Canopy-ground layer Relationships of Oak-pine Forests in the New Jersey Pine Barrens

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Abstract: The relative effects of biotic and abiotic factors on the distribution of ground layer species were determined in oak-pine forests in the New Jersey Pine Barrens. Cover of ground layer species and tree-seedling density were measured in three oak-pine stands with different disturbance histories. In addition, soil *p*H and nutrient levels, light and litter depth were measured beneath different canopy species. There were significant differences in amounts of Mg and Ca beneath canopies of different tree species. Few significant relationships were found between canopy type and distribution of ground layer species. The shrubs *Gaylussacia baccata* and *Vaccinium vacillans* were consistently randomly distributed. Significant differences were occasionally observed for some herbaceous species (*Carex pensylvanica, Melampyrum lineare*), which produced less cover than expected by chance beneath the canopy of *Quercus alba.* These differences were not related to soil variables beneath *Q. alba.* Overall, it appears that biotic interactions within the ground layer of these forests have more effect on species distribution than canopy type or soil nutrient levels.

Introduction

Numerous studies have documented the existence of pattern in vegetation and the correlation of this pattern with environmental variables (Greig-Smith, 1979). In forests, for example, ground layer species distribution may be correlated with canopy composition (Crozier and Boerner, 1984; Beatty, 1984), litter and soil depth gradients (Sydes and Grime, 1981) and interspecific competition (Maguire and Forman, 1983). These factors act at different scales and may impose an increasing degree of variability along an increasing spatial scale. That is, beneath the canopy of an individual tree, gradients of species composition and soil nutrients may occur with increasing distance from the tree trunk (Bratton, 1976; Cloutier, 1985). At the scale of multispecies canopy cover, species assemblages may differ beneath deciduous vs. coniferous vegetation (Hicks, 1980; Beatty, 1984).

The interplay between organisms and the environment, however, may be moderated by periodic disturbances (Connell, 1978). Thus, relationships between canopy and ground layer species may occur in northern hardwood forests where small scale disturbances (gaps) are common (Runkle, 1985), but chronic disturbances are rare (Canham and Loucks, 1984). For example, Forcier (1975) described patterns of species replacement in canopy gaps in northern hardwood forests. Runkle (1981) suggested that such canopy-seedling relationships would only develop in low diversity communities. Some oak-dominated forests are subjected to periodic destructive fires (Little, 1979; Henderson and Long, 1984; McCune and Cottam, 1985) as well as small scale gap-forming processes. The Pine Barrens of southern New Jersey provide an excellent system for the study of canopy-ground layer relations in highly disturbed, low diversity forests. Tree species richness is low in these forests but canopy-seedling relationships are poorly defined (Collins and Good, in press). The large scale pattern of vegetation in the Pine Barrens is attributed to fire frequency and intensity (Little, 1979), although soil moisture and nutrient gradients probably interact with fire to produce the regional vegetation pattern (Whittaker, 1979). The purposes of this research were to determine if: (1) differences exist in the environment beneath different canopy species; (2) the distribu-

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tion of individual ground layer species is related to canopy type, and (3) the assemblage of ground layer species is different beneath different canopy species.

MATERIALS AND METHODS

Study area. —The New Jersey Pine Barrens (Pinelands) occupies 445,000 ha on the outer coastal plain of southern New Jersey. Upland vegetation includes the pine plains, pine-oak and oak-pine forest types (McCormick, 1979). Oak-pine forests are abundant in the southern half of the Pine Barrens, but occur as scattered stands throughout much of the northern regions of the Pinelands. Oak-pine forests are dominated by various combinations of oak and pine species (McCormick, 1979). Canopy-ground layer relationships were studied in three oak-pine stands in the northern part of the Pinelands. Stands 1 and 2, within Lebanon State Forest, are part of large, continuous tracts of vegetation that have been subjected to periodic controlled fires. Both stands have been burned within the last 5 years. Stand 3 is a forest fragment in nearby Lebanon Lake Estates development that has been isolated from the main body of the Pine Barrens by paved roads for at least 15 years. This stand has not burned recently. Based on 40 (Stands 1 and 2) or 30 (Stand 3) point-quarter samples per stand, these forests are dominated by *Quercus velutina, Q. alba* and *Q. prinus*. Pines make up ca. 20% of total importance in each stand. Because of the similarity in species composition, along with the differences in disturbance history, these stands provide useful sites for a comparison of the role of disturbance in affecting composition and distribution of ground layer species in oak-pine forests.

Field methods. —In July 1984, ground layer vegetation in the three stands was sampled with 100 (Stand 3) or 150 (Stands 1 and 2) randomly located 0.5 m^2 quadrats. Cover in 10% cover classes was estimated visually for all species rooted in each quadrat. Number of tree seedlings of each canopy species was counted in each quadrat. Additionally, the identity of the canopy tree immediately above each quadrat was recorded. On 4-5 August 1985, environmental variables were measured in Stand 1 beneath the canopies of five randomly selected individuals of each tree species (*Quercus alba, Q. coccinea, Q. prinus, Q. velutina, Pinus echinata*). Light was measured at five points above the ground layer beneath each canopy tree with a LiCor light meter and quantum sensor. Light measurements were recorded between 1000-1100 hr and expressed as a percentage of maximum light measured outside the tree canopy. Litter depth was determined at 10 random points beneath each canopy tree by inserting a wire probe through the litter layer down to the soil surface. One soil sample was collected to a depth of 5 cm from beneath each canopy tree for the determination of *p*H, Mg, P, K, Ca, NO_3-N, NH_3-N and conductivity. Soil samples were analyzed by the Soil and Plant Testing Laboratory at Rutgers University.

Data analysis. —Average cover was calculated for each ground layer species in each stand. To determine if canopy composition has an effect on distribution and abundance of ground layer species, the percent of total cover for a species was compared to the expected percent cover based on random distribution. The latter values were determined as the proportion of the total number of quadrats that occurred beneath a given canopy species. That is, if 20 of 100 randomly located quadrats occurred beneath *Quercus alba* and, if a ground layer species such as *Melampyrum lineare* is distributed randomly, then we would expect that 20% of the total cover of *M. lineare* should occur beneath *Q. alba*. If the percentage is significantly lower or higher then expected, the distribution of *M. lineare* may be affected by the environment beneath *Q. alba*. Differences between observed and expected values were tested by chi square. Density of tree seedlings beneath each canopy species was compared to a randomly expected distribution in the same way.

In addition to differences among individual ground layer species, the overall assemblage of plants may be dissimilar beneath different species of canopy trees (Hicks, 1980; Beatty, 1984). An analysis of the distribution of individual species, however, would not demonstrate the existence of community-level differences, if they exist. Ordinations, on the other hand, provide a means of delimiting community-level patterns in forest floor vegetation and permit comparison of species assemblages beneath different tree species.

To determine the degree of compositional variation and the relationship between ground layer pattern and canopy type, the quadrat data for the ground layer samples in each stand were subjected to detrended correspondence analysis (DCA, Hill, 1979). Comparisons of ordination techniques using data sets with known properties have indicated that DCA produces reliable ordinations (Hill and Gauch, 1980; *but see* Beals, 1984). To further decrease distortion, del Moral and Watson (1978) recommend deleting rare species prior to ordination analyses. Because the ground layer in these forests contained few species, only those occurring in less than two quadrats were deleted prior to the ordinations. This resulted in 12, 14 and 11 species used in the analyses of ground layer assemblages in Stands 1, 2 and 3, respectively. To minimize distortion of the ordination by the remaining uncommon taxa, rare species were downweighted in proportion to their frequencies (Hill, 1979). In the ordinations for each stand, samples from beneath each canopy species were circumscribed to determine if the assemblage of ground layer species can be differentiated by canopy type.

Because of the small sample sizes for some environmental variables, data were analyzed by a nonparametric statistical test. Values for litter depth and light were averaged by canopy individual prior to statistical analysis. Statistical differences for each variable compared between tree species were determined by Friedman one-way analysis of variance (Siegel, 1956). To be conservative, $P<0.01$ was considered to represent a significant difference from random expectation.

RESULTS

Distribution of individual species. —A total of 19 species occurred in the ground layer of the three forest stands, of which 14 species occurred in at least two stands (Table 1). In general, the composition of the ground layer in these stands is very similar; differences primarily reflect a shift in dominance among the species. *Gaylussacia baccata* and *Vaccinium vacillans* were important shrubs in each stand. *Gaultheria procumbens,* a common Pine Barrens species, was second in importance in Stand 3. Total cover was greatest and bare ground was lowest in this stand.

In Stand 1, none of the common ground layer herbs or shrubs showed an affinity for any canopy species or canopy openings. Density of *Quercus prinus* seedlings was significantly different from a random distribution ($\chi^2 = 14.8$, $P = 0.01$). Seedlings of *Quercus prinus* occurred more often than expected by chance beneath *Q. velutina* and less often than expected beneath pines.

The distribution of the herb *C. pensylvanica* was highly significantly different from random ($\chi^2 = 31.2$, $P = 0.01$) in Stand 2. Cover of *Carex pensylvanica* was lower than expected by chance beneath the canopy of *Quercus alba* and *Q. coccinea* and more abundant in canopy openings than expected. Density of *Q. velutina* seedlings in Stand 2 was significantly different ($\chi^2 = 30.2$, $P = 0.01$) from a random distribution. Seedlings of *Q. velutina* occurred more often than expected by chance beneath the canopy of *Q. prinus* and less often than expected beneath *Q. alba* as well as under its own canopy.

In the forest fragment (Stand 3), cover of the herb *Melampyrum lineare* was significantly different ($\chi^2 = 85.2$, $P = 0.01$) from the predicted distribution. Cover of *M. lineare* was lower than expected by chance beneath *Quercus alba* and greater than expected beneath *Q. velutina.* Tree seedlings were rare in this stand, thus only total seedling density could be compared to the random distribution. Total density of tree seedlings was significantly different ($\chi^2 = 93.6$, $P = 0.01$) from the predicted distribution. In general, tree seedlings were more abundant than expected by chance beneath the canopy of *Q. alba* and lower than expected beneath *Q. prinus.*

Community patterns. —The first axis of the DCA ordination for Stand 1 is a compositional gradient separating samples with high cover values for *Gaylussacia baccata, Quercus* *alba* seedlings and *Vaccinium vacillans* from samples dominated by *Q. velutina* seedlings. Axis II of the DCA ordination separated samples with *Q. velutina* and *Pinus echinata* seedlings, and *Melampyrum lineare* from samples in which *G. frondosa* was abundant. Samples were plotted in the space defined by species gradients and then circumscribed based on the canopy type above each quadrat (Fig. 1A). Samples are distributed in a triangular pattern across the center of the figure, with the majority of samples in the left center part of the ordination. Thus, the most common species assemblage in the ground layer of Stand 1 contains *G. baccata* and *V. vacillans* with scattered seedlings of *Q. alba.* The polygons encompassing the samples beneath different tree species overlap extensively indicating that, in general, species assemblages are similar beneath different canopy species. Outliers, samples dominated by uncommon taxa, occurred beneath most tree species.

The first axis of the DCA ordination for Stand 2 separated samples containing common species such as *Gaylussacia baccata,* seedlings of *Quercus alba, Melampyrum lineare* and *Carex pensylvanica* from samples with uncommon species including *Smilax glauca* and *G. frondosa.* Many of these same taxa defined the gradient along the second axis, as well. The majority of samples was located along an area running from the left center to the lower right portion of the ordination (Fig. 1B). The most common species assemblage in the ground layer of this forest contained the shrubs *G. baccata* and *Vaccinium vacillans,* herbs such as *M. lineare* and *C. pensylvanica,* and scattered seedlings of *Quercus* spp. The polygons circumscribing quadrats beneath different tree species overlap extensively. Variation within a canopy type is simply a function of the number of samples beneath each canopy species. Outlier samples were not restricted to any particular canopy type.

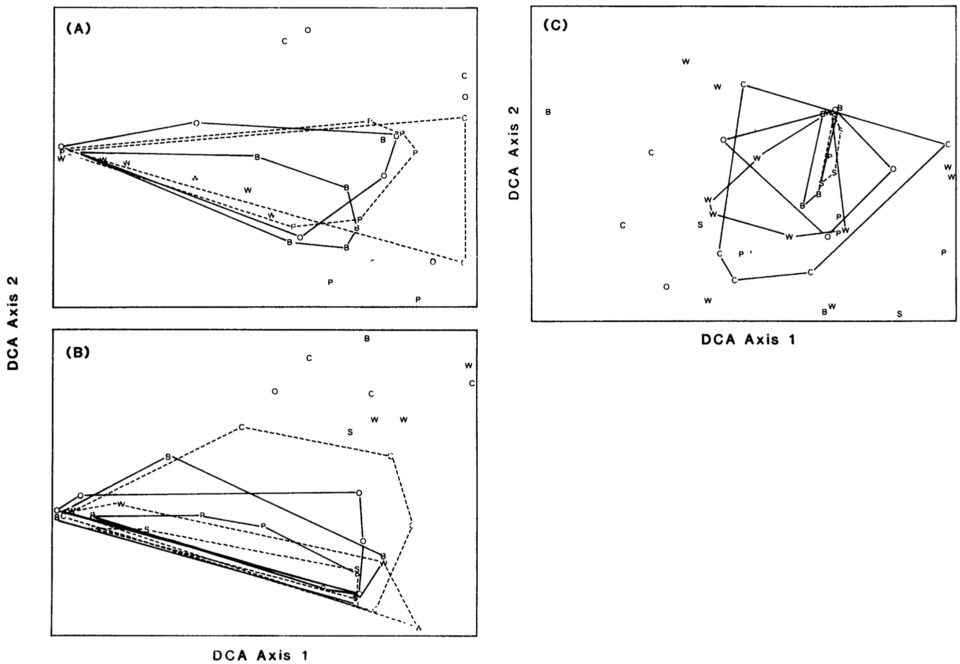

Fig. 1 A-C. — Detrended correspondence analysis ordinations of herbaceous layer vegetation in three oak-pine forests in the New Jersey Pine Barrens. The polygons encompass the samples located beneath different species of trees. Outliers, samples dominated by uncommon herbaceous layer species, are denoted by individual letters. B = *Quercus velutina,* C = *Q. prinus,* O = open, P = *Pinus* spp., S = *Q. coccinea,* W = *Q. alba*

In Stand 3, axis I of the DCA ordination is a gradient from samples containing *Quercus ilicifolia, Carex pensylvanica,* and seedlings of *Q. velutina* and *Q. alba,* to samples dominated by *Gaylussacia frondosa.* The second axis separates samples with *Gaultheria procumbens* and seedlings of *Pinus rigida* from samples with *Quercus spp.* and *C. pensylvanica.* Most of the samples are located in the right center of the ordination (Fig. 1C) indicating dominance by *G. baccata.* Again, the polygons circumscribing the samples located beneath each tree species overlap extensively, and variance is a function of sample size. Outliers are common and scattered along both ordination axes. Samples to the left contain *Quercus* seedlings while those to the far right contain *G. frondosa.* The outliers do not appear to be associated with any particular canopy type.

Environmental variables.—Soil *p*H, percent light and amounts of soil nutrients were low beneath the canopies of the different tree species in Stand 1 (Table 2). Concentration of NO_3-N and conductivity were below the range of detection. Concentrations of Mg and Ca were significantly different among the different tree species (Table 2). Mg was highest under the canopy of *Pinus echinata* and lowest under *Quercus coccinea.* Differences in the amount of Ca were more dramatic ranging from about 33 kg ha^{-1} beneath *Q. velutina* to 180 kg ha^{-1} beneath *Q. alba* and *Q. coccinea.* The homogeneous pattern of species distribution at the scale of canopy type (Fig. 1) correlates well with the lack of

TABLE 1.—Average cover of ground layer species in three oak-pine stands in the New Jersey Pine Barrens

Species	Stand 1	Stand 2	Stand 3
Carex pensylvanica	2.4	1.8	0.8
Crataegus sp.	0.3		
Gaultheria procumbens			11.8
Gaylussacia baccata	14.8	43.0	51.9
G. frondosa	2.0	0.8	5.6
Lyonia mariana		0.1	
Melampyrum lineare	0.5	1.2	1.1
Pinus spp.*	0.9	1.7	0.3
Pteridium aquilinum		0.1	
Quercus alba	0.1	0.4	0.1
Q. coccinea		0.1	0.6
Q. ilicifolia	2.4	0.4	3.0
Q. prinus	0.9	0.4	0.2
Q. velutina	1.5	1.6	0.3
Sassafras albidum	0.3	0.2	
Smilax glauca	0.1	0.1	0.1
Solidago sp.	0.1		
Vaccinium vacillans	23.9	18.8	8.6
Bare ground	51.1	48.2	24.4

*Includes both *P. rigida* and *P. echinata*

TABLE 2.—Mean (± SD) of environmental variables beneath the canopy of five tree species in oak-pine forests in the New Jersey Pine Barrens. Nutrient values are kilograms per hectare, light is percent of full sunlight. Amounts of NO_3-N and conductivity were too low to be detected. Statistical differences among species for each environmental variable are based on Friedman's one-way analysis of variance

Tree species	*p*H	Mg	P	K	Ca	NH_3-N	Light	Litter depth (cm)
Pinus echinata	3.6 ± 0.2	41.2 ± 11.1	9.4 ± 1.1	44.4 ± 15.0	91.0 ± 26.9	9.0 ± 1.9	15.6 ± 2.5	5.4 ± 1.3
Quercus alba	3.7 ± 0.1	29.1 ± 4.4	9.6 ± 1.3	51.8 ± 13.7	179.7 ± 33.2	7.6 ± 3.1	16.3 ± 8.2	3.2 ± 1.8
Q. coccinea	3.8 ± 0.2	20.2 ± 4.2	10.5 ± 1.3	43.5 ± 8.5	179.3 ± 19.8	9.0 ± 2.6	7.6 ± 3.4	3.6 ± 0.7
Q. prinus	3.8 ± 0.2	27.8 ± 3.5	9.9 ± 1.3	44.1 ± 6.7	132.6 ± 50.4	11.9 ± 1.7	18.4 ± 5.7	4.1 ± 1.6
Q. velutina	3.8 ± 0.1	35.8 ± 3.2	9.6 ± 0.9	38.6 ± 8.5	32.7 ± 15.2	10.5 ± 1.9	15.8 ± 8.1	3.9 ± 0.8
P	0.470	0.004	0.740	0.510	0.002	0.128	0.095	0.170

significant differences between soil variables. Those nutrients that differed do not explain the reduced cover of herbaceous species beneath *Q. alba*. Therefore, although light and nutrient levels are low, amounts of these variables must be above the threshold necessary for the survival and maintenance of species characteristic of the ground layer in these oak-pine forests.

DISCUSSION

Few significant relationships were found between canopy type and ground layer species in these oak-pine forests. The common shrubs *Gaylussacia baccata* and *Vaccinium vacillans* were consistently distributed randomly with respect to canopy species. Previous studies have indicated that shrub cover was generally related to the amount of canopy cover and percent of oak in the canopy. (Buell and Cantlon, 1950; McIntosh, 1959; Reiners, 1967). Buell and Cantlon (1950) reported that cover of *G. baccata* increased with increasing open space in the canopy whereas cover of *V. vacillans* showed no particular pattern. Cover of *G. baccata* was greater in oak vs. pine samples in the Shawangunk Mountains, New York (McIntosh, 1959). Reiners (1967) found that cover of these and other shrubs decreased as oak basal area increased in the Pine Barrens of Long Island. He predicted that shrub cover would be sparse in stands where oak basal area was greater than 23 m^2/ha. Consistent with Reiner's prediction, oak basal area in Stands 1, 2 and 3 was below 15 m^2 ha^{-1} and shrub cover ranged from 50-75%.

Despite similar composition among the ground layers in these stands, the few significant relationships between canopy and ground layer species were not consistent among stands. For example, *Melampyrum lineare* was common in all three stands, yet its distributional relationship to canopy species was variable. In Stand 3, cover of M. lineare was greater than expected by chance in open areas and less than expected beneath *Quercus alba*. In contrast, cover of this herb was random in open areas and greater than expected beneath *Q. alba* in Stand 2, and completely random in Stand 1 where *Q. alba* was uncommon. Other studies of species distribution have found only weak relationships between ground layer and canopy species (Hicks, 1980; Carleton and Maycock, 1981; Beatty, 1984; B. S. Collins *et al.*, 1984; Crozier and Boerner, 1984). Beatty (1984) found differences in herbaceous layers between hemlock vs. deciduous canopies. Crozier and Boerner (1984) found that herb assemblages as well as some environmental variables were different beneath *Q. alba* than under other canopy species. Several of the significant relationships in the Pine Barrens involved *Q. alba,* yet none of these patterns was associated with differences in soil nutrients, *p*H, light or litter depth (Table 2). Instead, herbaceous species such as *M. lineare* and *Carex pensylvanica* tend to occur abundantly in hot spots following prescribed burning where shrubs and trees do not sprout (Little, 1979).

Few significant relationships between tree seedling distribution and canopy species were found. This is in contrast to several studies in which tree seedlings had a higher probability of occurrence under nonconspecifics (*e.g.,* Forcier, 1975; Fox, 1977; Horn, 1981; Woods, 1984). The lack of a distributional pattern may, in part, have been due to limited sample size in this study. In those stands where seedlings of *Pinus* were abundant, however, no relationship with canopy type was detected.

The distribution of ground layer species showed little relationship to canopy type in the burned and not recently burned forests. In addition, species distribution showed little correlation with environmental parameters. Species life history strategies and interactions among species in the ground layer probably have a greater impact on distribution than canopy-ground layer interactions. For example, variance/mean ratios indicated that at a scale of 0.5 m^2, cover of the two dominant ground layer shrubs *Gaylussacia baccata* and *Vaccinium vacillans* was clumped at all three sites. Both shrubs are clonal and respond well to fire (Buell and Cantlon, 1953) which may account for pattern at this scale. In addition, cover of these two shrubs was significantly negatively correlated at each site in quadrats where both species occurred. These species were negatively associated in Stands 2 and 3, but not in Stand 1, the most recently burned stand. Thus, in these low diversity, frequently disturbed forests, pattern of ground layer species is a function of biotic interactions which develop between disturbances. Biotic interactions involve preemption of space by sprouting following fire and subsequent shading of *V. vacillans* by *G. baccata,* the larger of the two species. Overall, these patterns and interactions occur in an environmental matrix of highly variable overstory and edaphic factors.

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