Jersey (Raup 1938, 1964). The forest, in private ownership since colonial times, was intermittently exploited for timber, especially in the nineteenth century, before coming under the protective management of Harvard Forest in 1950 (Raup 1964). It is now held by a private consortium for conservation and research. Some areas of even-aged canopy indicate either that relative equilibrium has not been fully reestablished (Lorimer 1981; C. Canham pers. comm.) or that periodic large-scale disturbances have precluded all-age stand development (Raup 1964). Soils are thin, with weathered and glaciated granitic outcroppings; slopes are stable

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

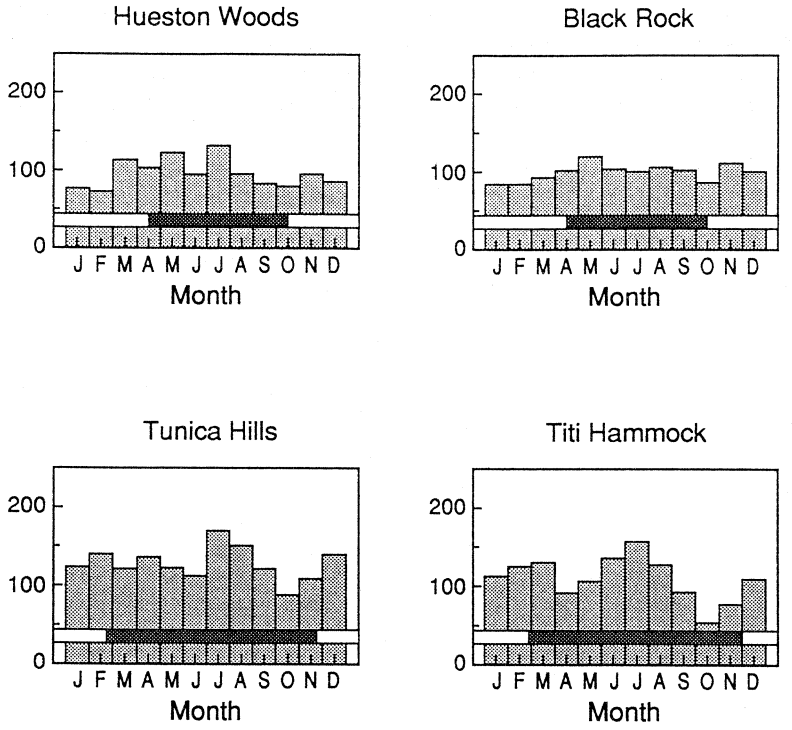

Fig. 2. Average monthly precipitation (mm) at each site. Dark bars indicate average annual frost-free period. (National Economic, Social, and Environmental [NESC] data bank, 1992, for Cincinnati, OH, West Point, NY, St. Francisville, LA, and Thomasville, GA).

Table 1. Location and physiognomic characteristics of the sites. Elevations are approximate for the sample plots. Disturbance regime details and all citations are given in the text.

Site	Latitude/ Longitude	Substrate	Elevation (m)	Precipitation (mm yr^{-1})	Disturbance		
					Hurricane	Fire	Landslide
Hueston Woods, Ohio, USA	39°30′N 84°45′W	humus, clay	300	900	rare	occasional	occasional
Black Rock Forest New York, USA	41°24′N 74°W	granitic, glacitated	300	1170	occasional	occasional	rare
Tunica Hills, Louisiana, USA	30°50′N 89°30′W	loess	30	1400	frequent	rare	frequent
Titi Hammock Georgia, USA	31°05′N 84°20′W	oceanic sediments	80	1370	frequent	frequent	rare

(Raup 1938). Rainfall averages 1170 mm yr^{-1} and is less seasonal than at any other site (NESC West Point, 1992) (Fig. 2). Atlantic hurricanes have been estimated to recur at intervals of 85 years in the Hudson River Valley region (Simpson & Lawrence 1971; also see Bormann & Likens 1979; Foster 1988; Henry & Swan 1974) (Table 1). The natural fire periodicity is not known (Raup 1964).

The distributions of tree species vary with aspect, elevation, and depth of soil and represent a transition from central Appalachian hardwoods to slightly more boreal forest (Braun 1950). The dominant species

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

include *Quercus prinus, Q. rubra*, and *Q. velutina* on upper slopes and *Acer saccharum, A. rubrum, Fagus grandifolia*, and *Carya* species on lower slopes. *Tsuga canadensis* occurs in deep ravines (Brown 1975; Raup 1938). Understory growth is sparse, except along the drainage courses, in recent gaps, and near rock outcrops. Species that typically occur in larger gaps include *Tilia americana, Populus grandidentata*, and *Fraxinus americana*; understory shrubs are dominated by *Vaccinium* spp. (Raup 1938). Although small vines occur in openings, large lianas are uncommon.

Tunica Hills

"Magnolia Glen" is a Louisiana Nature Conservancy preserve located on the east bank of the Mississippi River, in the Tunica Hills of West Feliciana Parish (Table 1). Rainfall is 1400 mm per year with slightly less monthly rainfall in the fall (NESC St. Francisville 1992) (Fig. 2). Hurricanes occur relatively frequently (most recently Hurricane Andrew in 1992), with an average return interval of 17 years (Neumann *et al.* 1986; Simpson & Lawrence 1971). Other disturbance is local: very steep slopes of loess soil result in frequent small landslides. No fire history data exist for the site (see Delcourt & Delcourt 1974).

The site's ridges and ravines support a very well-developed mixed hardwood forest with a canopy dominated by *Fagus grandifolia, Magnolia grandiflora, Liquidambar styraciflua*, and several *Carya* and *Quercus* species. The subcanopy species include *Ilex opaca, Cornus florida, Lindera benzoin, Styrax* spp., as well as many smaller deciduous shrubs (Delcourt & Delcourt 1974). The ridge-tops have been invaded by *Pinus taeda* after hardwood timbering early in the 20th century, but the lower slopes and drainage bottoms were never logged and have remained in hardwood cover (D. Pashley, pers. comm.).

Titi Hammock

The forest is located on the Georgia/Florida state line in a shallow drainage surrounded by longleaf pine *(P. palustris)* savanna, a typical formation of the southeastern coastal plain (Blaisdell *et al.* 1974; Platt & Schwartz 1990). The hammock is privately owned as part of Springhill Plantation, and is managed by the Georgia Nature Conservancy under a conservation easement. Soils are eroded marine sediments exposed since the Miocene and well-drained except in drainage bottoms; no landslides occur on the shallow slopes (Blaisdell *et al.* 1974). Precipitation is 1370 mm yr^{-1}, with a marked dry period in the fall and a lesser one in the spring (NESC Thomasville, GA, 1992) (Fig. 2). Hurricanes (most recently Hurricane Kate in 1985), frequently open the canopy, especially at higher elevations in the hammock; hurricane recurrence is estimated at 14 years (Simpson & Lawrence 1971). Regular fires in the savannah have penetrated the hammock as groundfire, further widening the spectrum of edaphic conditions (Blaisdell *et al.* 1974; W.J. Platt unpub. data).

A sharp elevational gradient is reflected in the changing species assemblages from the wet bottom *(Nyssa* spp., *Magnolia virginiana)* to the savannah edges (*Quercus* spp.). *Fagus grandifolia, Magnolia grandiflora*, and an array of other hardwoods share canopy dominance; *Pinus glabra* and *P. taeda* are also present (Platt & Schwartz 1990). The subcanopy is dominated by five species: *Cornus florida, Ostrya virginiana, Ilex opaca, Symplocos tinctoria*, and *Carpinus caroliniana* (Platt & Schwartz 1990). The understory contains many shrub species, both temperate and subtropical (see Quigley 1994 for detailed list), and occasionally dense thickets of juveniles of canopy species, and semi-woody vines.

Field procedure

At each site a transect of ± 3 km was established through representative forest. Along the transect sixteen 25 by 25 m plots (1 ha total) were selected randomly from about 30 non-contiguous potential plots.

Within each plot, each woody plant ≥ 1 cm dbh was marked using sequentially numbered aluminium tags. On plants with multiple stems, only the largest stem was tagged. Number of stems per plant, diameter at breast height (dbh) measured at 1.4 m, species, and notes on phenology or damage condition (e.g., leaning or senescent) were recorded for each plant. The location of each plant was mapped using methods described in Quigley & Slater (1994). Each plant was assigned a stratum category based on the height of the tallest stem: 1) shrub layer, less than 2.5 m tall; 2) subcanopy, more than 2.5 m but with crown all or partly below other trees; 3) canopy, with crown unobstructed; or 4) liana, a non-self-supporting woody climber).

Taxonomic nomenclature follows Elias (1985) for the northern sites and Radford *et al.* (1981) for the southern sites; for Louisiana species not found in the range covered by Radford *et al.* (1981) see Clewell (1985). Voucher specimens were collected for each species and deposited in the Louisiana State University

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Herbarium. Appendix 1 is a tabulation of the numbers of species occurring per family per site.

Analysis

Demographic and pattern data were analyzed separately. Whenever parametric analyses were used, all data were first tested by UNIVARIATE procedure for normal distributions (using the residuals) and homoscedasticity (using residuals plotted against predicted values). Distributions not meeting the assumptions of ANOVA were transformed until the assumptions were met (Sokal & Rohlf 1981; SAS 1993).

Replicated data

A split-split plot ANOVA (Sokal & Rohlf 1981) based on 16 plot replicates per site was used to analyze basal area, plant and stem density, and species numbers and species proportions/stratum. Fixed effects were latitude and stratum, and random effects were site (within latitude) and plot (within site). Basal area data were log-transformed, while plant density and stem density data sets were square-root transformed. Data for numbers of species per stratum, as well as for proportions of site total species per stratum, did not require transformation. Null hypotheses were that no differences in plot means existed between latitudes, between sites within latitudes, or among strata. Two sets of *a priori* orthogonal contrasts were run with each ANOVA (Table 2). The first set tested the single fixed effects: latitude was tested with site(latitude) as the error term; stratum was tested with plot(site(latitude)) as the error time. Effects of interaction between stratum and latitude were also tested with plot(site(latitude)) as the error term.

Species area curves were generated for each site following methods of Platt & Schwartz (1990). For each site, curves based on observed distributions of species among the 16 plots were generated by selecting the plots in random order and obtaining the cumulative quantity of species with increasing area. This process was repeated 10 times to obtain a mean observed distribution. The resulting curve was then compared to a predicted curve, created by 1,000 Monte Carlo simulations in which the same numbers of species (in the same relative abundances) were independently distributed among the plots. Confidence intervals were constructed that contained 95% of the cumulative species expected within areas of increasing size. Linear regressions were fitted to the observed (means) species/area curves, using the 10 runs (per 16 plots) to generate the point scatter. These regression data were tested by ANOVA to determine differences between latitudes and among sites.

Table 2. Orthogonal contrasts of strata and latitude versus stratum used in the ANOVAs of replicated data, based on 16 plots per site.

Error term is plot (site(lattitude))
Stratum
1+2+3 vs 4
1 vs 2+3
2 vs 3
Latitude × stratum
(40° vs 30°) × (1+2+3) vs 4
(40° vs 30°) × 1 vs (2+3)
(40° vs 30°) × 2 vs 3

Non-replicated data

Two data sets, abundance by species rank and frequency by size class, were comprised of combined data for each site rather than individual plot replicates. Frequencies of plants within 2 cm dbh incremental size classes were log-transformed and plotted against log-transformations of size classes. Species dominance was graphed as log abundance of species (regardless of stratum or size class) plotted against that species' rank. Linear regressions were fitted to the resultant curves for both sets of data. Size class data sets were tested for differences by ANOVA, with a nested model of sites within latitude. Log of species abundance was tested by ANCOVA for differences between latitudes and among sites, with species rank as the covariant; assumptions of the 2-slope model were that slopes were unequal between the latitudes, and not equal to 0.

Spatial dispersion

Vertical structure was examined in two ways. First, locations of crowns of plants of individual species at each site were tabulated by vertical position. These data were tested by ANOVA, nesting site (random effect) within latitude (fixed effect), with a null hypothesis of no difference between latitudes. Second, species that occurred exclusively in one stratum were identified for non-statistical comparison of relative exclusivity

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

(layering) of species among strata at each individual site.

Horizontal pattern was examined using nearest neighbor distances computed from Cartesian coordinates (Clark & Evans 1954). Nearest neighbor distances (y) were calculated for all woody plants based on stratum assignments. Five combinations of inter-stratum nearest neighbor distances – shrubs, subcanopy trees, canopy trees, lianas, and shrub layer/subcanopy combined – were tested for deviation from random distribution relative to canopy trees.

The first test of spatial pattern (deviation from random distribution) used the algorithm developed by Donnelly (1978) based on observed versus expected distance of nearest neighbors within individual plots. "Edge effects" can be ignored in this method so that no data are sacrificed; see Diggle (1983) for justification. In the determination of randomness, the distribution of y is approximately normal, with mean and variance:

$$E[y] = \frac{1}{2}\left[\frac{A}{n}\right]^{1/2} + \frac{\left[0.051 + \frac{0.0421}{\sqrt{n}}\right]}{n} l(A) \quad (1)$$

$$Var[y] - 0.070n^{-2}A + 0.037[n^{-5}A]^{1/2}l(A) \quad (2)$$

where A is plot area, $l(A)$ is the length of the plot boundary, and n the number of plants under comparison in each individual plot. When compared to the appropriate "z" statistic, significantly small or large values of the average y for each plot indicate aggregation or uniformity, respectively, of spatial dispersion (Diggle 1983). In this case, there were 16 z_i statistics for each site. To test the null hypothesis of no aggregation at each site a Z test was done by considering that, under H_0, z_i is approximately $N(0, 1)$, $i = 1, ..., 16$. Hence,

$$\bar{z} - \frac{\Sigma z_i}{16} \sim N\left(0, \frac{1}{\sqrt{16}}\right) \quad (3)$$

and our Z test statistic is

$$Z = \frac{\bar{z}}{1/4} - 4\bar{z}. \quad (4)$$

The critical value of Z, for significance at $\alpha = 0.05$, is 1.96.

Nearest neighbor distances for each categorical comparison were tested by ANOVA to examine differences between latitudes, using a model of (random) sites nested within fixed effects of latitude. Because numbers of plants varied among the 16 plots per site, the dependent variable was z_i (which was already standardized for plot density), defined by:

$$z_i = \frac{y - E(y)}{\sqrt{var(y)}} \quad (5)$$

where y was the average nearest distance per plot for each categorical comparison. For each test, the null hypothesis was that of no difference in plot means of inter-categorical distance, between latitudes or among sites.

Comparison of observed occurrences of nearest neighbors to expected distances based on random distribution of all plants within each plot was used to identify negative, positive, or non-significant correlations among stems of canopy and understory pairs of plants. Inter- and intraspecific dispersion were tested among canopy and understory stems, combining shrub layer and subcanopy as a single category and excluding lianas. Methods of Glitzenstein *et al.* (1986) were followed. For species populations with sufficient sample sizes ($n \geq 20$ for canopy trees, $n \geq 25$ for understory stems), inter- and intraspecific combinations were tested. A matrix comparison was performed (of single classification x^2 tests) of expected versus observed proximity values of small stems of given species to canopy trees of given species. The equation

$$f' = \left[\frac{L}{N}\right] S \quad (6)$$

expresses the expected (f') occurrence (when combined at random) of a given species in the canopy as the nearest neighbor to a small stem of the same or another species, where S is the number of small stems, L is the number of large stems of the species in question, and N is the total number of canopy stems of all species. A second test, using the same algorithm, was run to detect non-random spatial dispersal among only canopy trees and conspecific juveniles in the shrub layer and subcanopy.

Results

Demography/stand characteristics

Woody biomass of the forests, expressed as plot mean basal area, primarily a result of canopy and subcanopy contributions, did not differ between the two latitudes ($F_{1,2} = 3.34$, $P = 0.21$). Values ranged from 28 m^2 ha^{-1} at Black Rock to 36 m^2 ha^{-1} at Titi Hammock

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Table 3. Stand structure of the sites. Standard errors of densities and basal area are based on 16 plot replicates per site. Species and families are listed in Appendix 1. Canopy and occasional emergent crown heights are approximate

Site	Plants ha^{-1}	Stems ha^{-1}	Species (Families)	Canopy height (emergent) (m^2)	Basal area (m^2)
Hueston Woods	2537 ± 139	2823 ± 158	44 (19)	20 m (25 m)	32.4 ±3.8
Black Rock	1402 ± 87	2153 ± 230	44 (21)	20 m (25 m)	28.0 ±3.0
Tunica Hills	1674 ± 123	2520 ± 203	68 (32)	25 m (30 m)	29.1 ±8.5
Titi Hammock	1794 ± 201	2792 ± 324	68 (32)	25 m (30 m)	35.5 ±5.3

(Table 3). Although basal area among plots within sites was not significantly different, sites differed within latitude (Tables 3, 4).

Individual stratum contributions to basal area differed significantly from each other (Table 4), but with little difference between the two latitude (Fig. 3). Canopy trees contributed 84.2% to 88.9% of total basal area at three sites, but only 76.5% of the total basal area at Tunica Hills. Although proportional contributions of different strata within each site varied somewhat, especially between canopy and subcanopy, stratum basal area for shrubs, subcanopy, and canopy did not differ between 30° and 40°. At 40°, the shrub layer contributed 0.5% or less of total basal area. At 30°, shrubs contributed less than 0.8% of the total basal area. Subcanopy contribution ranged from 10% of basal area at Hueston Woods to 21% at Tunica Hills.

Interaction of latitude and stratum in basal area was significant (Table 4). However, this was a result solely of the increase in lianas at 30° – basal area of the other strata showed no interaction with latitude (Fig. 3). Liana basal area at Tunica was 1.5% of the total, twice that of the shrub layer. At the other three sites, basal area of shrub layer stems was greater than that of lianas.

Relative density of individual plants and of total stem counts varied more among the sites than between latitudes. Numbers of woody plants ranged from 1400 plants ha^{-1} at Black Rock to 2500 plants ha^{-1} at Hueston Woods, while numbers of stems ranged from 2150 to 2800 at the same sites (Table 3). There was no significant difference between latitudes in plant density (Table 5) or in stem density (Table 6). Despite the lack of difference among plots within sites in plant or stem density, both plant and stem density between sites within latitudes were significantly different (Tables 5, 6).

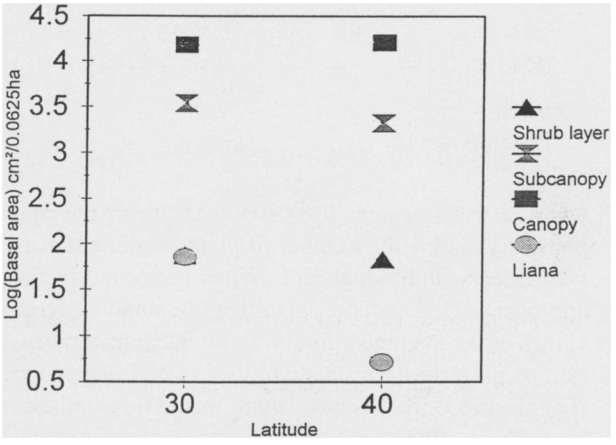

Fig. 3. Basal area per stratum by latitude, expressed as plot means of log transformed data.

The plant and stem densities of individual strata varied independently of each other with respect to latitude (Fig. 4). Subcanopy and canopy tree density was greater at 40° N, while shrub layer and liana density was greater at 30°. Comparisons of individual stratum densities were significantly different at every level (Tables 5, 6). The interactions of stratum with latitude were also significant. Although patterns of rel-

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Table 4. Split-plot ANOVA table of the effects of latitude and stratum on basal area measured as the log of plant basal area per 1/16 ha. Main effect was latitude, with a split plot effect of site and a split-split plot effect of stratum. Latitude and strata were fixed; site and plot replicates were random. Stratum legend: 1) shrub layer; 2) subcanopy; 3) canopy; 4) liana. (*) denotes statistical significance at $\alpha - 0.05$; $R^2 = 0.91$. Dependent variable: basal area

Source	df	Mean square	F	P
Latitude	1	7.59	3.34	0.2092
Site(latitude)	2	2.27	14.04	0.0001*
Plot(Site(Latitude))	60	0.16	0.78	0.8612
Stratum	3	117.22	568.95	0.0001*
(1+2+3) vs 4	1	168.75	819.01	0.0001*
1 vs (2+3)	1	164.23	797.09	0.0001*
2 vs 3	1	18.70	90.74	0.0001*
Latitude × Stratum	3	24.81	22.71	0.0001*
(40 vs 30) × (1+2+3) vs 4	1	13.57	65.89	0.0001*
(40 vs 30) × 1 vs (2+3)	1	0.03	0.12	0.7279
(40 vs 30) × 2 vs 3	1	0.44	2.12	0.1471
Stratum × Plot(Site(Latitude))	186	0.21		
Total	255			

Table 5. Split-plot ANOVA table of the effects of latitude and stratum on plant density measured as the square root of number per 1/16 ha. Main effect was latitude, with a split plot effect of site and a split-split plot effect of stratum. Latitude and strata were fixed; site and plot replicates were random. Stratum legend: 1) shrub layer; 2) subcanopy; 3) canopy; 4) liana. (*) denotes statistical significance at $\alpha = 0.05$; $R^2 = 0.80$. Dependent variable: plant density

Source	df	Mean square	F	P
Latitude	1	0.03	0.02	0.9797
Site(Latitude)	2	38.44	15.61	0.0001*
Plot(Site(Latitude))	60	2.46	1.28	0.1090
Stratum	3	353.99	183.96	0.0001*
(1+2+3) × 4	1	669.67	348.02	0.0001*
1 × (2+3)	1	10.01	5.20	0.0237*
2 × 3	1	382.29	198.67	0.0001*
Latitude × Stratum	3	39.33	20.44	0.0001*
(40 vs 30) × (1+2+3) vs 4	1	74.33	38.63	0.0001*
(40 vs 30) × 1 vs (2+3)	1	42.17	21.92	0.0001*
(40 vs 30) × 2 vs 3	1	1.50	0.78	0.3786
Stratum × Plot(Site(Latitude))	186	1.92		
Total	255			

ative subcanopy and canopy tree densities did not differ between latitudes, lianas and shrub layer density differed inversely to densities of trees (subcanopy and canopy combined) at 40° (Fig. 4, Tables 5, 6).

At all sites, small trees were the most abundant component; frequency decreased as sizes increased. Maximum tree sizes were slightly less than 1 m dbh at all sites (Fig. 5). There were fewer small stems at Black Rock and Tunica than at Hueston and Titi. Hueston, Tunica, and Titi had somewhat more large trees than did Black Rock. Nonetheless, frequency distributions of the sizes were not different either at the two latitudes or for sites within latitudes (Table 7). Both slopes and intercepts of the fitted regression lines were similar among sites and latitudes.

Composition

Despite some canopy trees in common, especially *Fagus grandifolia* and several *Quercus, Carya,* and *Fraxinus* spp., the species composition differed considerably between forests at 30° and 40° N. Numbers of both species and families at 40° north were 65% of those at 30° (Table 3). Families also varied somewhat among forests at the same latitude (see Appendix 1). Hueston Woods and Black Rock each had 44 species, in 19 and 21 families, respectively; Titi Hammock and Tunica Hills each had 68 species, in 32 families each. These latitudinal differences were significant (Table 8).

Species area curves (Fig. 6) reached asymptotes more quickly at 40° than at 30° N, suggesting greater heterogeneity of species distribution in the warm-temperate forest sites. At 30° N there were more species per hectare, and but no more species per 0.0625-ha plot.

ANCOVA of the dominance/diversity curves (log[abundance] by species rank; Fig. 7) showed no significant differences among the means of relative abundance of species at 30° and 40° N (Table 9). However, interaction of species rank with latitude was significant. Tunica and Titi had somewhat more even distributions of species numbers, that is, fewer very com-

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

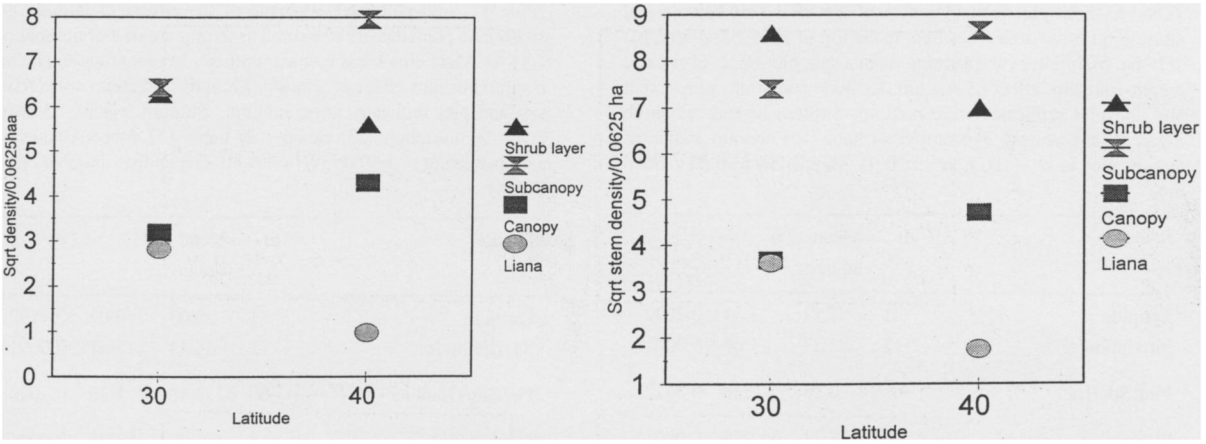

Fig. 4. **a**) Plant density and **b**) stem density (all multiple trunks) by latitude, expressed as plot means of square root transformed data.

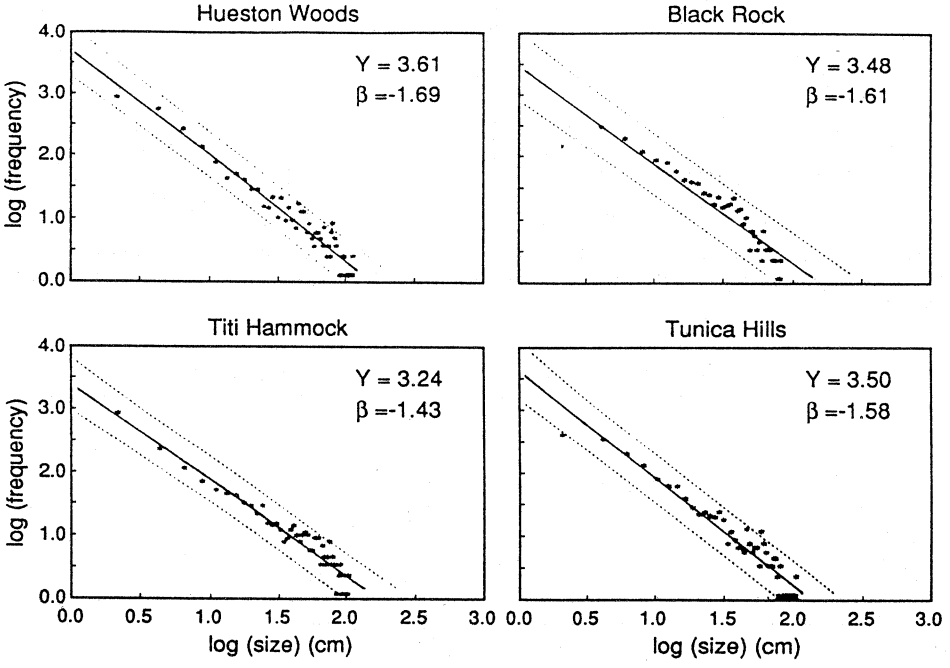

Fig. 5. Log(frequency) of stems in 2 cm size classes graphed as a function of log(mean size) of the size class. The solid line is the best fit of linear regression and dotted lines are 95% confidence intervals.

mon species with large populations, than did the forests at 40° N. Conversely, Hueston and Black Rock had more individual plants in their most common species, and far fewer rarer species, than did the forests at 30° N; the warm temperate forests had significantly more shrub and liana species.

Despite the difference in total numbers of species per latitude based on 1 ha samples, neither numbers of species per stratum nor proportions of species per stratum was significantly different at 40° and 30° N (Fig. 8). Despite significant variation among plots within sites, average numbers of species per stratum within plots were similar between latitudes (Table 10) and between sites within latitude. Likewise, proportions of species per stratum were similar both between sites within latitudes (Table 11) and between latitudes. Proportions of shrub layer species were similar to subcanopy and canopy combined but all other contrasts

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

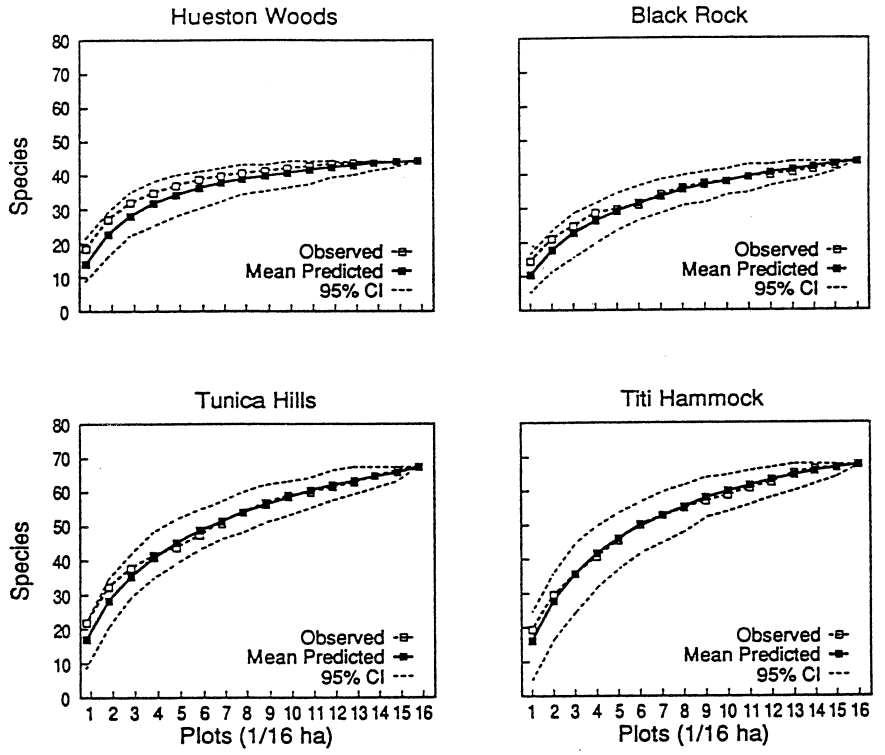

Fig. 6. Species area curves: observed curves are the average of ten random selections of the 16 plots per site; predicted curves are the result of 1000 Monte Carlo runs with each species appearing with the same frequency as actually observed. 95% confidence intervals were constructed for the predicted curves.

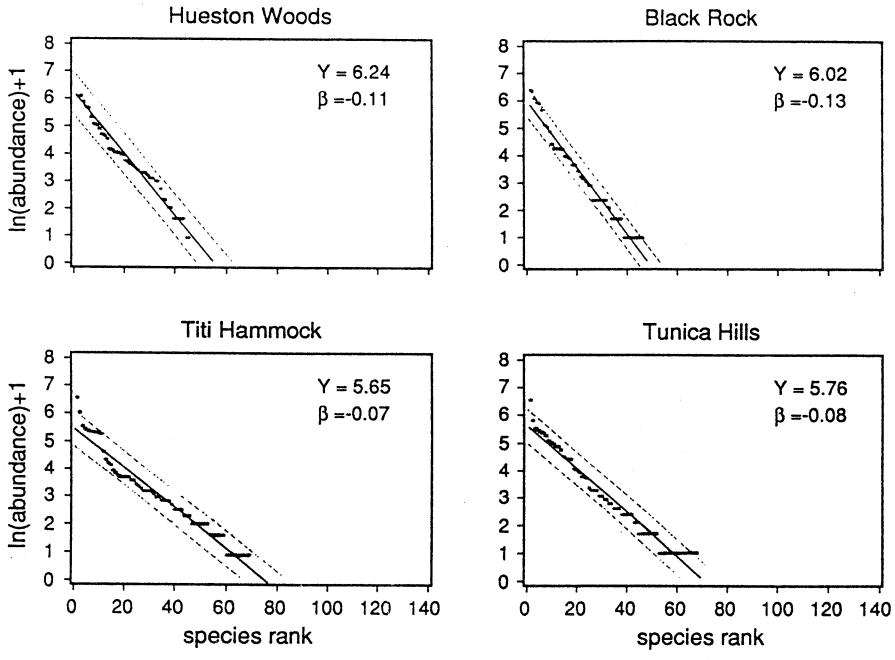

Fig. 7. Log(abundance) + 1 of all species per site graphed as a function of species rank. The solid line is the best fit of linear regression and dashed lines are 95% confidence intervals.

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms



Fig. 8. **a)** Numbers of species, and **b)** proportions of species per stratum by latitude, expressed as untransformed plot means.

Table 6. Split-plot ANOVA table of the effect of latitude and stratum on stem density measured as the square root of number per 1/16 ha, with all multiple trunks per plant included. Main effect was latitude, with a split plot effect of site and a split-split plot effect of stratum. Latitude and strata were fixed; site and plot replicates were random. Stratum legend: 1) shrub layer; 2) subcanopy; 3) canopy; 4) liana. (*) denotes statistical significance at the level of $\alpha = 0.05$; $R^2 = 0.77$. Dependent variable: stem density

Source	df	Mean square	F	P
Latitude	1	9.77	0.58	0.5266
Site(Latitude)	2	16.90	3.90	0.0255
Plot(Site(Latitude))	60	4.33	1.37	0.0584
Stratum	3	506.49	160.19	0.0001*
(1+2+3) × 4	1	909.81	287.75	0.0001*
1 × (2+3)	1	124.22	39.29	0.0001*
2 × 3	1	485.44	153.53	0.0001*
Latitude × Stratum	3	52.50	16.60	0.0001*
(40 vs 30) × (1+2+3) vs 4	1	74.30	23.50	0.0001*
(40 vs 30) × 1 vs (2+3)	1	82.92	26.23	0.0001*
(40 vs 30) × 2 vs 3	1	0.28	0.09	0.7677
Stratum × Plot(Site(Latitude))	186	3.16		
Total	255			

Table 7. ANOVA of latitudinal difference of square root transformed log(frequency) by log(mean size) for non-replicated site data sets. Dependent variable: log(frequency)

Source	df	Mean square	F	P
Latitude	1	0.17	0.49	0.5558
Site(Latitude)	2	0.35	1.74	0.1780
Error	181	0.20		
Total	184			

Table 8. ANOVA of latitudinal difference of site total numbers of species, with sites as replicates within latitude, and plots replicated within sites. Dependent variable: #species/plot

Source	df	Mean square	F	P
Latitude	1	119.63	4.81	0.0294*
Site(Latitude)	2	43.99	1.77	0.1730
Plot(Site × Latitude)	60	14.00	0.56	0.9948
Error	192	24.85		
Total	255			

of species numbers and proportions among strata were significantly different (Tables 10 and 11). Canopy and subcanopy species differed from each other, as did the liana numbers compared to all other strata (Fig. 8a). In numbers of species per stratum, individual plots differed significantly (Table 10); however, proportions of species per stratum were the same for all plots within sites within latitudes (Table 11). In addition, since number of species per 0.0625-ha is not different between latitudes, but the total numbers of species

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Table 9. ANCOVA of latitudinal difference of square root transformed log(abundance) of the species by rank for non-replicated site data sets. (Model does not assume equal slopes.) Error for latitude is site(latitude). $R^2 = 0.95$. Dependent variable: log(abundance). Covariant: species rank

Source	df	Mean square	F	P
Rank	1	36.48	5554.85	0.0001*
Latitude	1	0.10	0.26	0.6583
Rank × Latitude	1	1.29	195.98	0.0001*
Site(Latitude)	2	0.38	58.29	0.0001*
Error	217	0.01		
Total	222			

Table 10. Split-plot ANOVA table of the effects of latitude and stratum on species composition measured as the number of species per stratum per 1/16 ha. Main effect was latitude, with a split plot effect of site and a split-split plot effect of stratum. Latitude and strata were fixed; site and plot replicates were random. Stratum legend: 1) shrub layer; 2) subcanopy; 3) canopy; 4) liana. (*) denotes statistical significance at $\alpha = 0.05$; $R^2 = 0.75$. Dependent variable: number of species/stratum

Source	df	Mean square	F	P
Latitude	1	119.63	2.72	0.2409
Site(Latitude)	2	43.99	3.14	0.0503
Plot(Site(Latitude))	60	14.00	1.79	0.0017*
Stratum	3	947.33	121.33	0.0001*
(1+2+3) × 4	1	2390.66	306.19	0.0001*
1 × (2+3)	1	34.44	4.41	0.0371*
2 × 3	1	416.88	53.39	0.0001*
Latitude × Stratum	3	158.67	20.32	0.0001*
(40 vs 30) × (1+2+3) vs 4	1	19.06	2.44	0.1199
(40 vs 30) × 1 vs (2+3)	1	374.07	47.91	0.0001*
(40 vs 30) × 2 vs 3	1	82.88	10.62	0.0013*
Stratum × Plot(Site(Latitude))	186	7.81		
Total	255			

Table 11. Split-plot ANOVA table of the effects of latitude and stratum on species composition measured as the proportion of species (present at the site) per stratum per 1/16 ha. Main effect was latitude, with a split plot effect of site and a split-split plot effect of stratum. Latitude and strata were fixed; site and plot replicates were random. Stratum legend: 1) shrub layer; 2) subcanopy; 3) canopy; 4) liana. (*) denotes statistical significance at $\alpha = 0.05$; $R^2 = 0.72$. Dependent variable: proportion of species/stratum

Source	df	Mean square	F	P
Latitude	1	0.10	0.61	0.5166
Site(Latitude)	2	0.16	1.31	0.2771
Plot(Site(Latitude))	60	0.12	0.00	1.0000
Stratum	3	11689.60	137.14	0.0001*
(1+2+3) × 4	1	31301.30	367.22	0.0001*
1 × (2+3)	1	15.44	0.18	0.6709
2 × 3	1	3751.95	44.02	0.0001*
Latitude × Stratum	3	1978.76	23.21	0.0001*
(40 vs 30) × (1+2+3) vs 4	1	1071.16	12.57	0.0005*
(40 vs 30) × 1 vs (2+3)	1	4380.75	51.39	0.0001*
(40 vs 30) × 2 vs 3	1	484.38	5.68	0.0181*
Stratum × Plot(Site(Latitude))	186	85.24		
Total	255			

were much greater at 30°, one may infer greater spatial homogeneity at 40°, as illustrated by the species area curves (Fig. 6).

For both species numbers and proportions, the interaction of stratum with latitude was significant (Fig. 8). Only numbers of liana species did not change relative to the changes in all other strata between latitudes (Table 10). Canopy tree species were significantly greater at 40°, while the subcanopy did not change. However, increases in local diversity at 30° N were not a result of canopy plus subcanopy increases at the plot level.

At 40° N the subcanopy contained more species than any other stratum; at 30° N, however, the shrub layer was the most speciose stratum (Table 12). In three forests, about 50% of all species were represented as canopy trees; at Titi, canopy tree species were only 30% of total species. Liana species at 30° N were three times the number (and twice the proportion of total species) of lianas at 40° N.

Species present in only one stratum were more numerous at 30° than at 40° N (Table 12), particularly in the understory. In both sites at 40° north, only 3 species occurred exclusively in the shrub layer, compared to 10 at Tunica and 17 at Titi. Also included in the shrub layer and subcanopy counts at 30° N were several juveniles of potential canopy trees that were

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

not represented as adults. The subcanopy, in contrast, had almost equal numbers of exclusive species in the north to those in the south: 4 and 5 at Hueston and Black Rock as opposed to 5 and 3 at Tunica and Tit. The numbers of exclusively canopy species reflected neither of these trends (Table 12, column 6). Number of species occurring only as canopy trees was 3 at Hueston Woods, 6 at Black Rock, 8 at Tunica, and only 2 at Titi. The major source of increased diversity in forests at 30° over 40° N was in the shrub layer and liana species.

Spatial dispersion

Patterns of dispersion appeared to vary locally among plots and among stratum categories, but analysis showed several consistent trends at both latitudes. Canopy trees were randomly distributed with respect to other canopy trees within plots in all four forests (Table 13). Although the average nearest neighbor distance among canopy trees was somewhat greater at 30° N than at 40°, there was no significant difference between latitudes in nearest neighbor distances once differences in tree density were removed (Table 14a). Similarly, distances were not different between sites within latitudes (Table 14a). Although canopy trees were somewhat less numerous in the warm temperate forests, neither pattern nor relative inter-tree distance was significantly different from those of the northern forests. The actual tree-tree distance was greater at 30° N, but was caused by lower densities of canopy trees, not a difference in spatial pattern.

In the sites at 30° N distances between subcanopy trees and canopy trees were also greater than at 40°. Although subcanopy tree distances relative to canopy stems ranged from 2.76 m to 4.30 m, plot means were not different between latitudes (Table 14c). At all sites subcanopy stem distribution was significantly uniform in relation to the canopy trees (Table 13, column 3).

Shrub layer plants were randomly dispersed relative to canopy trees at Black Rock; at the other sites they were uniformly distributed in relation to canopy trees, at distances ranging from 2.77 m to 4.46 m (Table 13, column 2). Nearest neighbor distances among shrub layer and canopy trees were not different between latitudes (Table 14b), but differed significantly between sites. Combined shrub layer and subcanopy stems were significantly and uniformly distributed in relation to canopy trees (Table 13, column 4). Nearest canopy neighbor distances to understory stems varied from 2.72 m at Black Rock to 4.13 m at Titi, but although mean distances at sites within latitude differed significantly (Table 14d) there was no difference between latitudes.

Spatial dispersion of liana populations relative to canopy trees was the most variable of all strata compared (Table 13, column 5). Lianas were randomly dispersed only at Tunica, where they were also most numerous ($n = 278$ ha^{-1}) and largest in diameter. At Hueston Woods, lianas were uniformly dispersed relative to the canopy, and at Titi and Black Rock the lianas were aggregated relative to the canopy trees. Mean nearest neighbor distances, adjusted for density, were not different between latitudes (Table 14e), but did differ significantly among sites. Lianas also had the most variable of all inter-stratum distances to nearest canopy tree neighbor, ranging from an average of 0.88 m at Black Rock to 3.48 m at Titi Hammock.

Specific associations

Analysis of associations of interspecific pairs between canopy and understory trees did not demonstrate definitive differences between forests at 30° and 40° N. Rather, different interspecific associations at individual sites (see Appendix 2) appeared to reflect local edaphic conditions, particularly those of slope and moisture. In general, fewer than half the species considered to be understory specialists were randomly dispersed without regard to species of nearest canopy tree neighbor. These included *Ilex opaca* (Titi, Tunica), *Lindera benzoin, Ostrya virginiana* (Hueston, Tunica), *Halesia diptera, Styrax grandiflora* and *Symplocos tinctoria* (Tunica), and *Amelanchier sanguinea* (Black Rock). Other subcanopy and shrub layer plants were strongly and positively associated with some canopy species and negatively with others. The most striking of these included *Carpinus caroliniana*, which was positively associated with *Liquidambar styraciflua* at Titi and Tunica, and negatively with all other trees. *Acer saccharum* at Tunica was positively associated with *Fagus grandiflora*, and negatively with all other trees. Two shrub species at Black Rock each had one positive canopy association and were negative for all other trees: *Vaccinium sanguineum* with *Acer rubrum* and *V. corymbosum* with *Quercus prinus*.

Associations of juveniles of canopy species with canopy trees of different species were significantly non-random (Appendix 2). At Titi, both *L. styraciflua* and *M. grandiflora* were positively associated with *Pinus glabra*; juveniles of all species were negatively distributed relative to *F. grandifolia*. At Black Rock,

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Table 12. Number of species appearing in each stratum (all) and number of species appearing exclusively in that stratum (exc)

Site	Total species	Shrub layer		Subcanopy		Canopy		Liana
		all	exc	all	exc	all	exc	
Hueston Woods	44	27	3	33	4	25	3	4
Black Rock	44	20	3	31	5	24	6	3
Tunica Hills	68	37	10	35	5	28	8	11
Titi Hamock	68	50	17	41	3	19	2	8

Table 13. Summary of z statistic tests of deviation from random dispersal among nearest neighbors within the canopy stratum and for other strata relative to canopy trees. Ns (0) = random distribution; negative values indicate aggregation; positive values indicate uniformity of spatial dispersion ($p < 0.05$). Average distance (m) to nearest neighbor (± standard deviation), and the numbers of plants used in each comparison (n) are given

Site	Canopy	Shrub layer	Subcanopy	Shurb and subcanopy	Liana
Hueston	0.32 ns	41.47*	94.28*	174.10*	6.13*
Woods	3.66 ± 0.91	3.29 ± 0.84	3.33 ± 0.82	3.30 ± 0.84	2.98 ± 2.86
	n = 273	n = 840	n = 1348	n = 2188	n = 76
Black	1.01 ns	–5.16 ns	20.78*	38.29*	–8.14*
Rock	3.33 ± 0.82	2.77 ± 0.63	2.76 ± 0.46	2.73 ± 0.43	0.88 ± 0.31
	n = 331	n = 289	n = 776	n = 1065	n = 6
Tunica	0.71 ns	42.54*	50.11*	122.72*	–1.38 ns
Hills	4.81 ± 1.09	4.46 ± 1.24	4.30 ± 1.02	4.35 ± 1.07	3.15 ± 0.77
	n = 166	n = 539	n = 691	n = 1230	n = 278
Titi	1.44 ns	69.64*	51.91*	154.33*	–9.57*
Hammock	4.96 ± 1.03	3.84 ± 1.15	4.06 ± 0.63	4.02 ± 0.68	3.48 ± 2.02
	n = 168	n = 865	n = 704	n = 1569	n = 57

Acer rubrum was positively associated with *Quercus prinus*, and *F. grandifolia* negatively with *A. saccharum*. At Hueston, *Acer nigrum* and *A. saccharum* were negatively associated with *Juglans nigra*, but other species' juveniles were randomly dispersed with respect to *J. nigra*.

Canopy/understory (adult/juvenile) associations within the same species of common dominant trees varied among the different forests. For example, at Titi Hammock, *F. grandifolia* juveniles were negatively associated with conspecific canopy trees, while at Tunica and Black Rock the association was positive, and at Hueston the association was random (not significant). *M. grandiflora* juveniles were not proximate to conspecific adults at Titi, nor were *A. saccharum* saplings near adult maples at Hueston Woods. In general, however, juvenile plants' positions relative to conspecific canopy dominants were either positive or random (rather than negative); such species included *Pinus glabra, Betula alleghensis*, and *Acer rubrum*.

At all four sites, locations of subcanopy trees and shrubs were less likely to be near (or associated with) canopy tree trunks than were canopy tree juveniles of the same or different species. That is, presumptive gaps or interstices among canopy trees tended to be occupied less by juveniles of potential canopy trees than by understory "specialists". However, the patterns of distribution of understory stems were somewhat more random at Hueston Woods (40° N), suggesting a longer

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Table 14. ANOVAs of latitudinal differences of nearest neighbor distances among strata, within 16 replicate plots per site. Latitude is a fixed effect, with random sites nested within latitude. Dependent variable is the z_i of distance between individual plants: the difference between observed and expected distances, divided by the square root of the variance (see methods). $\alpha = 0.05$

Source	df	Mean square	F	P
a) Canopy trees				
Latitude	1	0.17	0.67	0.4996
Site(latitude)	2	0.25	0.25	0.7778
Error	60	1.00		
Total	63			
b) Shrub layer and canopy trees				
Latitude	1	1439	1.98	0.2947
Site(latitude)	2	727.03	5.29	0.0076*
Error	60	137.38		
Total	63			
c) Subcanopy and canopy trees				
Latitude	1	42.47	0.03	0.8756
Site(latitude)	2	1351.00	9.04	0.0004*
Error	60	149.50		
Total	63			
d) Shrub layer, subcanopy, and canopy trees				
Latitude	1	865.50	0.18	0.7132
Site(latitude)	2	4830.04	9.09	0.0004*
Error	58	531.14		
Total	61			
Lianas and canopy trees				
Latitude	1	26.11	1.38	0.3606
Site(latitude)	2	18.88	7.39	0.0014*
Error	58	2.55		
Total	61			

cycle of replacement in that forest than at the other tree.

Discussion

Data from this study suggest that seasonal hardwood forests at different latitudes in eastern North America are similar in many respects. Basal area, overall plant and stem densities, architectural stratification, and, to a somewhat lesser degree, taxonomic composition of the dominant elements, did not change with latitude. Despite significant differences in abundance and density of understory plants (e.g., fewer small stems at Black Rock, and proportionally more at Titi), relative mean size class distributions for canopy trees were also comparable for all sites. Horizontal patterns of dispersion among stratum categories did not differ among the sites or between latitudes. While canopy trees were randomly dispersed at all sites, non-random patterns of dispersal among understory trees, shrubs and lianas (relative to the canopy trunks) were significantly uniform relative to tree trunks. Despite these similarities, however, there were significant, latitude-specific differences in species richness, vertical distribution of species, proportions of subcanopy trees, shrubs, and lianas relative to canopy tree numbers, and of local horizontal patterns of species associations among the sites.

Increased numbers of species at the southern sites were not equally distributed among the four vertical strata. The major source of increased diversity in forests at 30° over 40° N was in shrub layer and liana species. Although Hueston Woods had many juveniles of canopy dominant species and significant populations of subcanopy trees, neither northern site had many shrubs, either in species or number. The understory at 30° N, in contrast, had more juveniles of canopy trees and greater density of subcanopy trees (see Marks & Harcombe 1975; Platt & Schwartz 1990). Titi Hammock had relatively numerous shrub species, and Tunica had high liana diversity. Both these attributes may be related to high frequencies of disturbance (Glitzenstein *et al.* 1986). In the southern forest samples there were juveniles of potential canopy trees (e.g., *Pinus, Carya, Aleurites, Paulownia*, and *Fraxinus*) for which no canopy-sized adults were present. Presence of some of these juveniles may represent a mass effect (local occurrence of species – especially exotics – that will not survive to reproductive age; Shmida & Wilson 1985). The profusion and diversity of lianas at Tunica (and of many smaller uncensused vines at Titi) also suggests continual canopy disturbance in the southeastern forests (see Hegarty & Caballe 1991). It has been suggested that within-gap light levels are more heterogenous but more restricted at higher latitudes (Poulson & Platt 1989). The canopy trees were less dense in the southern forests, resulting in higher understory light levels even without gaps.

The patterns of woody understory vegetation – shrubs, small-statured trees, and the juveniles of canopy dominant species – are palimpsests of past dynamics: current spatial dispersion has been determined by previous cycles of succession or replace-

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

ment (Fox 1977; Glitzenstein *et al.* 1986; Harcombe & Marks 1977; Lorimer 1980; White 1979; Woods 1979). Current patterns are also precursors of the future subcanopy and canopy species assemblages. Harcombe & Marks (1977) have demonstrated a negative association between abundances of overstory and understory species, suggesting that understory species can suppress overstory juveniles (also see Ehrenfeld 1980). Therefore, even assuming widespread and random dispersal of seeds, juveniles of canopy species (regardless of adult overstory location) are not necessarily randomly dispersed (Platt & Hermann 1986).

Prior hypotheses that might account for structural distinctions between northern and southern hardwood forests range from strictly autogenic to primarily abiotic dynamics (see Runkle 1985). On one hand are niche specialization (competitive divergence) hypotheses (Barden 1979; Fox 1977; Harcombe & marks 1977; White 1979; Whittaker 1975); on the other is the predominance of abiotic stand disturbance history (Canham & Marks 1985; Glitzenstein *et al.* 1986; Lorimer 1980; Platt & Schwartz 1990; Raup 1964). While temperate forest gap size is relatively constant (Runkle 1985), understory light levels may be seasonally highly variable (Canham *et al.* 1990). Such variation may be increased by canopy openings not related to treefall gaps, but to thinning of tree limbs and partial defoliation by windstorms (Platt & Hermann 1986). In the southeastern forests, these abiotic disturbance events may supersede gap/phase dynamics as the primary source of opening both for seedling recruitment and for eventual attainment of canopy stature. If so, we hypothesize that such differences are reflected in the spatial and numerical relationships between the canopy and understory species in forests affected by frequent (if not regular) non-catastrophic canopy perturbations (i.e., hurricanes). We have found higher stem density and within-stratum diversity, more randomness of spatial dispersion among species, and less defined physical stratification on species assemblages into vertical layers (see Smith 1973; Terborgh 1985) in southern forests than in northern forests where widespread canopy disturbance infrequently "resets the clock" of successional chronology (Harcombe & marks 1977; Poulson & Platt 1989; Putz & Sharitz 1991; Whittaker 1975).

Interspecific associations of horizontal spatial position were more obvious in the northern forests than in the southern sites, both among canopy tree juveniles and for understory species. Such patterns, coupled with the lack of juveniles of extant canopy species, support the idea of alternation of species in tree by tree replacement in gap-phase canopy openings (Bormann & Likens 1979). The hurricane affected forests at 30°, conversely, had greater vertical mixing and relatively fewer instances of positive interspecific association; this suggests that their spatial distributions may be less a result of specific responses to competitive interaction within gaps as such, than to more or less continual subcanopy recruitment and regeneration irrespective of senescence of adjacent canopy trees.

Despite broad similarity in canopy composition, biomass, and horizontal patterns of dispersion, the warm- and cool-temperate forests are distinctly different in their vertical structure and species distributions. Canopy and subcanopy trees are less dense at 30° N, and the understory shrubs (and saplings) more uniformly dispersed among them. We suggest that frequent, non-catastrophic disturbance to the canopy in the southeastern forests promotes a relatively higher density, diversity, and uniformity of dispersion of the understory: shrubs, juvenile trees, and lianas.

Acknowledgements

For support of the field research at Titi Hammock, many thanks to Jonathan Streich, Alex Levy, and the Georgia Nature Conservancy. Earthwatch (Center for Field Research) and the LSU Department of Botany provided partial support to MFQ for the work at Hueston Woods. For logistic assistance, thanks to Joel Udstuen of the Ohio State Parks and John Vankat of Miami University, Jack Karnig and Philip Ammirato of the Black Rock Forest Consortium, and David Pashley of the Louisiana Nature Conservancy. For field assistance, thanks to Elizabeth Harris, Hergart Quigley, Susan Grace, Terry Thibodeaux, William Odom, and Enrique Reyes. For assistance in statistical analysis, thanks to Raul Macchiavelli and Xinhang Liu.

The comments of three anonymous reviewers greatly improved the manuscript.

References

Axelrod, D. I. 1966. Origin of deciduous and evergreen habits in temperate forests. Evol. 20: 1–15.

Barden, L. S. 1979. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos 35: 16–19.

Blaisdell, R. S., Wooten, J. & Godfrey, R. K. 1974. The role of magnolia and beech in forest processes in the Tallahassee, FL, and Thomasville, GA, area. Proc. Tall Timbers Fires Ecol. Conf. 13: 363–397.

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Bormann, F. H. & Likens, G. E. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Am. Sci. 67: 660–669.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Company, Philadelphia, USA.

Brown, H. P. 1975. Trees of New York State. Dover Publications, New York, NY, USA.

Canham, C. D. 1989. Different responses to gaps among shade-tolerant tree species. Ecol. 70(3): 548–550.

Canham, C. D. & Marks, P. L. 1985. The response of woody plants to disturbance: patterns of establishment and growth, pp. 197–216. In: Pickett & White (eds) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, USA.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A. & White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20: 620–631.

Clark, P. J. & Evans, F. C. 1954. Distance to nearest neighbor as a measure of spatial relationship in populations. Ecol. 35(4): 445–453.

Clewell, A. F. 1985. Guide to the vascular plants of the Florida panhandle. Florida State University Press, Tallahassee, USA.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Christensen, N. L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. Am. Mid. Nat. 97: 176–188.

Delcourt, H.R. & Delcourt, P.A. 1974. Primeval magnolia-holly-beech climac in Louisiana. Ecol. 55: 638–644.

Delcourt, P. A. & Delcourt, H. R. 1987. Long-term forest dynamics of the temperate zone. Ecol. Stud. 63. Springer Verlag, NY, USA.

Diggle, P. J. 1983. Statistical analysis of spatial point patterns. Academic Press, New York, USA.

Donnelly, K. 1978. Simulations to determine the variance and edge-effect of total nearest neighbor distance. In: Hodder, I. (ed.) Simulation Methods in Archaeology, Cambridge University Press, London, UK.

Dunn, C. P., Guntenspergen, G. R. & Dorney, J. R. 1983. Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. Can. J. Bot. 61(1): 211–217.

Ehrenfeld, J. G. 1983. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torr. Bot. Club 107(1): 29–41.

Elias, T. S. 1980. Trees of North America. Van Nostrand Reinhold Company, New York, 948 p.

Foster, D. R. 1988. Disturbance history, community, organization and vegetation dynamics of the old-growth Pisgah Forest, southwestern New Hampshire, USA. J. Ecol. 76: 105–134.

Fox, J. F. 1977. Alternation and coexistence of tree species. Am. Nat. 111: 69–89.

Glitzenstein, J. S., Harcombe, P. A. & Streng, D. R. 1986. Disturbance, succession and maintenance of species diversity in an east Texas forest. Ecol. Monogr. 56(3): 243–258.

Harcombe, P. A. & Marks, P. L. 1977. Understory structure of a mesic forest in southeast Texas. Ecol. 58: 1144–1151.

Harcombe, P. A. & Marks, P. L. 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). Oecologia 57: 49–54.

Hegarty, E. E. & Caballe, G. 1991. Distribution and abundance of vines in forest communities. pp. 313–335. In: Putz, F. E. & Mooney, H. A. (eds) The Biology of Vines. Cambridge University Press, New York, USA.

Henry, J. D. & Swan, J. M. A. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. Ecol. 55: 772–783.

Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecol. 61: 1595–1598.

Lorimer, C. G. 1981. Survival and growth of understory trees in oak forests of the Hudson Highlands, New York. Can. J. For. Res. 11: 689–695.

Lorimer, C. G.1985. Methodological considerations in the analysis of forest disturbance history. Can. J. For. Res. 15: 200–213.

Ludwig, J. A. & Reynolds, J. F. 1988. Statistical Ecology. John Wiley and Sons, New York, USA.

Marks, P. L. & Harcombe, P. A. 1975. Community diversity of coastal plain forests in southern east Texas. Ecol. 56: 1004–1008.

Martin, W. H. 1992. Characteristics of old-growth mixed mesophytic forests. Nat. Areas. J. 12(3): 127–135.

Monk, C. D. 1968. Successional and environmental relationship of the forest vegetation of north central Florida. Am. Mid. Nat. 79(2): 441–457.

National Economic Social, and Environmental (NESC) Data Bank, 1992. NS Climat 098666; Climatic data. UMI/Data Courier.

Neumann, C. J., Cry, G. W., Caso, E. L.& Jarvinen, B. R. 1978. Tropical cyclones of the North Atlantic Ocean, 1871–1977. National Climatic Center, NOAA. Asheville, NC, USA.

Platt, W. J. & Hermann, S. 1986. Relationships between dispersal syndrome and characteristics of populations of trees in a mixed-species forest. pp. 309–321. In: Estrada, A. & Fleming, T. (eds) Frugivores and Seed Dispersal. Junk Publishers, Dordrecht, Netherlands.

Platt, W. J. & Schwartz, M. W. 1990. Temperate hardwood forests. pp. 194–229. In: Myers, R. & Ewel, J. (eds) Ecosystems of Florida. Univ. of Central Florida Press, Orlando, FL, USA.

Platt, W. J. & Strong, D. R. (eds) 1989. Gaps in Forest Ecology. Ecol. 70(3) Special Feature: 535–576.

Poulson, T. L. & Platt, W. J. 1989. Gap light regimes influence canopy tree diversity. Ecol. 70(3): 553–555.

Putz, F. E. & Sharitz, R. R. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, USA. Can. J. For. Res. 21: 1765–1770.

Quigley, M. F. 1994. Latitudinal Gradients in Temperate and Tropical Seasonal Forests. PhD Dissertation, Louisiana State University, Baton Rouge, LA, USA.

Quigley, M. F. & Slater, H. H. 1994. Mapping forest plots: a fast triangulation method for one person working alone. South. J. Appl. For. 18(3): 133–136.

Radford, A. E., Ahles, H. E. & Bell, C. R. 1985. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, USA.

Raup, H. M. 1938. Botanical studies in the Black Rock Forest. Bulletin No. 7. Cornwall-on-the-Hudson, New York, USA.

Raup, H. M. 1964. Some problems in ecological theory and their relation to conservation. J. Ecol. 52 (Supp) March 1964: 19–28.

Runkle, J. R. 1979. Gap phase dynamics in climax mesic forests. PhD. Thesis, Cornell University, Ithaca, NY, USA. 289 p.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecol. 62: 1041–1051.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecol. 63: 1533–1546.

Runkle, J. R. 1985. Disturbance regimes in temperate forests, Chapter 2. In: Pickett, S. & White, P. (eds) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, USA.

Shmida, A. & Wilson, M. V. 1985. Biological determinants of species diversity. J. Biogeog. 12: 1–20.

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Simpson, R. H. & Lawrence, M. B. 1971. Atlantic hurricane frequencies along the United States coastline. NOAA Technical Memorandum, National Weather Service, SR–58. Forth Worth, TX, USA.

Smith, A. P. 1973. Stratification of temperate and tropical forests. Am. Nat. 107(957): 671–683.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry, 2nd edition. W. H. Freeman, San Francisco, CA, USA.

Statistical Analytical Software, SAS Institute, Inc., 1993. SAS For Windows User's Guide. Cary, NC, USA.

Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. Am. Nat. 126(6): 760–776.

Vankat, J. L. 1990. A classification of the forest types of North America. Vegetatio 88: 53–66.

Vankat, J. L., Blackwell, W. H. & Hopkins, W. E. 1975. The dynamics of Hueston Woods and a review of the question of teh successional status of the southern beech-maple forest. Castanea 40: 291–308.

Ware, S., Frost, C. & Doerr, P. D. 1993. Southern mixed hardwood forest: the former longleaf pine forest. pp. 447–493. In: Martin, W. H., Boyce, S. G. & Echternach, A. C. (eds) Biodiversity of the Southeastern United States. John Wiley and Sons, New York, USA.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45(3): 229–299.

Whittaker, R. H. 1975. Communities and Ecosystems, 2nd edition. Macmillan Publishing Co, New York, USA. 387 p.

Williamson, G. B. 1975. Pattern and seral composition in an old-growth beech-maple forest. Ecol. 56: 727–731.

Woods, K. D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. Oikos 33: 31–39.

Appendix 1. Family and species by site

	# of species			
	Hues	Blac	Tuni	Titi
Aceraceae	3	3	3	1
Anacardiaceae	1	1	1	1
Annonaceae	1		1	1
Aquifoliaceae			2	2
Araliaceae			1	1
Arecaceae			1	
Berberidaceae		1		
Betulaceae	2	4	2	2
Bignoniaceae			1	1
Caprifoliaceae	2		3	2
Celastraceae				1
Cornaceae	1	1	1	1
Cupressaceae			1	
Ebenaceae				1
Ericaceae		4		6
Euphorbiaceae				1
Fabaceae	2		1	1
Fagaceae	3	8	8	8
Hamamelidaceae		1	2	2
Hippocastanaceae	1		1	1
Juglandaceae	5	4	5	3
Lauraceae	1	2	1	
Liliaceae	1		1	3
Magnoliaceae	1	1	3	3
Moraceae	2		1	1
Myricaceae			1	1
Nyssaceae		1	1	2
Oleaceae	3	2	3	4
Pinaceae		1		2
Platanaceae	1		1	
Rhamnaceae			1	
Rosaceae	6	5	2	4
Salicaceae	1	1		
Sapotaceae			1	2
Saxifragaceae			2	2
Scrophulariaceae			1	
Styracaceae			2	3
Symplocaceae			1	1
Tiliaceae	1	1	1	1
Ulmaceae	3	1	5	
Verbenaceae			1	1
Vitaceae	2	2	4	3
Total fam	19	21	32	32

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Appendix 2. Spatial distribution of understory (subcanopy) and juveniles of canopy tree species around canopy trees. Tabulated values are differences between observed nearest neighbor frequencies for small stems relative to large stems from randomly expected nearest neighbor frequencies, based on proportion of each species of canopy tree in the site population. Positive numbers indicate more large trees than expected as nearest neighbors; negative numbers indicate fewer large trees than expected. Sample sizes are given in parentheses. For each row, differences from random assortment are tested with a single classification χ^2 test for goodness of fit (Sokal & Rohlf 1981): (*) denotes significance at the level of $\alpha = 0.05$

a) Hueston Woods

Understory species		Canopy trees (N = 258)				χ^2
		Acer sacch. (50)	*Fagus grand.* (35)	*Juglans nigra* (23)	Other trees (150)	
Fraxinus quadragulata	(36)	–2.3	–2.3	–3.0	8.2	8.5 *
Carpinus caroliniana	(27)	–1.9	–0.9	–0.3	3.2	1.7 ns
Lindera benzoin	(43)	0.1	–2.9	–2.6	5.4	4.2 ns
Ulmus rubra	(80)	7.3	–12.7	12.3	–7.0	38.0 **

b) Black Rock

Understory species		Canopy trees (N = 331)								χ^2
		Acer rubrum (69)	*Quercus velut.* (59)	*Betula alleq.* (27)	*Lirio. tulip.* (24)	*Acer sacch.* (24)	*Quercus prinus* (24)	*Fagus grand.* (20)	Other trees (84)	
Amelanchier sanguinea	(28)	1.7	4.0	–2.3	–1.0	1.0	1.0	–1.7	–0.1	8.9 ns
Carpinus caroliniana	(28)	10.2	–5.0	–1.3	–1.0	3.0	–1.0	–1.7	–3.1	31.8 *
Hamamelis virginiana	(193)	–1.2	–7.4	2.3	–4.0	7.0	15.0	–8.7	–3.0	29.3 **
Vaccinium stamineum	(119)	27.2	–14.2	0.3	–0.6	–7.6	–1.6	–6.2	2.8	52.0 **
Vaccinium corymbosum	(27)	1.4	–0.8	–0.2	–2.0	–2.0	10.0	–1.6	–4.9	61.0 **
Total	(395)	18.3	8.3	0.0	2.6	0.0	20.1	16.6	2.4	68.39 **
Canopy species:										
Acer rubrum	(182)	–4.9	5.6	–2.8	–5.2	–7.2	23.8	–8.0	–1.2	56.9 **
Acer saccharum	(143)	–11.8	–3.5	3.3	7.6	10.6	–2.4	–7.6	3.7	30.3 **

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Appendix 2. Continued

Betula alleghensis	(40)	1.7	–0.1	2.7	2.1	0.1	–0.9	–1.4	–4.2	7.0 ns
Fagus grandifolia	(140)	–23.2	–4.0	2.6	–3.2	0.8	–1.2	32.5	–4.5	146.6 **
Nyssa sylvatica	(38)	–2.9	–5.8	–0.1	–2.8	–2.8	3.2	–2.3	13.4	36.1 **
Total	(543)	14.9	0.6	0.7	0.1	0.1	12.8	5.3	0.4	34.9 **

c) Tunica Hills

Understory species		Canopy trees (N = 166)			χ^2
		Liquidambar styraciflua (35)	*Fagus grandifolia* (27)	Other trees (104)	
Acer saccharum	(55)	–7.6	24.1	–12.5	74.2 **
Carpinus caroliniana	(136)	18.3	–5.1	–13.2	14.9 **
Cornus florida	(90)	–9.0	–0.6	9.6	5.9 *
Halesia diptera	(59)	–1.4	–2.6	4.0	1.3 ns
Ilex opaca	(36)	4.4	–4.9	0.4	6.6 *
Lindera benzoin	(33)	3.0	–4.4	1.3	5.0 ns
Ostrya virginiana	(76)	–7.0	–2.4	9.4	5.4 ns
Prunus caroliniana	(100)	–7.1	2.7	4.3	3.1 ns
Styrax grandiflora	(34)	2.8	–0.5	–2.3	1.5 ns
Symplocos tinctoria	(53)	–0.2	–2.6	2.8	1.0 ns
Total	(672)	0.1	0.1	0.0	0.2 ns

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms

Appendix 2. Continued

d) Titi Hammock

Understory species		Canopy trees (N = 168)					χ^2
		Magnolia grandiflora (39)	*Fagus grandiflora* (36)	*Pinus glabra* (22)	*Liquidambar styraciflua* (21)	Other trees (5)	
Carpinus caroliniana	(29)	–6.7	–6.2	–3.8	17.4	–0.6	100.0 **
Cornus florida	(330)	8.4	19.3	25.8	–3.3	–50.2	47.5 **
Ilex opaca	(87)	2.8	–3.6	5.6	1.1	–5.9	5.1 ns
Ostrya virginiana	(190)	–16.1	–14.7	34.1	6.3	–9.5	61.24 **
Symplocos tinctoria	(105)	–17.4	–9.5	1.3	–4.1	29.8	46.13 **
Total	(741)	4.9	1.4	40.9	3.3	6.0	56.6 **
Canopy species:							
Fagus grandifolia	(276)	1.5	–5.6	–2.1	1.3	4.9	5.2 ns
Liquidambar styraciflua	(36)	4.1	–1.6	10.4	–7.1	–5.7	19.6 **
Magnolia grandiflora	(59)	–10.7	–9.6	9.3	9.6	1.4	39.5 **
Pinus galbra	(90)	–0.9	–5.3	-3.8	–2.3	12.2	8.7 ns
Quercus alba	(27)	–1.3	–3.8	–1.5	1.6	4.7	7.3 ns
Quercus falcata	(45)	–2.4	–6.6	2.1	6.4	0.6	13.2 *
Quercus haemispherica	(90)	4.1	–13.3	0.2	–2.3	11.2	15.1 **
Quercus nigra	(88)	6.6	–9.9	4.5	6.0	–7.2	14.3 *
Total	(711)	0.0	27.5	5.3	2.6	3.1	38.5 **

This content downloaded from
128.59.222.107 on Fri, 20 Sep 2024 19:53:14 UTC
All use subject to https://about.jstor.org/terms