



The Seedling Regeneration Niche: Habitat Structure of Tree Seedlings in an Oak-Pine Forest

Author(s): Scott L. Collins and Ralph E. Good

Source: *Oikos*, Vol. 48, No. 1, (Jan., 1987), pp. 89-98

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3565692>

Accessed: 05/05/2008 22:01

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=black>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We enable the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest

Scott L. Collins and Ralph E. Good

Collins, S. L. and Good, R. E. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. – *Oikos* 48: 89–98.

The physical environment to which a seedling is subjected affects its probability of survival and recruitment into a population. Aspects of the physical and biotic environment form components of the plant habitat and regeneration niches defined by Grubb. The importance of different variables may change during the life cycle of a long-lived plant. We measured nine variables that characterize the habitat of six species of one year old tree seedlings in an oak-pine forest in the New Jersey Pine Barrens. Variables were measured for 25 randomly located individuals of each species as well as at 25 random points in the same stand as the seedlings and in two other stands. Principal components analysis (PCA) of seedling plus random point data produced two habitat gradients: Axis I was a gradient from canopy cover to moss and lichen cover and higher light intensity. Axis II was a gradient from high total cover and shallow litter to habitats with less cover and deeper litter layers. Random points were concentrated in areas with deep litter and low light whereas most seedlings grew in areas with more light and less litter. Discriminant functions analysis indicated that seedling habitat breadth was large but that the habitat of *Pinus echinata* could be distinguished from that of *Quercus coccinea* and *Sassafras albidum*.

Seedling density differed among the three stands. Analysis by PCA of the random points from the three stands produced similar habitat gradients as in the PCA derived from tree seedling habitats. In the stand where seedling density was lowest, litter layers were significantly deeper, shrub density was greater and light was lower than in the other stands. These trends were confirmed by discriminant functions analysis. The multivariate analysis of seedling habitat and regeneration niches can be used to explain, in part, seedling density in the ground layer of different forest stands.

S. L. Collins and R. E. Good, Div. of Pinelands Research, Center for Coastal and Environmental Studies, Rutgers – The State Univ. of New Jersey, New Brunswick, NJ 08903, USA. (Present address of SLC: Dept of Botany and Microbiology, Univ. of Oklahoma, Norman, OK 73019, USA).

1. Introduction

Numerous scale related variables affect the distribution of plants and thus the composition of vegetation within a plant community. In particular, mechanisms operating at small scales such as germination microsites (Harper et al. 1965), litter depth (Sydes and Grime 1981), or neighborhood competition (Goldberg and Werner 1983) may limit the abundance and performance of individuals within a population. These factors are thus important variables related to the formulation of the real-

ized niche of a plant. Grubb (1977) divided the plant niche into four components: life-form, phenology, habitat and regeneration. Although his review focused on the regeneration niche, by presenting the additional components Grubb implicitly recognizes their importance, as well. There are problems with this formalization. First, the approach is categorical because it defines types of niches whereas recent concepts of niche emphasize an organism-centered approach (Hutchinson 1978, MacMahon et al. 1981). More importantly, these components of the plant niche are not mutually exclu-

Accepted 21 January 1986

© OIKOS

sive. For example, studies of the habitat niche may become complicated by the changing physiological tolerances of a plant as it matures. Thus, aspects of the habitat and regeneration niches must often be analyzed in concert to understand plant-environment relationships. Nevertheless, Grubb's concept of the plant niche can serve as a conceptual focus for detailed studies of species-environment relationships.

The physiological limits of a plant are often broad when considered over the life span of a long-lived individual, however, its sensitivity to environmental factors changes with age (Parrish and Bazzaz 1985). The above-ground portion of a tree will encounter different light, humidity, and wind conditions as it grows from the herbaceous layer into the canopy. The physical environment to which the tree is subjected at any stage in its life cycle will affect continued survival of the individual. To some extent, this represents the environmental sieve defined by Harper (1977). Therefore, it is important to analyze the habitat niche for different stages in the life cycle of a long-lived plant. Most analyses of species niche focus on adults, thus ignoring the important earlier stages of the life cycle. Here we analyze some physical aspects of the habitat of one year old tree seedlings in an oak-pine forest in the New Jersey Pine Barrens. After germination, seedling mortality is high (Good and Good 1972) and the physical habitat surrounding a seedling contributes to the probability of long-term survival. In this paper we describe and compare the habitat of seedlings of six tree species. To do so we apply methods used in animal habitat analyses (e.g., James 1971, Dueser and Shugart 1979, Collins 1983) to study aspects of the plant niche defined by Grubb (1977). Such an approach permits quantification of habitat structure and variation associated with the location of individuals of a species. Also, this type of analysis permits interspecific comparisons without invoking the *a priori* assumption that interspecific competition governs species distributions. When performed on large geographic patterns, James et al. (1984) call this method a quantification of the Grinnellian, as opposed to the Hutchinsonian (1978) niche. The specific objective here is to provide a first step toward understanding the abundance of tree seedlings in oak-pine forests of the New Jersey Pine Barrens. The results are extended to two other oak-pine stands in an effort to explain, in part, seedling abundance in a broader context.

2. Materials and methods

2.1. Study area

The New Jersey Pine Barrens (Pinelands) cover an area of about 445,000 ha on the outer Coastal Plain of southern New Jersey. Throughout its history, the vegetation of the Pinelands has been subjected to natural and man-induced disturbances, in particular, fire (Little 1979a) and logging (Wacker 1979). Many of these disturbances

have been reduced during the 1900's and natural vegetation has returned to most of the disturbed sites (Robichaud and Buell 1973). Nevertheless, the large-scale pattern of vegetation in the region is attributed mainly to past and current disturbances (Little 1979a), although soil moisture and texture gradients probably interact with fire to produce the regional vegetation pattern (Whittaker 1979). The general ecology of the Pinelands has been well described (Forman 1979), but detailed data on the ecology of some community-types and species characteristics are lacking (c.f. Buell and Cantlon 1950).

2.2. Field methods

Three oak-pine stands in the north-central Pinelands, all within 3 km of each other, were selected for analysis of tree seedling density and habitat structure. Stands 1 and 2 were located in Lebanon State Forest in vegetation subjected to periodic prescribed burning. Stand 3 is a forest fragment in the Lebanon Lake Estates development that has been isolated by paved roads for at least 15 yr. Tree species composition and importance in each stand were determined by the point-centered quarter method (Cottam and Curtis 1956) based on 30 (Stand 3) or 40 (Stands 1 and 2) points per stand. Tree seedling density was determined by counting the number of tree seedlings that occurred in 100 (Stand 3) or 150 (Stands 1 and 2) randomly located 0.5 m² quadrats.

In Stand 1, habitat structure was measured for 25 individuals of six tree species: *Quercus alba*, *Q. coccinea*, *Q. prinus*, *Q. velutina*, *Pinus echinata*, and *Sassafras albidum*. Twenty-five samples per species were recorded because they provided adequate replication while allowing rapid measurement under uniform conditions. All measurements were conducted from late July to early August 1984. Seedlings were selected for analysis by locating the individual nearest to a randomly located point. Random points were located by walking a specified distance along a transect and tossing a wire stake in a random direction and distance from the transect line. Seedlings were aged by searching for terminal bud scale scars and several individuals were excavated (after environmental measurements) to determine if they originated from seeds or root sprouts. Root sprout data were not included in any analyses. Unlike pines, it is difficult to age oak seedlings (Merz and Boyce 1956), but based on bud scale scars and excavation, we are confident that most of the oak seedlings we sampled were less than two years old.

Nine habitat variables (Tab. 1) were recorded at each point by centering a 14 cm diameter circular quadrat on each randomly located seedling. This size quadrat is small enough to incorporate the environment immediately surrounding a seedling and it is large enough to include several measurable environmental parameters. Within each quadrat, moss cover, lichen cover and percent ground layer cover were visually estimated. Litter

Tab. 1. Nine variables used to describe the habitat structure of one year old tree seedlings in an oak-pine forest.

Variable	Measurement
Litter depth	Depth of the litter layer immediately adjacent to each seedling.
Nearest neighbor distance	Distance (cm) from the seedling to its closest neighbor in the ground layer.
Moss cover	Percentage of soil surface covered by mosses in a 14 cm diameter circular quadrat centered on each seedling.
Lichen cover	Percentage of soil surface covered by lichens in a 14 cm diameter circular quadrat centered on each seedling.
Percent light	Photosynthetically active radiation (PAR) measured immediately above each seedling. Values were expressed as a percent of the maximum PAR measured outside the tree canopy.
Canopy cover	An estimate of the percentage of cover by overstory trees above each seedling.
Ground cover	An estimate of the percentage of cover by ground layer vegetation in a 14 cm diameter circular quadrat centered on each seedling.
Total cover	The summation of ground cover and canopy cover.
Canopy type	A binary variable (0 = deciduous, 1 = coniferous) to indicate that the canopy above each seedling was either deciduous or coniferous.

depth was measured adjacent to a seedling by inserting a wire probe down to the soil surface. Light immediately above each seedling was measured with a LiCor PAR sensor. These measurements, all taken between 1000 and 1400 hours on clear, sunny days, were expressed as a percentage of ambient light, measured in an open area near the stand. Distance from the seedling to its nearest neighbor in the ground layer (e.g. herb, shrub or tree seedling) was recorded. Canopy type (deciduous or coniferous) above the seedling was noted, and an estimate of the amount of canopy cover in the vicinity of the seedling was determined. Total cover above each seedling was derived by summing the cover estimates of the ground layer and canopy layer vegetation. Similar measurements were taken at randomly located points in each of the three stands.

2.3. Data analysis

Statistical differences among species for each habitat variable were analyzed by one-way analysis of variance (ANOVA) and Duncan's multiple range test. To improve normality, continuous variables were $\log(x + 1)$ transformed and percentage variables were arcsine transformed (Sokal and Rohlf 1969). Habitat data were also subjected to principal components analysis (PCA) and discriminant functions analysis (DFA). Both techniques have been used extensively in comparative studies of habitat structure and niche relationships of animal assemblages (e.g. James 1971, Dueser and Shugart 1979, Wiens and Rotenberry 1981, Shugart 1981, Collins et al. 1982). Principal components analysis reduces the complexity in a multivariate data set by combining the original variables into a few new, orthogonal principal components. Correlation coefficients indicate the relationship of each original variable to each principal component. The position of each sample is then projected onto each component and the samples can be circumscribed to determine the distribution of a species in habitat space. For this study, a data matrix containing

175 samples (25 samples from each of 6 species and 25 random points from Stand 1) by nine variables (standardized to $\bar{X} = 0$, $s^2 = 1$) was used to derive gradients based on habitat structure. The PCA was derived from a correlation matrix of the nine habitat variables. By including the random points, it is possible to determine if each species habitat is different from or is a distinct subset of the available habitat in this stand (see Smith 1977). The distribution of each species in habitat space was represented by 95% "concentration" ellipses (based on Sokal and Rohlf 1969: 528).

Stepwise discriminant function analysis maximizes the distances between predefined groups while minimizing within-group variance. Samples for each species are treated as one group. In this study, DFA was used to indicate which combination of the nine habitat variables could best discriminate the habitat of the six species. In addition, DFA conducts an a posteriori test to determine the group in which each sample has the highest probability of membership. If samples of species A are consistently reclassified as members of species B and vice versa, then the general habitat structure surrounding these two species is similar. The efficacy of the DFA classification matrix was assessed with Cohen's Kappa statistic (Titus et al. 1984). This statistic is a measure of the degree to which the DFA classification matrix is better than a randomly constructed matrix.

Once the general characteristics associated with the habitat of one year old tree seedlings have been identified, an analysis of habitat structure in other forests may explain variation in tree seedling density among stands. Both univariate and multivariate methods were employed to produce such an analysis with the Pine Barrens data set. Statistical relationships among the variables measured at randomly located points in three stands were assessed by ANOVA and Duncan's multiple range test. Although multivariate analyses do not always permit the determination of the contribution of each variable, they have the advantage, lacking in univariate test, of combining all variables into one analysis.

For this study, standardized data recorded at the 75 randomly located points (25 points from each of three stands) were subjected to PCA and DFA. PCA was used to produce gradients of habitat structure based on the variables measured at each random point. The random point samples were then projected onto the PCA axes which were defined by a combination of habitat variables. The distribution of random samples in habitat space was summarized by 95% concentration ellipses. This provides a graphic description of the habitat gradients available for seed germination and seedling establishment in each stand. The DFA was used as before to determine which combination of habitat variables best distinguishes the microhabitat structure among the three stands.

3. Results

3.1. Seedling habitat analysis

The same tree species occurred in each of the three stands, but species importance values were variable among stands (Tab. 2). *Quercus coccinea* was uncommon in Stands 1 and 2 which may have limited the distribution and abundance of *Q. coccinea* seedlings in these stands. The other tree species, however, had a frequency value greater than 30.0 indicating that each species occurred at about one-third of the sample points. Thus, adult distribution for most species is unlikely to have limited the distribution of seeds and seedlings within each stand.

Based on the average habitat variables for each species (Tab. 3), it is clear that differences exist in the habitats of these tree seedlings. In particular, a considerable range of average values between species is evident for nearest neighbor distance, moss cover, light, canopy cover, and ground cover. Although most average values had large standard errors, five of the eight variables tested were significantly different among species. Differences in nearest neighbor distance and moss cover were induced primarily by large values for *Quercus coccinea* and *Pinus echinata*, respectively. In contrast, litter

depth, canopy cover, and light appear to show a pattern of continuous variation among the tree species.

Principal components analysis produced four factors with eigenvalues greater than 1.0 that accounted for a total of 74.2% of the variance in the original matrix (Tab. 4). Axis I defined the primary habitat gradient separating areas with dense ground and total cover from areas with high light, more moss and lichen cover, and distant nearest neighbors. Axis II separated microhabitats with high canopy and total cover, and shallow litter layers from areas with less cover and deep litter. Axis III also reflected a plant cover gradient. In this case, when nearest neighbor distance was low, cover of ground layer vegetation was extensive but canopy cover was reduced. This might indicate increased density of ground layer species in canopy openings. Finally, Axis IV separated sites based on canopy type (deciduous or coniferous) and light.

Distribution of the species in the space defined by the first two principal components (Fig. 1) shows that most random points occurred in habitats with high amounts of ground, canopy, and total cover. The distribution of seedlings, on the other hand, was generally different from the random points. Tree seedlings tended to occur in areas with less total cover than the random points. In particular, seedlings of *P. echinata*, *Q. velutina*, and *Q. coccinea* occurred more toward the moss-lichen cover end of axis I where litter layers are shallow. In contrast, seedlings of *Q. alba*, *Q. prinus*, and *S. albidum* were found in areas of greater ground cover. The seedling habitats were separated along the second axis, as well. *Pinus* seedlings were located at the high canopy cover-shallow litter layer end of the axis. Seedlings of *Q. prinus* and *S. albidum* occurred in areas with less light and deeper litter layers. Based on the size of the ellipses, the habitats of *Q. velutina* and *P. echinata* were more variable than those of *Q. prinus* and *Q. alba*. This variation was primarily associated with shrub cover, litter depth and light intensity gradients.

Seven of the nine habitat variables entered into the stepwise discriminant functions analysis (LITDPTH, NEARNB, MOSS, LIGHT, CANCOV, TOTCOV,

Tab. 2. Frequency (number of points of occurrence per species/total number of points) and importance value ((Relative frequency + Relative density + Relative basal area)/3) for canopy sized trees in each stand. Stands 1 and 2 are in continuous forest, Stand 3 is a forest fragment.

Species	Stand					
	1		2		3	
	F	IV	F	IV	F	IV
<i>Pinus</i> spp.*	47.5	22.4	42.5	11.7	50.0	20.2
<i>Quercus alba</i>	32.5	10.4	52.5	13.7	73.3	25.2
<i>Q. coccinea</i>	7.5	2.1	17.5	4.4	20.0	8.8
<i>Q. prinus</i>	90.0	38.2	87.5	28.7	31.6	34.4
<i>Q. velutina</i>	70.0	26.9	62.5	41.9	36.7	11.1

* Mostly *P. echinata* in Stands 1 and 2, *P. rigida* in Stand 3.

Tab. 3. Means of nine habitat variables for one year old tree seedlings (N = 25 per species) in an oak-pine forest in the New Jersey Pine Barrens.

Variable	<i>Quercus coccinea</i>	<i>Quercus velutina</i>	<i>Quercus prinus</i>	<i>Quercus alba</i>	<i>Pinus echinata</i>	<i>Sassafras albidum</i>	P*
Litter depth	2.2 ^b	2.2 ^{b,c}	3.5 ^a	2.5 ^{a,b}	1.1 ^c	3.6 ^a	0.0001
Nearest neighbor distance	31.9 ^a	20.8	14.3	17.8	13.5	15.8	0.0014
Moss cover	14.1	17.4	2.6	1.6	33.4 ^a	12.4	0.0005
Lichen cover	0.8	2.0	0.9	0.2	1.8	0.6	0.2955
Percent light	37.6 ^{a,b}	48.9 ^a	22.6 ^b	28.8 ^b	33.9 ^{a,b}	33.3 ^{a,b}	0.0172
Canopy cover	72.6 ^{a,b}	63.2 ^{a,b,c}	54.4 ^c	73.8 ^a	59.4 ^{b,c}	61.3 ^{b,c}	0.0188
Ground cover	5.1	16.6	16.4	12.9	16.8	16.7	0.4342
Total cover	77.6	79.8	70.8	86.7	76.2	78.0	0.6426
Canopy type	0.1	0.2	0.1	0.3	0.1	0.1	–

* Values in each row with different superscripts are significantly different based on Analysis of variance and Duncan's multiple range test. Statistical differences were not determined for canopy type.

CANTYPE). Based on Cohen's Kappa, the DFA classification matrix (not shown) was 42% better than a randomly constructed classification matrix ($Z = 11.2$, $P < 0.01$). Percent of samples correctly classified ranged from a low of 36.0 for *Q. velutina* to a high of 64.0 for *P. echinata*. Because *Q. velutina* had the most variable habitat (PCA, Fig. 1), it is not surprising that the DFA could not derive a well-defined habitat type for this species. Although the PCA also indicated variable habitat for *P. echinata*, 16 of the 25 samples were correctly classified as pine habitat by the DFA. In fact, this was the only species with zero values in the classification matrix; therefore, although the habitat of *P. echinata* is heterogeneous, it can be distinguished from the habitats of *Q. coccinea* and *S. albidum*. Given the degree of microsite variation in this stand, the habitat breadth of one year old tree seedlings is large, but even so, habitat requirements of some species are sufficiently precise that the amount of suitable habitat in a stand may affect seedling abundance, recruitment, and species diversity.

3.2. Stand habitat analysis

Seedling density of several species did, in fact, differ among the three forest stands (Tab. 5). In particular, density of *Pinus* spp., *Q. velutina*, and *Q. prinus* seedlings was lowest in the forest fragment that had not been recently burned (Stand 3). The lower density may reflect between-site differences in the amount of habitat suitable for seedling establishment. Based on measurements at randomly located points in each stand, litter depth, ground cover, and total cover were significantly greater while nearest neighbor distance and percent light were significantly lower in the forest fragment compared with the other two stands (Tab. 6).

Principal components analysis of the stand habitat data set produced three factors with eigenvalues greater than 1.0 (70.4% of the variance, Tab. 7). Axis I defined a cover-litter depth-light intensity gradient. Where cover values for each stratum were large, a deep litter

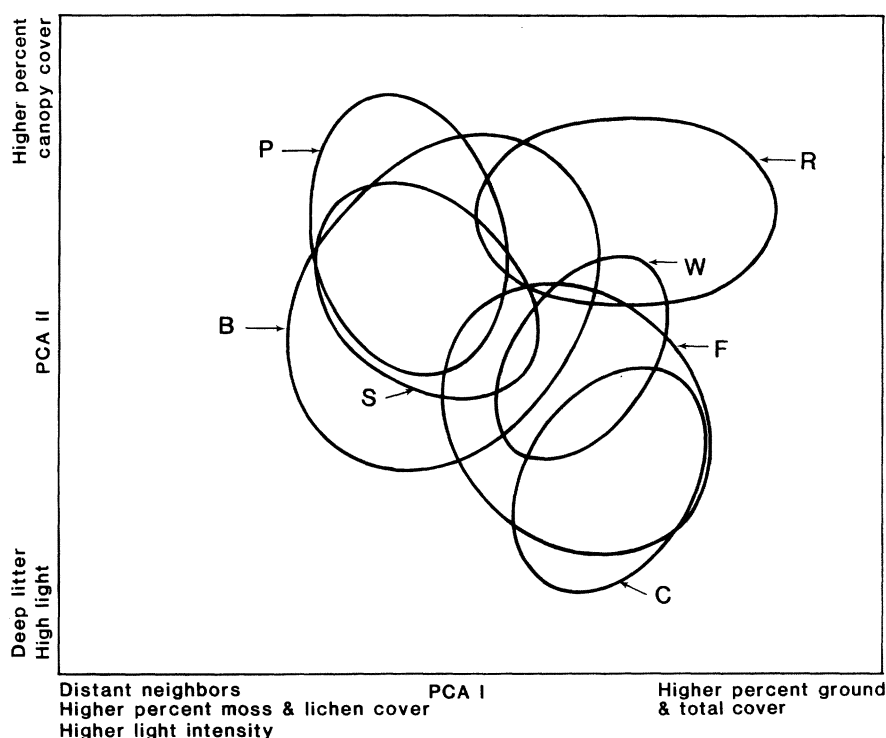
layer developed and light intensity was reduced near the forest floor. Axis II again indicated that light intensity was negatively correlated with canopy and ground cover. Axis III was based on differences in canopy type between stands. The distribution of samples in the space defined by the first two principal components (Fig. 2) showed that samples from Stand 3 occurred at the high percent cover-deep litter layer end of the first axis, whereas samples from Stands 1 and 2 occurred more toward the higher light end of this axis. Axis II separated samples from Stands 1 and 2 based on light intensity which was generally lower in the former stand. Based on size of ellipses, habitat heterogeneity was greatest in Stand 1 because it had several samples with high moss and lichen cover and no litter layer.

Five of the nine habitat variables (LITDPTH, NEARNB, MOSS, LIGHT, GRNDCOV) entered into the stepwise DFA (Tab. 8). Based on Cohen's Kappa the DFA classification matrix was 42% better than a randomly constructed classification matrix ($Z = 5.47$, P

Tab. 4. Principal components analysis of the correlation matrix of nine variables representing the habitat structure surrounding one year old tree seedlings in an oak-pine forest. Four factors had eigenvalues greater than 1.0.

Variable	Factor			
	I	II	III	IV
Litter depth	0.62	-0.46	-0.03	0.03
Nearest neighbor distance	-0.51	0.24	0.41	0.20
Moss cover	-0.59	0.52	-0.35	-0.13
Lichen cover	-0.44	0.51	-0.49	0.01
Percent light	-0.57	-0.29	0.05	-0.35
Canopy cover	0.30	0.68	0.59	-0.17
Ground cover	0.71	0.15	-0.51	-0.10
Total cover	0.75	0.60	0.04	-0.20
Canopy type	-0.10	-0.19	0.05	-0.91
Variance	29.7	19.6	12.7	12.0

Fig. 1. Principal components analysis of habitat for one year old seedlings of six tree species. Axis I (29.7% of the variance) is a gradient from canopy cover to moss and lichen cover and higher light. Axis II (19.6% of the variance) is a gradient from high total cover and shallow litter to habitats with less cover and deeper litter (see Tab. 4). B = *Quercus velutina*, C = *Q. prinus*, F = *Sassafras albidum*, P = *Pinus echinata*, R = random points, S = *Q. coccinea*, W = *Q. alba*. Sample distribution is represented by 95% concentration ellipses.



< 0.01). The heterogeneity of habitat in Stand 1 was reflected by the low number of correctly classified samples in the matrix. Although only 52% of the samples from Stand 1 were correctly classified, most of the reclassified samples were moved to the Stand 2 habitat group. In addition, only two of the samples from Stand 3 were classified as members of the Stand 1 habitat group. Thus, it appears that the physical environment to which seedlings are subjected in these two stands is considerably different. When the samples are plotted in the space defined by the first two DFA axes (Fig. 3), most samples from Stand 3 are separated from those in Stands 1 and 2 along the first axis. In contrast, sample distribution along DFA axis II is largely similar. There-

fore, the general habitat types available in Stand 3 are sufficiently different from those in Stands 1 and 2 primarily as a function of denser vegetation and deeper litter layers in Stand 3.

4. Discussion

Based on the habitat variables measured in this study, it is clear that microhabitat gradients occur in the forest

Tab. 5. Density per hectare of tree seedlings in three oak-pine stands in the New Jersey Pine Barrens.

Species	Stand		
	1	2	3
<i>Pinus</i> spp. ^a	18400	23400	400
<i>Quercus velutina</i>	3000	3333	600
<i>Q. prinus</i>	4600	1600	200
<i>Q. coccinea</i>	— ^b	267	1600
<i>Q. alba</i>	600	933	800
<i>Sassafras albidum</i>	600	400	— ^b

a. Includes *Pinus echinata* and *P. rigida*.

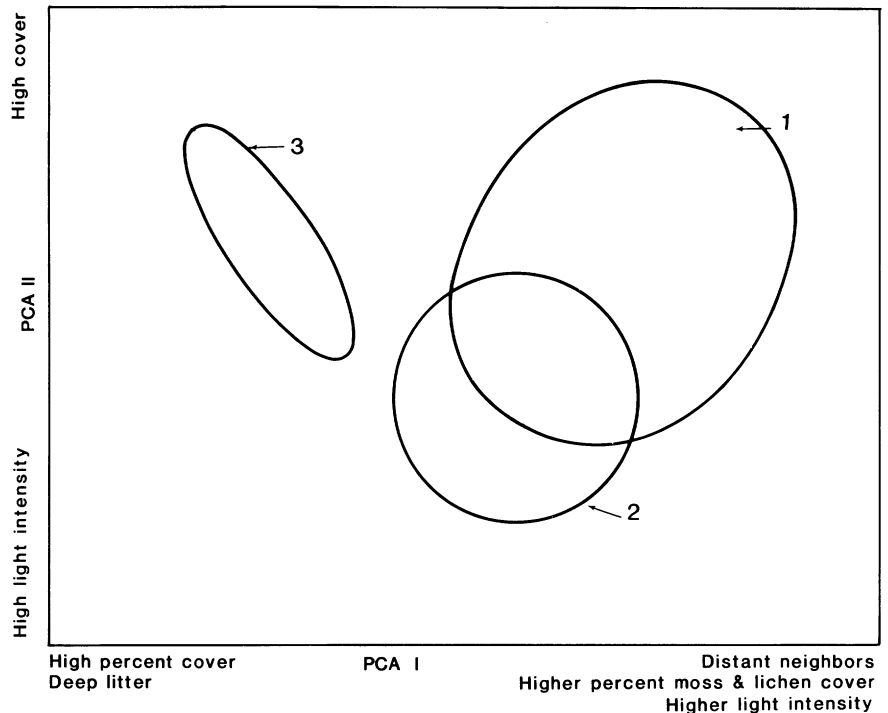
b. Did not occur in quadrat samples but was present in the stand.

Tab. 6. Means of nine habitat variables measured at 25 random points in three oak-pine forests in the New Jersey Pine Barrens.

Variable	Stand			P*
	1	2	3	
Litter depth	2.8 ^a	3.3 ^a	6.1 ^b	0.0001
Nearest neighbor distance	17.5 ^a	9.9 ^a	6.0 ^b	0.0001
Moss cover	8.8	3.2	0.1	0.0822
Lichen cover	2.7 ^a	0.6 ^b	0.1 ^b	0.0219
Percent light	31.1 ^a	21.2 ^a	8.2 ^b	0.0027
Canopy cover	63.2	71.6	78.0	0.1175
Ground cover	43.7 ^a	35.0 ^a	71.2 ^b	0.0002
Total cover	106.9 ^a	106.6 ^a	149.2 ^b	0.0034
Canopy type	0.1	0.2	0.1	—

* Statistical differences are based on analysis of variance and Duncan's multiple range test. Values in each row with different superscripts were significantly different. Statistical differences were not determined for canopy type.

Fig. 2. Principal components analysis of habitat for twenty-five randomly located points in each of three oak-pine stands. Stands 1 and 2 are in continuous forest, Stand 3 is a forest fragment. Axis I (44.4% of the variance) is a cover-litter depth-light intensity gradient. Axis II (14.5% of the variance) is also a canopy cover-light gradient (see Tab. 6).



floor of oak-pine forests in the Pine Barrens (Tab. 4, Fig. 1, 2). Except for light, the habitat variables we measured are relatively stable at least over time spans of 1–2 growing seasons. A single measurement of light provides little information about how light quantity fluctuates seasonally. Nevertheless, we believe that one measurement of PAR in combination with ground layer

and canopy cover estimates provides an approximation of the light environment experienced by a seedling. Litter depth and moss cover can affect percolation and evaporation of moisture in the soil (Moul and Buell 1955). Finally, nearest neighbor distance is an indirect measure of the potential competitive environment in which a species occurs (Yeaton and Cody 1976). We be-

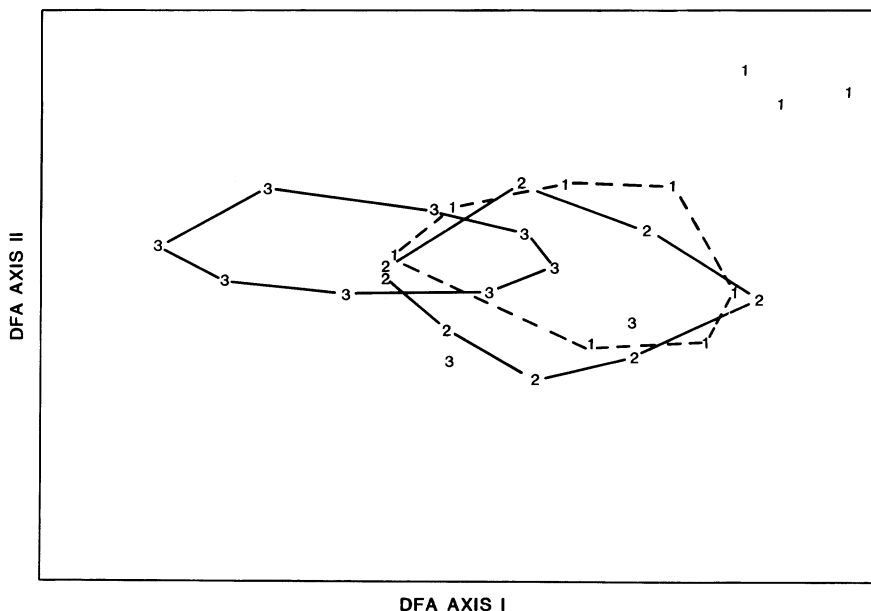


Fig. 3. Discriminant functions analysis of habitat for 25 randomly located points in each of three oak-pine stands. Five variables entered into the discriminant function. 1 = Stand 1, 2 = Stand 2, 3 = Stand 3. Polygons enclose the majority of points in the discriminant space. Outliers are noted by numbers.

Tab. 7. Principal component analysis of the correlation matrix of nine habitat variables representing the habitat structure of random points in three oak-pine forests. Three factors had eigenvalues greater than one.

Variable	Factor		
	I	II	III
Litter depth	-0.34	0.11	0.07
Nearest neighbor distance	0.33	0.42	-0.23
Moss cover	0.40	0.33	0.17
Lichen cover	0.37	0.47	0.01
Percent light	0.36	-0.09	-0.07
Canopy cover	-0.24	0.46	-0.15
Ground cover	-0.35	0.23	0.11
Total cover	-0.41	0.45	-0.01
Canopy type	0.06	0.08	0.93
Variance	44.4	14.5	11.5

Tab. 8. Classification matrix from a discriminant functions analysis (DFA) of habitat at 25 randomly located points in three oak-pine forests. Cohen's Kappa was 0.422 indicating that the DFA classification matrix is about 42% better than a randomly constructed matrix. Five of nine habitat variables entered into the stepwise DFA. $f = 5.93$; $df = 10,136$; $p < 0.01$.

Group	Percent correct	Number of cases classified into –		
		Stand 1	Stand 2	Stand 3
Stand 1	52.0	13	8	4
Stand 2	60.0	6	15	4
Stand 3	72.0	2	5	18
Total		21	28	26

lieve that together, the habitat variables we measured provide a rough but general description of the physical and biotic heterogeneity in the microsites surrounding one year old tree seedlings.

Differences among species in litter depth, light and nearest neighbor distance correlate with physical, resource and competitive gradients along which the distribution of seedlings appears to be non-random (Fig. 1). The statistical analysis (e.g. ANOVA) of random versus occupied habitat is both unjustified and precarious. At least some and possibly all random points could occur in areas suitable for establishment of seedlings. Also, even though a seedling may not occur at or near a random point, it does not necessarily imply that this microhabitat is unsuitable for seedling growth. Instead, absence may simply be a function of the vagaries of seed dispersal. The analysis of occupied sites provides a meaningful description of the habitat niche of a plant, and such an analysis would only be complicated by a statistical comparison of species habitat with presently unoccupied space (Johnson 1981, James et al. 1984).

There is considerable similarity in the habitats occupied by seedlings of different tree species. Differentiation of plant and animal species along environmental gradients is a common phenomenon (e.g. Whittaker 1967, Bratton 1976, Gorman and Karr 1978, Dueser and Shugart 1979, Collins et al. 1982, Mann and Shugart 1983). Complex factors such as canopy type have been shown to influence the distribution of herbaceous layer species in the understory of mesic forests (Beatty 1984, Crozier and Boerner 1984). Canopy type has a limited effect on seedling distribution in the Pine Barrens (Collins and Good 1985). Because *Quercus* seeds contain large energy reserves, one year old seedlings may not be highly site specific. Nevertheless, our analyses based on intrastand patterns suggest that most one year old tree seedlings occur within a subset of the available habitat on the forest floor (Fig. 1). Perhaps more distinct differences in microspatial preferences among oaks may occur later in the life cycle as growth intensifies competition for light and nutrients. For example, in a 30-yr Michigan old field, seedlings of *Q. alba* and *Q. velutina* colonized open patches of bare soil but survivorship was highest in patches where other vegetation was present (Harrison and Werner 1984). Pine seedlings, on the other hand, usually colonize open patches of mineral soil and remain shade intolerant during growth (Little and Moore 1949).

Differences exist in the number and composition of seedlings among oak-pine stands (Tab. 5). This may reflect the composition and abundance of adults for species such as *Q. coccinea*, but canopy individuals of the other species were widely scattered throughout each stand (Tab. 2). In addition, seed distribution is unlikely to be limited by adult distribution in animal dispersed species such as *Quercus* and *Sassafras*.

Clear differences in microhabitat exist among the stands, as well (Tab. 6). Several variables including litter depth, ground cover, and total cover are significantly higher in Stand 3 than in Stands 1 and 2. Many fewer seedlings of *Pinus*, *Q. prinus* and *Q. velutina* occur in Stand 3. This stand is a forest fragment that has been isolated from the main body of the Pine Barrens by paved roads for at least 15 yr. Such a narrow barrier would appear inconsequential relative to seed dispersal or population structure. The roadway, however, provides an unnatural fire break and, in effect, serves to disrupt the natural disturbance regime characteristic of Pine Barrens forests (Little 1979b). Reduced fire frequency rapidly leads to increased shrub cover and deep litter layers (Little and Moore 1949). Pines require a mineral seedbed and reduced litter layer for germination and survival (Little 1979b). Some oak seedlings, on the other hand, had high survivorship when the litter was 2.5–5.0 cm deep (Wood 1938). This effect of litter is not uniform among oak species, apparently, because only *Q. coccinea* and *Q. alba* appeared to be unaffected by the litter depth ($\bar{X} = 6.2$ cm) and vegetation cover gradients in Stand 3. Seedling densities of *Q. prinus* and

Q. velutina were reduced in Stand 3 relative to the other stands.

Our habitat analysis for plants is similar to that used by Mann and Shugart (1983) in their study of four species of *Galium*. They noted niche differentiation among species based on canopy density, litter type and overstory type. Canopy and litter were important variables in our study, however, our methods differ in scale. Mann and Shugart (1983) included large-scale features of the environment where populations of *Galium* occurred. We assessed only aspects of the physical environment immediately adjacent to one year old tree seedlings. We believe this constitutes a more direct approach to the analysis of the regeneration niche of plants (Grubb 1977).

Obviously, the suite of variables measured for this study does not incorporate the complete environment in which a seedling occurs. Numerous other microsite factors including soil depth, moisture, nutrients and pH along with wind speed, humidity, microtopography, predation, etc., affect seed germination and seedling establishment. Soil nutrient, moisture, and pH values tend to fluctuate over short time periods within a growing season (Lockman and Molloy 1984). Indeed, these variables are altered by the presence of an actively growing tree seedling. Thus, although these factors may have an important impact on seedling survival, their adequate measurement relative to germination is difficult. In addition, the importance of soil nutrients may be buffered at this stage of the life cycle by the seed reserves provided in large-seeded species such as *Quercus* and *Sassafras*. Soil depth and microtopography have been found to be important within-community variables affecting the distribution of herbaceous species (Bratton 1976, Thompson 1980), however, these factors are relatively invariant in the Pine Barrens. Upland soils of the Outer Coastal Plain of New Jersey are generally level, deep, well drained, coarse sands; large rocks are rare (Tedrow 1979).

The use of individually-centered samples has not been widely applied in plant ecology (Turkington and Harper 1979, MacMahon et al. 1981) despite their utility for addressing patterns at the population and community levels. Quadrat size and habitat variables could be selected for appropriate measurements in different systems (e.g. microhabitat patterns among spring ephemerals). When used in conjunction with ordinations, the individually-centered sample approach may facilitate the development of suitable hypotheses for the experimental analysis of the species regeneration niche (Grubb 1977). In this study, we determined microenvironmental variation along axes which can display niche differentiation based on a subset of easily measured physical and biotic variables. It is clear that one year old tree seedlings show fine-scale microhabitat differentiation among species. In addition, the absolute number of seedlings differs between forest stands. This difference

is due, in part, to dissimilar microhabitat gradients between forest stands.

Acknowledgements – We thank D. Gibson, F. James, S. Pickett, P. Risser and L. Wallace for providing many helpful comments on earlier versions of the manuscript. Also, we thank P. Collins for help with the field work. This research was supported by grants to REG from the Victoria Foundation and Insider Funds.

References

- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. – *Ecology* 65: 1406–1420.
- Bratton, S. P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. – *Am. Nat.* 110: 679–693.
- Buell, M. F. and Cantlon, J. E. 1950. A study of two communities of the New Jersey Pine Barrens and a comparison of methods. – *Ecology* 31: 567–586.
- Collins, S. L. 1983. Geographic variation in habitat structure for the wood warblers in Maine and Minnesota. – *Oecologia* (Berl.) 59: 246–252.
- and Good, R. E. 1985. A preliminary analysis of oak-pine vegetation in the New Jersey Pine Barrens. – Technical Report, Center for Coastal and Environmental Studies, Rutgers University, New Brunswick, NJ.
- , James, F. C. and Risser, P. G. 1982. Habitat relationships of wood warblers (Parulidae) in northern central Minnesota. – *Oikos* 39: 50–58.
- Cottam, G. and Curtis, J. T. 1956. The use of distance measures in phytosociological sampling. – *Ecology* 37: 451–460.
- Crozier, C. R. and Boerner, R. E. J. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. – *Oecologia* (Berl.) 62: 337–343.
- Dueser, R. D. and Shugart, H. H. 1979. Niche pattern in a forest floor small mammal fauna. – *Ecology* 60: 108–118.
- Forman, R. T. T. 1979. Pine Barrens: ecosystem and landscape. – Academic Press, New York.
- Goldberg, D. E. and Werner, P. A. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. – *Am. J. Bot.* 70: 1098–1104.
- Good, N. F. and Good, R. E. 1972. Population dynamics of tree seedlings and saplings in a mature eastern hardwood forest. – *Bull. Torrey Bot. Club* 99: 172–178.
- Gorman, O. T. and Karr, J. R. 1978. Habitat structure and stream fish communities. – *Ecology* 59: 507–515.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- Harper, J. L. 1977. Population biology of plants. – Academic Press, New York.
- , Williams, J. T. and Sager, G. R. 1965. The behavior of seeds in soil. I. The heterogeneity of soil surface and its role in determining the establishment of plants from seed. – *J. Ecol.* 53: 273–286.
- Harrison, J. S. and Werner, P. A. 1984. Colonization by oak seedlings into a heterogeneous successional habitat. – *Can. J. Bot.* 62: 559–563.
- Hutchinson, G. E. 1978. An introduction to population ecology. – Yale Univ. Press, New Haven, CT.
- James, F. C. 1971. Ordinations of habitat relationships among breeding birds. – *Wilson Bull.* 83: 215–236.
- , Johnston, R. F., Wamer, N. O., Niemi, G. J. and Boek-

- len, W. J. 1984. The Grinnellian niche of the Wood Thrush. – *Am. Nat.* 124: 17–47.
- Johnson, D. H. 1981. The use and misuse of statistics in wildlife studies. – In: Capen, D. E. (ed.), *Use of multivariate statistics in studies of wildlife habitat*. – US Dept of Agriculture Forest Service General Technical Report RM-87, pp. 4–10.
- Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. – *Ecology* 58: 810–819.
- Sokal, R. R. and Rohlf, F. J. 1969. *Biometry*. – Freeman, New York.
- Sydes, C. and Grime, J. P. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. – *J. Ecol.* 69: 237–248.
- Tedrow, J. C. F. 1979. Development of Pine Barrens soils. – In: Forman, R. T. T. (ed.), *Pine Barrens: ecosystem and landscape*. – Academic Press, New York, pp. 61–80.
- Thompson, J. N. 1980. Treefalls and colonization patterns of temperate forest herbs. – *Am. Midl. Nat.* 104: 176–184.
- Titus, K., Mosher, J. A. and Williams, B. K. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. – *Am. Midl. Nat.* 111: 1–7.
- Turkington, R. and Harper, J. L. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. – *J. Ecol.* 67: 201–218.
- Wacker, P. O. 1979. Human exploitation of the New Jersey Pine Barrens before 1900. – In: Forman, R. T. T. (ed.), *Pine Barrens: ecosystem and landscape*. – Academic Press, New York, pp. 3–23.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. – *Biol. Rev.* 42: 207–264.
- 1979. Vegetational relationships of the Pine Barrens. In: Forman, R. T. T. (ed.), *Pine Barrens: ecosystem and landscape*. – Academic Press, New York, pp. 315–322.
- Wiens, J. A. and Rotenberry, J. T. 1981. Habitat associations and community structure of birds in shrubsteppe environments. – *Ecol. Monogr.* 51: 21–41.
- Wood, M. O. 1938. Seedling reproduction of oak in southern New Jersey. – *Ecology* 19: 276–293.
- Yeaton, R. I. and Cody, M. L. 1976. Competition and spacing in plant communities: the northern Mojave Desert. – *J. Ecol.* 64: 689–696.
- Mann, L. K. and Shugart, H. H. 1983. Discriminant analysis of some east Tennessee forest herb niches. – *Vegetatio* 52: 77–89.
- Merz, R. W. and Boyce, S. G. 1956. The age of oak “seedlings”. – *J. Forestry* 54: 774–775.
- Moul, E. T. and Buell, M. F. 1955. Moss cover and rainfall interception in frequently burned sites in the New Jersey Pine Barrens. – *Bull. Torrey Bot. Club* 82: 155–162.
- Parrash, J. A. D. and Bazzaz, F. A. 1985. Ontogenetic niche shifts in old-field annuals. – *Ecology* 66: 1296–1302.
- Robichaud, B. and Buell, M. F. 1973. The vegetation of New Jersey: a study of landscape diversity. – Rutgers Univ. Press, New Brunswick, NJ.
- Shugart, H. H. 1981. An overview of multivariate methods and their application to studies of wildlife habitat. – In: Capen,