

Physiographic position, disturbance and species composition in North Carolina coastal plain forests

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ABSTRACT

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Relations among physiographic heterogeneity, disturbance and temporal change in forest composition were analyzed on 765 forest stands in the southern coastal plain of North Carolina. Physiographic position strongly restricted the species composition of forest stands, though broad overlap of some physiographic classes was noted. Forest stands in different physiographic positions experienced significantly different disturbance regimes. Temporal dynamics were represented as displacement vectors in an ordination space. The distance and direction of displacement over time were analyzed to determine the impact of disturbance on vegetation composition. After removing the effects of physiographic position and initial state of the vegetation, three general pathways were identified. Wild-fire, insect and harvest disturbance types induce stand dynamics that are directionally opposite to undisturbed stands' developmental trends. Prescribed burning induced compositional dynamics unlike those observed for any other disturbance types, while other disturbance types, including weather, disease and non-harvest cutting, do not substantially differ from undisturbed stands in the overall direction of their displacement in the ordination space. Only harvesting and prescribed fires induce displacements in the ordination space that are very much different in magnitude from undisturbed stands.

INTRODUCTION

The most critical environmental planning and policy issues confronting humankind today depend on the analysis of global, regional and subregional conditions over long time periods, e.g. the U.S. Renewable Resources Planning Act of 1974, the analyses supporting assessments of global change (Han-

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sen et al., 1984; IGBP, 1988; Woodmansee, 1988). Many of these large-scale analyses focus on regional vegetation heterogeneity and will be unable to resolve finer levels of detail. Studying and understanding the sources of spatial and temporal heterogeneity in forest composition presents a formidable challenge to forest researchers. In such studies, observation of local change may not convey relevant information in terms of regional or global questions (Bailey, 1985; Meentemeyer and Box, 1987; Shugart et al., 1988). At broad scales, efficient and relatively accurate forest cover models may require only a few constraining variables.

Developing a proper spatial and temporal perspective may be among the most important unresolved problems in forest development research. Even though theories of stand development (Christensen, 1977; Bormann and Likens, 1979; Oliver, 1981; Christensen and Peet, 1981) and disturbance (Denslow, 1980; Bazzaz, 1983; Pickett and White, 1985) are well developed at the patch or stand scale, analysis of the patterns and dynamics of regional systems presents problems that are relatively new to ecological thought. This is because scale changes affect the perceived importance of different patterns of heterogeneity and the apparent importance of different biotic and abiotic factors controlling forestland structure and compositional diversity. Recently, landscapes have begun to be considered (Turner, 1987) and even the interactions of processes at different spatial scales have been addressed in a theoretical approach (Allen and Starr, 1982). Yet few regional-scale studies have been undertaken. Sufficient simplification of complex data, while maintaining patterns which may be analyzed to highlight relations with disturbance regime, environmental or other ecologically interesting variables, is essential. Consequently, our study objective was to assess the relative importance of physiographic heterogeneity, disturbance regimes and forest vegetation for large-scale analyses.

MATERIALS AND METHODS

Study area

The study area includes approximately 3.38 million ha of the southern coastal plain of North Carolina. About 2.12 million ha (63%) of this area is forestland (Tansey, 1984). Coastal plain forestlands occupy diverse topographic positions ranging from perennially flooded swamps to xeric sites on deep coarse sands. Moisture availability (Peet and Christensen, 1980; Brush, 1982), edaphic conditions (Christensen, 1977; Gresham and Lipscomb, 1985), and disturbance regimes (Quaterman and Keever, 1962; Blair and Brunett, 1976; Christensen and Peet, 1981; Myers, 1985) have all been proposed as important factors that may influence forest composition on the Atlantic coastal plain.

Study data

We performed our analysis on data that were collected from individual stands on the southern coastal plain of North Carolina. Our analysis is based on direct observations of forest composition and change over an approximate 10 year interval from 765 forest stands located in environmentally diverse sites. Data were provided by the USDA Forest Service, Southeastern Forest Experiment Station, Forest Inventory and Analysis Work Unit (FIA). FIA units support a continuous inventory of the forest resources of the USA. As part of the inventory approach, the FIA conducts periodic remeasurements at permanent sampling locations. We used data from the two most recent surveys (mid 1970s and 1980s).

Field methods employed during data collection are discussed in a detailed field manual (U.S. Department of Agriculture, 1985). We present a brief summary here. For each stand sampled, average stand age (AGE), stand origin, site index (SI) and physiographic classification were recorded. AGE was calculated from the average of ring counts made on cores taken from three or more representative trees. Stand origin, recorded as a 0–1 variable, indicated whether a stand had been planted or originated from natural regeneration. SI, an estimate of site productivity, was assigned on the basis of published yield tables. Physiographic class was designated on the basis of soil moisture and drainage, topography, aspect and soil characteristics. Three hydric types (deep swamp, pocosin, and narrow drains) with a year round abundance of available moisture were identified. Four mesic types, rolling uplands, flatwoods, narrow floodplains and broad floodplains and one xeric type, deep sands, were also used.

Three survey points were sampled at each stand. Species was recorded and diameter at breast height (dbh) was measured on all living trees greater than or equal to 2.5 cm and less than 12.7 cm dbh on fixed area plots 2.1 m in radius at each sampling point. Additionally, all living trees, 12.7 cm dbh and larger, that fell within the limiting distance of a 37.5 basal area factor were included. At remeasurement, each tree recorded in the previous inventory was relocated and, if still present, dbh was remeasured. New trees reaching minimum dbh on the fixed plot were identified, their diameters measured and recorded as ingrowth. Changes between the initial and terminal inventories were computed by methods adapted from Beers and Miller (1964).

Statistical analysis

Our numeric analyses included ordination-based methods to examine species composition–environment relationships. First, we performed an ordination, detrended correspondence analysis (DCA, Hill, 1979), to reduce the dimensionality of the 765 stands \times 62 species data matrix. DCA allows the

display of the typical location of each species encountered in the inventory, as well as the initial and final location of each of the 765 stands in a simplified two-dimension ordination space.

In DCA, stands that share a large proportion of their species are plotted near one another. Conversely, stands that do not have any species in common will be widely separated (Hill, 1979; Gauch, 1982). Consequently, we analyzed how site physiography limits species composition by comparing characteristic locations within the ordination space of forest stands from different physiographic positions using discriminant function analysis. In addition, over time, change in the location of a single stand in the DCA space indicates a corresponding change in the real or relative species composition of that stand. Therefore, we analyzed how physiographic position and disturbance occurrence affected forest composition changes that occurred between inventories using an analysis of variance of changes in each stand's location within the ordination space. The contingency analysis of disturbance, reported below, did not depend on the use of ordinated study data.

Ordination analysis

We performed a single DCA ordination of the study data. Rare species (in our survey) were down-weighted in this analysis (c.f. Hill, 1979). We calculated each stand's initial location in the ordination space from the results of the first inventory and its final position based on the most recent inventory using species scores weighted by species relative density (RD; Long, 1985) in the stand. Changes in forest composition, inferred from the ordination results, were represented as vectors connecting the initial and final stand locations in the ordination space. The vectors described both the direction and distance of the change in each stand's position.

Discriminant analysis of physiographic position

Discriminant function analysis is a statistical technique used to test the possibility of differentiating among groups using a set of variables upon which the groups are thought to differ (Johnson and Wichern, 1982). For this analysis, forests stands were grouped according to their physiographic class and the discriminant function which maximized the overall differences among the groups was derived from stand ordination scores in the first two DCA dimensions (and, by inference, species composition).

The absence of trees at the initial inventory in 40 cases precluded meaningful interpretation in terms of species composition, so we used 715 of the 765 cases in calculating discriminant functions. Following the discriminant analysis, we redefined the original physiographic groupings based on the results of the analysis.

Analysis of disturbance occurrence

A two-way frequency table analysis (physiographic class \times disturbance type) was employed to determine if a systematic relationship existed between physiographic position and disturbance occurrence during the study period. Several disturbance types each affected less than four stands during the 10-year study and we eliminated a total of 24 stands affected by these disturbances. This reduced the large number of empty cells that would have resulted from their inclusion. Additionally, 95 plantation stands were not included because of small sample sizes. We used a χ^2 test of independence to examine the relationship between physiographic class and the occurrence of different disturbance types in the remaining 646 naturally regenerated stands.

Analysis of temporal dynamics in species composition

The final analysis examined how variation in the temporal dynamics of species composition were influenced by physiographic position and disturbance. We employed separate analyses of variance (ANOVA) of the change in the stand scores for each DCA axis between the initial and final inventory. Initial conditions have an important relationship with the rates of vegetation change, therefore, we included several measures of each stand's initial condition as covariates in the ANOVAs. These included: initial location in the DCA space, AGE, total stand RD (RD_T), SI and stand origin (naturally regenerated versus planted; coded as a 0–1 variable). Separate ANOVAs were necessary because interaction between disturbance type and physiographic class confounded interpretation of a multivariate ANOVA of these data (Wyant, 1987).

RESULTS

Ordination analysis

The first and second DCA axes, respectively, captured 38 and 30% of the variation in the original data. The third axis explained 14% and the fourth axis 10% of total variance. The remaining axes, taken together, explained only 8.4% of total variation in the data. We decided that the third and additional axes explained too little variation to warrant interpretation.

Correspondence analysis permits the user to plot both species (Fig. 1a) and stand locations (Fig. 1b) in a low dimension space that is exactly correspondent (Greenacre, 1981). However, rare species may not be properly placed in the DCA space due to chance occurrences (Whittaker, 1987), so only common species (DCA weightings of 0.50 or greater) are presented (Table 1, Fig. 1). Species names and the codes used in Fig. 1a are presented in Table 1. The

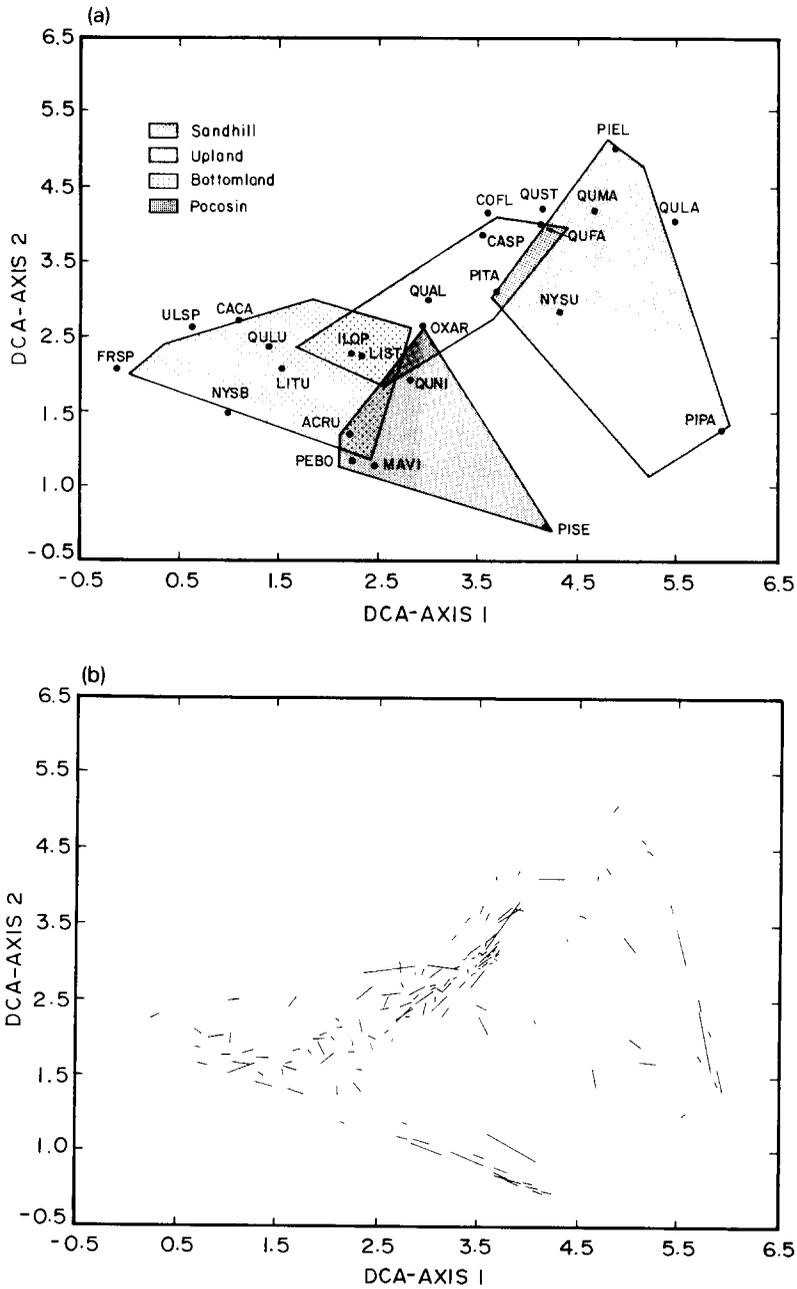


Fig. 1. (a) Dominant species occurrence and smallest convex polygons encompassing stands from major physiographic classes showing occurrence in the detrended correspondence analysis ordination space. Only species with dominance weightings greater than 0.5, relative to the most frequently occurring species (Hill, 1979) are shown. Related results are presented in Table 1. (b) Selected stand displacement vectors for a randomly chosen, 25% subsample of the study stands showing temporal changes in location within the ordination space.

TABLE 1

Dominant species, common names, DCA ordination scores and weights of tree species encountered on study plots. Only species with a DCA weighting of at least 0.5 are presented. Related results are presented in Fig. 1

Species	Common name	DCA code	Weights
<i>Acer rubrum</i> L.	Red maple	ACRU	1.000
<i>Carpinus caroliniana</i> Walt.	Blue beech	CACA	0.532
<i>Carya</i> spp.	Hickory	CASP	0.744
<i>Cornus florida</i> L.	Dogwood	COFL	0.816
<i>Fraxinus</i> spp.	Ash	FRSP	0.642
<i>Ilex opaca</i> Ait.	Holly	ILOP	1.000
<i>Liquidambar styraciflua</i> L.	Sweetgum	LIST	1.000
<i>Liriodendron tulipifera</i> L.	Yellow poplar	LITU	0.756
<i>Magnolia virginiana</i> L.	Sweet bay	MAVI	0.811
<i>Nyssa sylvatica</i> var. <i>biflora</i> (Walt.) Sarg.	Blackgum (lowland)	NYSB	0.713
<i>Nyssa sylvatica</i> Marsh.	Blackgum (upland)	NYSU	1.000
<i>Oxydendrum arboreum</i> (L.) DC	Sourwood	OXAR	0.666
<i>Persea borbonia</i> (L.) Spreng.	Redbay	PEBO	0.631
<i>Pinus elliotii</i> Engelm.	Slash pine	PIEL	0.510
<i>Pinus palustris</i> Mill.	Longleaf pine	PIPA	1.000
<i>Pinus serotina</i> Michx.	Pond pine	PISE	1.000
<i>Pinus taeda</i> L.	Loblolly pine	PITA	1.000
<i>Quercus alba</i> L.	White oak	QUAL	0.921
<i>Quercus falcata</i> Michx.	Southern red oak	QUFA	0.999
<i>Quercus laevis</i> Walt.	Turkey oak	QULA	0.796
<i>Quercus laurifolia</i> Michx.	Laurel oak	QULU	0.634
<i>Quercus marilandica</i> Muenchh.	Blackjack oak	QUMA	0.607
<i>Quercus nigra</i> L.	Water oak	QUNI	1.000
<i>Quercus stellata</i> Wangenh.	Post oak	QUST	1.000
<i>Ulmus</i> spp.	Elms	ULSP	0.561

first and second DCA axes were scaled to the proportion of variance in the original data that they explained. This scaling was employed for presentation purposes only and did not affect analyses conducted on ordinated data.

Discriminant analysis of physiographic position

The results of the discriminant analysis of forest stands grouped by physiographic class were statistically significant. Wilks' lambda statistic, measuring the overall separation of group centroids was 0.29 (equivalent F statistic = 87.06 with 14,1408 equivalent d.f.) and produced highly significant ($P < 0.01$) overall separations among the physiographic classes. Because the overall results of the discriminant analysis were statistically significant, we

TABLE 2

F statistics and associated significance levels of separations between pairs of physiographic classes provided by the discriminant analysis calculated from final DCA scores. Each *F* statistic has 2 and 704 degrees of freedom. Significance levels are presented parenthetically beneath their respective statistics

Physiographic class	Physiographic class						
	Sand	Upland	Flatwood	Narrow floodplain	Small drain	Broad floodplain	Swamp
Upland	100.28 (<i>P</i> <0.01)						
Flatwood	144.31 (<i>P</i> <0.01)	12.34 (<i>P</i> <0.01)					
Narrow floodplain	334.89 (<i>P</i> <0.01)	117.84 (<i>P</i> <0.01)	140.69 (<i>P</i> <0.01)				
Small drain	249.31 (<i>P</i> <0.01)	90.94 (<i>P</i> <0.01)	93.27 (<i>P</i> <0.01)	0.92 (<i>P</i> =0.40)			
Broad floodplain	296.76 (<i>P</i> <0.01)	111.39 (<i>P</i> <0.01)	123.78 (<i>P</i> <0.01)	1.16 (<i>P</i> =0.31)	1.50 (<i>P</i> =0.22)		
Swamp	156.88 (<i>P</i> <0.01)	66.23 (<i>P</i> <0.01)	64.14 (<i>P</i> <0.01)	4.92 (<i>P</i> <0.01)	4.11 (<i>P</i> =0.02)	2.16 (<i>P</i> =0.12)	
Pocosin	156.78 (<i>P</i> <0.01)	101.80 (<i>P</i> <0.01)	81.20 (<i>P</i> <0.01)	79.07 (<i>P</i> <0.01)	52.19 (<i>P</i> <0.01)	75.69 (<i>P</i> <0.01)	45.52 (<i>P</i> <0.01)

examined differences between pairs of physiographic classes in the discriminant function space (Table 2).

The univariate *F* tests in Table 2 show that, based on species composition, the discriminant function produced significant (*P*<0.05) separations among most of the physiographic classes. The species composition of forest stands in the swamp, upland, deep sand, flatwood and pocosin classes were significantly different from each other and the other classes. However, there was substantial overlap in the species composition of most of the stands in small drain, broad floodplain and narrow floodplain physiographic classes. We combined the small drain, narrow floodplain and broad floodplain classes for subsequent analyses because of the *F* test results (Table 2).

Analysis of disturbance occurrence

Of the 646 naturally regenerated stands we studied, just under 57% remained undisturbed during the remeasurement period. Human-caused disturbances (harvest, other cutting and prescribed burning) occurred on 35% of the stands. Natural disturbances impacted the remaining 8% (Table 3). The χ^2 statistic associated with the contingency table analysis was 109.21 (35 d.f., *P*<0.01), suggesting that physiographic position is strongly correlated with variation in the type of disturbances experienced.

TABLE 3

Joint frequency distributions of naturally regenerated stands according to physiographic classification and disturbance experience during the study period

Disturbance	Physiographic class						Row total
	Sand	Flatwood	Upland	Floodplain and drain	Pocosin	Swamp	
Undisturbed							
Count	32	137	48	106	35	9	367
Column (%)	53.3	46.3	54.5	73.6	76.1	75.0	-
Row (%)	8.7	37.3	13.1	28.9	9.5	2.5	56.8
Harvest							
Count	8	82	20	16	2	0	128
Column (%)	13.3	27.7	22.7	11.1	4.3	0.0	-
Row (%)	6.3	64.1	15.6	12.5	1.6	0.0	19.8
Other cutting							
Count	7	35	9	9	1	2	63
Column (%)	11.7	11.8	10.2	6.3	2.2	16.7	-
Row (%)	11.1	55.6	14.3	14.3	1.0	3.2	9.8
Prescribed fire							
Count	10	17	4	1	1	0	33
Column (%)	16.7	5.7	4.5	0.7	2.2	0.0	-
Row (%)	30.3	51.5	12.1	3.0	3.0	0.0	5.1
Disease							
Count	0	9	1	4	1	0	15
Column (%)	0.0	3.0	1.1	2.8	2.2	0.0	-
Row (%)	0.0	60.0	6.7	26.7	6.7	0.0	2.3
Insect							
Count	0	12	2	1	5	0	20
Column (%)	0.0	4.1	2.3	0.7	10.9	0.0	-
Row (%)	0.0	60.0	10.0	5.0	25.0	0.0	3.1
Wildfire							
Count	3	4	2	2	1	0	12
Column (%)	5.0	1.4	2.3	1.4	2.2	0.0	-
Row (%)	25.0	33.3	16.7	16.7	8.3	0.0	1.9
Weather							
Count	0	0	2	5	0	1	8
Column (%)	0.0	0.0	2.3	3.5	0.0	8.3	-
Row (%)	0.0	0.0	25.0	62.5	0.0	12.5	1.2
Column total							
Count	60	296	88	144	46	12	646
Percentage	9.3	45.8	13.6	22.3	7.1	1.9	100.0

Analysis of temporal dynamics in species composition

ANOVA results are presented in Tables 4 and 5 for the univariate analyses of displacement in the first and second dimension of the DCA space, respectively. About half of the total variation in stand displacement over the 10-year study period was explained by the covariates and factors included in the analysis of covariance (Tables 4 and 5). Partitioning the explained sums of squares among the factors and covariates provides a means of assessing the relative importance of each in controlling temporal dynamics. The covariates taken together described initial conditions and account for most of the variation explained in each analysis. Initial species composition at a site (initial DCA scores) was the most important covariate in each analysis. Contributions of the other covariates differed between the two analyses. Main effects of physiographic class and disturbance type were significant in both analyses and no significant interactions between disturbance and physiographic class were detected.

These significance tests, however, do not furnish sufficient information re-

TABLE 4

Analysis of covariance of compositional dynamics measured as displacement along the first DCA axis. The analysis was conducted on standardized data

Source of variation	Sum of squares	Mean square	d.f.	F statistic
Covariates	282.39	40.43	7	88.77 ($P < 0.01$)
Site class	5.19	5.19	1	13.01 ($P < 0.01$)
Stand origin	23.39	23.39	1	51.19 ($P < 0.01$)
Stand age	8.43	8.43	1	18.55 ($P < 0.01$)
Site class	5.19	5.19	1	36.46 ($P < 0.01$)
RD _T	16.57	16.57	1	39.64 ($P < 0.01$)
Initial score				
First axis	57.96	57.96	1	127.54 ($P < 0.01$)
Second axis	0.79	0.79	1	1.75 ($P = 0.19$)
Interaction, disturbance by physiographic class	19.54	0.78	25	1.71 ($P = 0.20$)
Main effects	122.39	10.20	12	22.44 ($P < 0.01$)
Physiographic class	35.37	7.07	5	15.57 ($P < 0.01$)
Disturbance	92.29	13.18	7	29.01 ($P < 0.01$)
Explained	424.23	9.64	44	21.21 ($P < 0.01$)
Residual	316.30	0.45	696	
Total	740.53	1.00	740	

TABLE 5

Analysis of covariance of compositional dynamics measured as displacement along the second DCA axis. The analysis was conducted on standardized data

Source of variation	Sum of squares	Mean square	d.f.	F statistic
Covariates	284.27	40.61	7	71.27 ($P < 0.01$)
Site class	1.61	1.61	1	2.82 ($P = 0.09$)
Stand origin	35.64	35.64	1	62.54 ($P < 0.01$)
Stand age	0.84	0.84	1	1.47 ($P = 0.22$)
RD _T	16.49	16.49	1	28.93 ($P < 0.01$)
Initial score				
First axis	7.89	7.89	1	13.85 ($P < 0.01$)
Second axis	77.08	77.08	1	135.29 ($P < 0.01$)
Interaction, disturbance by physiographic class	12.94	0.52	25	0.91 ($P = 0.59$)
Main effects	42.84	3.57	12	6.26 ($P < 0.01$)
Physiographic class	37.22	7.44	5	13.06 ($P < 0.01$)
Disturbance	9.48	1.35	7	2.38 ($P = 0.02$)
Explained	340.04	7.73	44	13.56 ($P < 0.01$)
Residual	396.55	0.57	696	
Total	736.59	0.99	740	

guarding the relationship of the factors to the observed forestland dynamics. We examined the pattern of factor effects to understand the effects of disturbance and physiographic class more fully (Table 6, Fig. 2). Differences in the eta and beta statistics highlight the enhanced effect of physiographic class in most cells, and the diminished effect of disturbance, again in most cells, when adjustments are made for other factors and covariates. Disturbance was the single most important source of variation in displacement in the first DCA dimension though it was not a significant factor in explaining dynamics in the second dimension. Physiographic position proved to be only a minor, though significant, factor in controlling forest dynamics.

DISCUSSION

Physiographic control of species composition

Two scales of heterogeneity are evident in the depiction of physiographic class location and stand dynamics in the DCA space. First, an important partitioning along physiographic classes is obvious (Fig. 1a). Stands from var-

TABLE 6

Multiple classification analysis results of the analysis of covariance of forest dynamics, measured as changes in DCA scores. Cell means are expressed as deviations from the grand mean (-0.01). The multiple r -squared is 0.55 for the first ordination axis analysis and 0.44 of the second axis analysis. Analyses were conducted on standardized data

Factor and category	<i>n</i>	Unadjusted deviation		Adjusted deviation ^a		Eta and (beta) statistics	
		Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Physiographic class						0.05 (0.32)	0.12 (0.31)
Sand	70	0.00	0.05	0.64	0.56		
Flatwood	370	0.01	0.05	0.09	0.11		
Upland	96	-0.12	-0.26	0.08	0.12		
Floodplain and drain	145	0.06	-0.07	-0.49	-0.45		
Pocosin	48	-0.02	0.08	-0.12	-0.42		
Swamp	12	0.08	-0.07	-0.75	-0.60		
Disturbance						0.45 (0.38)	0.18 (0.12)
None	416	0.26	0.12	0.17	0.07		
Harvest	128	-0.96	-0.35	-0.81	-0.25		
Other cutting	75	0.07	-0.03	0.13	0.06		
Prescribed fire	51	0.24	-0.04	0.40	-0.04		
Disease	29	0.23	0.06	0.17	0.09		
Insect	21	-0.23	-0.12	-0.07	-0.06		
Wildfire	13	-0.32	-0.05	-0.13	-0.03		
Weather	8	0.06	-0.02	0.12	0.06		

^aDeviations are adjusted for the influence of covariates and the other factor.

ious landforms occupy different regions of the DCA space. Second, within a physiographic class, individual stands' temporal dynamics are represented as displacement vectors (Fig. 1b). Though irregular patterns are produced by the displacement vectors within a physiographic class, there is little evidence that developmental changes in species composition overpower the control of physiography.

Our first study hypothesis asserts that physiographic classes represent broadly different sets of environmental conditions limiting the species capable of occupying those sites and that subsamples selected from separate physiographic classes will occupy separate regions of the DCA space (Grime, 1977; Austin, 1985; Price, 1985). In the North Carolina coastal plain, forestland composition covaries with physiographic position above the water table. The first DCA axis (Fig. 1a) follows a moisture gradient from perennially flooded sites on the left, to xeric sands on the right. The species farthest to the left on the first axis, characteristically grow in pure, even-aged stands on sites

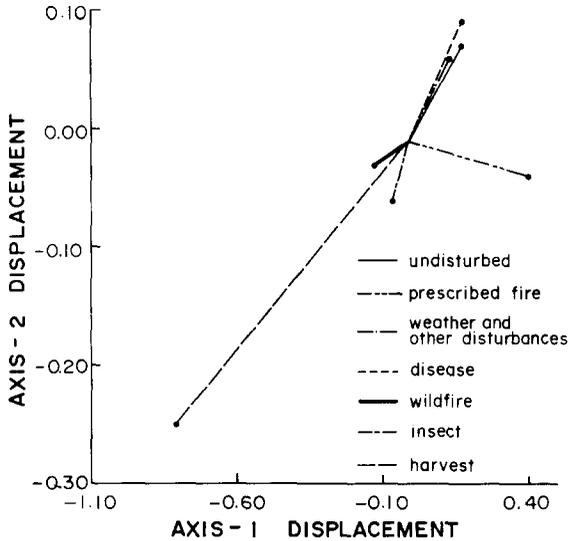


Fig. 2. Standardized temporal forest responses, expressed as deviations from the grand mean in each ordination dimension. Responses are adjusted for the effects of physiographic class and covariates listed in Tables 4 and 5.

that are normally flooded (Johnson and Shropshire, 1983). Mixed hardwoods, including red maple, sweetgum, elm and ash are associated with tupelo and bald cypress on sites which are not permanently flooded (Jones et al., 1984). Elevated margins of many wet lands are dominated by bottomland oak species. At the opposite extreme, longleaf pine savannas or longleaf pine stands with well-developed turkey oak understories occupy xeric sites (Myers, 1985).

The second DCA axis separates species typically occurring in pocosin forests from those of upland sites. Pocosins, though normally flooded, lack typical swamp species, being extremely acidic, nutrient poor sites on deep, peaty soils (Christensen et al., 1981; Sharitz and Gibbons, 1982). Upland forests that fall in the middle of the first dimension and at the top of the second, are characterized by oaks and other hardwoods whose shifting importance are often characterized as resulting from relatively small edaphic and soil moisture changes (Wells, 1928; Oosting, 1942; Radford et al., 1964).

The discriminant analysis results (Table 2) suggest that physiographic classes at the end of each DCA axis tend not to support tree species that are also typically found in other physiographic positions. This is based on relatively high significance of difference between physiographic class differences in the flatwood, upland, sand classes and to a lesser degree the swamp class. On the other hand, the remaining physiographic classes, narrow and broad floodplains, and small drains are not clearly different on the basis of extant vegetation (Table 2), indicating that these sites share many species. How-

ever, even though these bottomland sites support a broadly overlapping suite of species, they do not frequently share species typically found on either upland or swamp sites (Table 2).

Physiography explained only a fraction of the total variation in species abundance patterns across the coastal plain. Environmental heterogeneity may also have an important role in defining disturbance regimes (Runkle, 1985; Shugart and Seagle, 1985; Swanson et al., 1988).

Physiographic position and disturbance regimes

We hypothesized that different disturbance types have substantially different temporal and spatial distributions in the study area (White, 1979; Austin, 1985) because disturbances are influenced by environmental gradients (Harmon et al., 1984). In our study, the systematic relations between physiographic class and disturbance occurrence indicate that different physiographic locations experience different disturbance regimes (Table 3).

The regional frequency of disturbances on the coastal plain of North Carolina is very high. Nearly half of the naturally regenerated stands in the sand, flatwood and upland physiographic classes and about a quarter of the stands in the remaining physiographic classes experienced disturbances during the 10-year study period. This corresponds to a rotation period (i.e. the period of time during which disturbances affect an area equivalent to the study area (Pickett and White, 1985)) of about 40 years for all wetland forests, considering the combined frequencies of all disturbances. The rotation period for upland forests for all disturbances is about 20 years. This division of overall disturbance frequencies into two groups does not hold for individual disturbance types.

Natural disturbance, while locally important, did not occur with great enough frequency to be important in a regional context. In addition, our data do not include flood frequency observations, yet flooding is the most frequently noted disturbance agent affecting bottomland forests (Bell, 1974; Tanner, 1986). Therefore, the disturbance regimes of lowland sites are probably not adequately represented in the sample.

Our analyses suggest that anthropogenic disturbances will have the most important influence on the future forests of the coastal plain of North Carolina. Human-caused disturbances are occurring much more frequently than natural disturbances on the coastal plain of North Carolina. These disturbances are also being imposed on the landscape in patterns different from those of naturally occurring disturbances. In addition, two human-caused disturbances, harvesting and prescribed burning, induce species composition shifts of much greater magnitude (distance in the DCA space) than other disturbance types (Table 3). Harvest and prescribed burning regimes applied to coastal plain forests do not appear to be well matched with the current

natural disturbance regimes. We suspect that this new disturbance regime will ultimately have profound effects on the pattern and composition of forestlands along the Atlantic coastal plain.

Tansley (1935) recognized that the effect of a new disturbance regime is not merely to arrest succession but to change the character of the vegetation. Differences in the type and frequency of disturbances must be accompanied by differences in species abundance because the effect of repeated stress from disturbances is to eliminate or debilitate susceptible species and cause them to be replaced by species tolerant of the disturbance regime (Denslow, 1985). In the southeastern USA these shifts are predominantly toward more intensively managed forests (USDA Forest Service, 1988), particularly on industrial forestlands.

Disturbance and physiographic effects on stand dynamics

Spatial and temporal sources of vegetation heterogeneity have generally been studied separately. In fact, Daubenmire (1966) criticized early continuum constructions for failure to account for successional dynamics. Most studies of forest succession have concentrated on stand-level examinations; either by direct observation or by arranging spatially separated plots into presumed time sequences. These approaches, however, are best suited to empirical analyses of within stand dynamics rather than the examination of stand developmental status as a source of pattern in forest landscapes. In our analysis, the importance of the interaction between physiography and disturbance in governing the vegetation occupying a site can be discerned by examining the joint effects of disturbance and physiography on vegetation dynamics (Fig. 4).

Forest dynamics are characterized by the direction and rate of change in the structure and composition of forest stands. Pickett and White (1985) theorize that the most obvious role that disturbance plays in governing forest composition is in the deflection of stand development from some successional pathway. Our analyses indicate that, when other factors are controlled, some disturbance types offset successional development trends. Wildfire, insect and harvest disturbance types induce stand dynamics that are directionally nearly opposite that of undisturbed stands' developmental trends. However, other disturbance types, including weather, disease and nonharvest cutting, do not substantially differ from undisturbed stands in the overall direction of their displacement in the DCA space.

During the relatively short study period (10 year), stand development did not act to bring about convergence on a physiographically typical community composition, nor did disturbances impart sufficient force to change the general relationship between physiography and vegetation. Because physiographic class contributed only a minor portion of the variance explained in

changes between initial and final DCA locations, there is no evidence of change in the degree of physiographic control over the relative abundance of tree species with time (Table 4). Only harvesting and prescribed fires induce displacements in the DCA space that are very much different in magnitude from undisturbed stands (Fig. 2).

Harvest disturbances, as an increasing percentage of the disturbance regimes acting on southeastern forests, and the extensive application of prescribed fire now dominate other disturbance patterns. The species composition of communities subject to new disturbance patterns is likely to reflect both old and new regimes of disturbance. Intensive forest management activities will induce a shift in species to those better suited to highly disturbed conditions (Bormann and Likens, 1979; Denslow, 1980, 1985; Oliver, 1981).

Disturbances are an important, though not the sole, source of variation in stand development trends. Disturbance effects are diminished after adjustment for covariate and physiographic class effects (Table 4). Much of the apparent variation in compositional response to disturbance is evidently caused by variation in initial vegetation of the disturbed stands which is, in turn, a function of their physiographic position in the landscape. Initial vegetation, disturbance type and physiographic position all interact to determine the compositional dynamics of individual stands. There is little reason to expect simple relations among these variables and their effects on individual stand dynamics (Wyant, 1987). However, we have demonstrated here that prescribed fires and harvesting, combined with physiographic location, significantly add to forestland heterogeneity at the regional scale.

CONCLUSION

We have examined how various environmental factors affect our conceptual model explaining environmental control of forest heterogeneity considered at regional scales. We tried to determine how environmental heterogeneity, disturbances and the temporal dynamics of forest stands control the relative abundance of tree species in the coastal plain forests of North Carolina. The effects of major environmental gradients and disturbance regimes on vegetation pattern are more easily understood if analyzed at larger scales. An integrated understanding of temporal and spatial forest patterns must involve complex larger scales as well as relatively well studied smaller scales. Clearly, it is not possible for each study to concentrate equally among all scales of spatial and temporal resolution. Scale problems alter model conceptualization and structure because some driving variables change greatly with spatial scale shifts. Events that seem random at one scale of examination (e.g. disturbance occurrence in individual stands) compose patterns at another (e.g. within a region). It may be that the temporal dynamics that seem to be unique and unpredictable on the basis of 10 year's change also compose pat-

terns that are easily discernable and readily interpretable at a larger temporal scale.

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