INFLUENCE OF CANOPY DENSITY ON GROUND VEGETATION IN A BOTTOMLAND HARDWOOD FOREST[1]

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Abstract-We investigated the influence of canopy density on ground vegetation in naturally formed gap and non-gap habitats (environments) in a blackwater river floodplain. Tree seedlings were more important (relatively more abundant) in the non-gap habitat, and grass was more important in the gap habitat, but there were elevation x habitat interactions. Also, there was an elevation x habitat interaction for species richness, with more species occurring higher on the elevational gradient and in the non-gap habitat. Because tree seedlings were similar in size in the two habitats, we concluded that naturally formed canopy gaps in this bottomland forest neither significantly increase light levels nor stimulate tree seedling growth. Also, because there was a habitat effect even after accounting for the covariates of light and elevation, we concluded that something besides elevation or light level is influencing the ground vegetation composition. Apparently, small canopy openings can increase the importance of competing plant species without improving conditions for tree seedling growth.

INTRODUCTION

Managers of bottomland hardwood forests report problems in regenerating stands to contain a component of valuable tree species, particularly oak, similar to pretreatment stands. We have a limited understanding of conditions that improve the regeneration of valuable trees in bottomland hardwood forests, although it is generally accepted that oak reproduction should be well established before the overstory is removed (Aust and others 1985). Large oak seedlings are rare in such forests due to developing oak seedlings' increasing intolerance to shade (Carvell and Tyron 1981). Hence, on moist sites, crown openings that provide sufficient sunlight for seedling establishment and survival of these relatively slow growing trees may be necessary to establish sufficient oak regeneration during the last years of rotation.

Because advance reproduction of fairly large seedlings (minimum l-cm diameter at ground level) should be present before clearcutting (Sander 1971), opening the canopy to encourage growth of advance regeneration oaks has become a common silvicultural practice in bottomland hardwood forests (McKevlin 1992, and Personal Communication with Steve Meadows, 1999. Research Forester, Southern Research Station, Stoneville, MS 38778). However, canopy openings also may stimulate the growth of potentially competing plant species such as intolerant trees, grasses, sedges, and forbs. Although regeneration of woody plants in floodplain forests has received some attention in the literature (DeSteven and Sharitz 1997, Jones and others 1994a, Streng and others 1989), little has been done on the regeneration of woody plants relative to herbaceous plants in floodplain forests.

Demographic analyses in forests undergoing gap formation or major disturbances is a useful approach for determining tree seedling pool contributions to long-term overstory dynamics (Jones and others 1994b). In Southern forested wetlands, flooding is the dominant disturbance factor, thus plant species usually are distributed along a growing-season flood gradient (Franz and Bazzaz 1977, Burke and others, In press). Flooding is not, however, the sole factor affecting vegetation dynamics within these systems. Light availability also can constrain regeneration of wetland plants (Menges and Waller 1983). The frequency, size, and distribution of canopy disturbances can influence the composition of bottomland hardwood forest stands because of differences in quality and quantity of light available to plants (Streng and others 1989).

We investigated the relative influence of light and elevation (as an index of flooding intensity) on ground vegetation diversity and the importance (relative abundance) of tree seedlings, grasses, and forbs in non-gap and naturally formed canopy gap habitats (environments). Although the community structure of ground vegetation in this bottomland hardwood forest was closely related to elevation (Burke and others, In press), little has been published about plant community structure in canopy gap and non-gap habitats along elevational gradients.

STUDY SITE

We conducted our research on the Coosawhatchie Bottomland Ecosystem Study site (fig. 1) near Coosawhatchie in Jasper County, SC (32° 40' N and 80° 55 W). The Coosawhatchie River drains a 400 km^2 watershed where forestry and agriculture are the major land uses. It is a fourth-order, anastomosing blackwater river that has a floodplain surface about 1.6-km wide and a relief of about 2-m.

The study area is composed of two weakly developed terraces, distinguished primarily by flooding frequency and surface sand size. Soils on the lower terrace consist of highly variable loamy and clayey marine and recent fluvial sediments over older, sandy fluvial sediments with an alluvial surface layer. Soils in the sloughs are silts and clays deposited by overbank flooding. Flood waters remain on the very poorly drained, low permeability soils; thus swampy, shallow pools persist. Generally, soils consist of a thick loamy surface layer underlain by interbedded, silty slackwater deposits and lenses of point bar and channel sands, surrounding reworked, relict islands of Pamlico terrace material (Murray and others, In press).

[1] Paper presented at the Tenth Biennial Southern Silvicultural Research Conference, Shreveport, LA, February 16-18, 1999.

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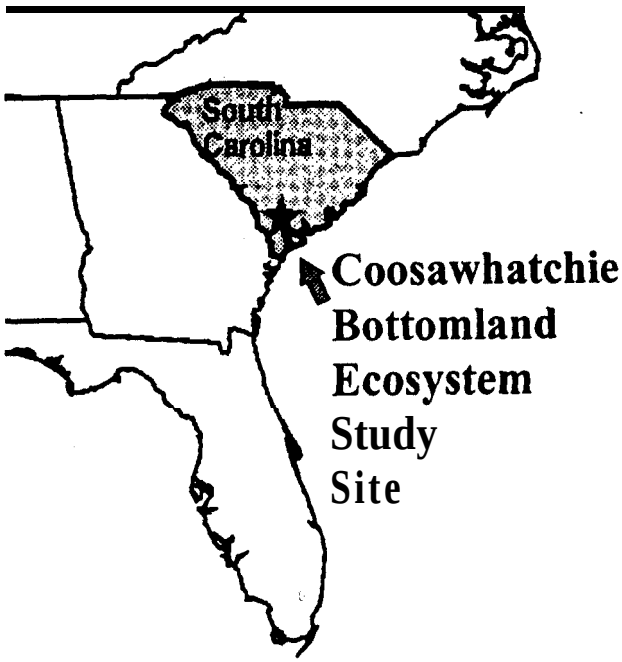

Figure l-location of the Coosawhatchie Bottomland Ecosystem Study site.

Most soils on the site were classified in the Brookman series: a fine, mixed, thermic, Typic Umbraqualf, which has thick, black loamy surface layers and dark gray clayey subsoils. Scoured areas have higher silt content. Approximately 15 percent of the site was classified in the Meggett series: a fine, mixed, thermic, Typic Atbaqualf. Those soils are found at a slightly higher elevation (< l-m) than the rest of the floodplain, on large islands and adjacent to upland areas. Black or dark gray surface layers are less than 25-cm thick. The Nakina series: a fine-loamy, siliceous, thermic, Typic Umbraqualf, is found in the western part of the study area, adjacent to the upland. To a depth of about 50-cm, surface layers consist of black loam. Approximately 20 percent of the soils are characteristic of the Okeetee, Coosaw, Elloree, Grifton, Osier, and Rutledge series. All are composed of siliceous, sandy, and sandy loam surface layers; however, the Osier and Rutledge series are devoid of leached E and argillic B horizons. This lack of profile development in the Osier and Rutledge series supports a recent fluvial origin, whereas the Okeetee, Coosaw, Elloree, and Grifton series, which exhibit well-developed horizons, are composed of older terrace sediments.

There are four main forest community types that are closely related to hydroperiod on the site (Burke and Eisenbies, In press) : (1) the Water Tupelo Community is flooded half the time, is almost always saturated, and > 30 percent of the basal area is water tupelo (*Nyssa aquatica*) ; (2) the Sweetgum/Swamp Tupelo Community is flooded 40 percent of the time, is saturated about 80 percent of the time, and > 50 percent of the basal area is water tupelo, swamp tupelo (*Nyssa sylvatica* var. *biflora*), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*); (3) the Laurel Oak Community is flooded about 10 percent of the time and is saturated less than half the time. More than 15 percent of the basal areas in laurel oak (*Quercus laurifolia*) and > 40 percent is a combination of laurel oak, sweetgum, and red maple ; and (4) the Mixed Oak Community, where surface flooding has not occurred during the last 5 years and soil is saturated about 20 percent of the time. More than 30 percent of the basal areas is water oak (*Q. nigra*), willow oak (Q. *phellos*), and cherrybark oak (C?. *falcata* var. *pagodaefolia*).

A prolific crop of laurel oak seedlings, established in the winter of 1995-1996, provided a cohort of advance regeneration, which allowed us to compare ground vegetation along elevation gradients and between the gap and non-gap habitats (environments).

METHODS

The objective of this study was to estimate the influence of natural canopy openings on the composition of ground vegetation, particularly related to the tree seedling component. During the summer of 1997, ground vegetation was surveyed in plots (2- x 2-m) established in 32 canopy gaps and in 63 non-gap areas (fig. 2). The non-gap plots had been established as part of an earlier study of vegetation on the site (Burke and others, In press), and the gap plots were located at the center of established canopy gaps (King and others, In press).

Each plot was divided into four equal 1-m^2 quadrants, and one randomly selected quadrant was used in the *survey.* Species composition, stem densities and percent cover for

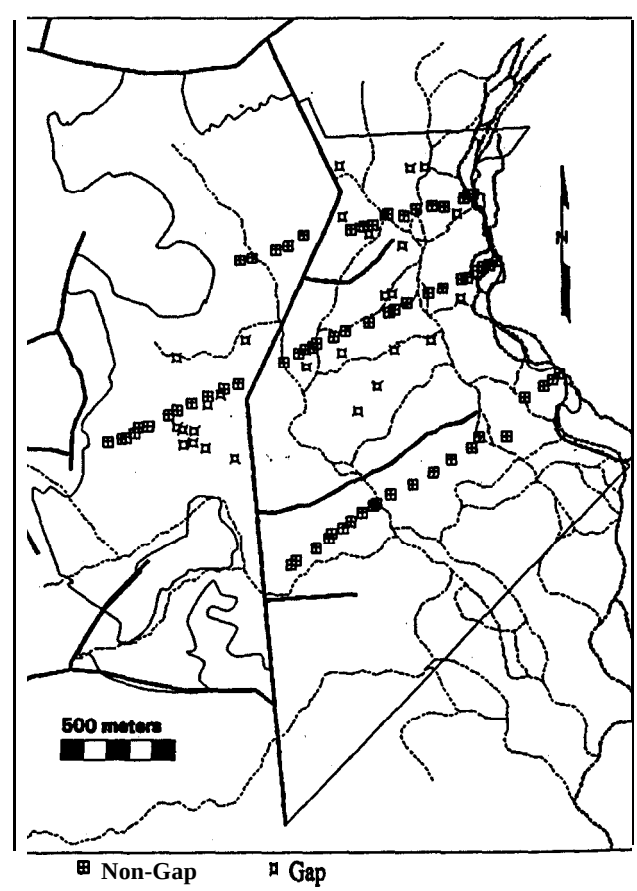

Figure 2-Map of the study site showing the locations of the gap and non-gapplots.

each species, and relative density and relative cover were measured for all woody seedlings (< 2.5cm diameter) and herbaceous species. Percent cover was categorized by class, based on a geologic method for estimating percent of facial surface area composed of a particular mineral (Terry and Chilingar 1955) using, instead of mineral composition, percent cover of plant taxa. Categories were 0= does not occur, 1 = > O-5 percent, 2 = 6-20 percent, 3 = 21-40 percent, 4 = 41-60 percent, 5 = 61-80 percent, 6 = 81-100 percent, and 7 = > 100 percent.

Light regimes were quantified using a portable LiCor® quantum line sensor and point sensor, connected to a LiCor® data logger. Spectral irradiance in gap and plot centers was scanned at waist height within a 350 to 800 µm waveband, which is considered photosynthetically active radiation (PAR). Eighteen readings over 5-second intervals were taken at each gap and non-gap plot center. Concurrent light measurements were taken using another LiCor® quantum point sensor place in an open field on the site. Spectral irradiance measurements were taken under clear conditions between 10:30 am and 13:30 pm, solar time, to avoid variation from sky conditions and sun elevation (St. Jacques and Bellefleur 1993).

Elevation (m) at each plot center served as an index for flooding intensity, based on the correlation between elevation and percent of time soil was inundated or saturated (Eisenbies and Hughes, In press).

Data for gap and non-gap habitats were tested for homogeneity of variance using Bartlett's test (Winer 1971) and were log-transformed before analysis when necessary. T-tests and Analysis of Covariance (ANCOVA) were used to test for habitat differences. ANCOVA was used to reduce the experimental error and remove potential sources of bias that were impossible to eliminate by study design. A probability level of 0.05 was used throughout. The effects of light and elevation served as covariates, and the response variables were richness (number of species within each plot), Shannon-Wiener diversity index (H' = $2^{H'}$, where H represents the information for a community) (Shannon and Weaver 1949), and absolute and relative (as percent of total) cover of trees, forbs, and grasses. Data were analyzed using SAS (SAS User's Guide 1985). Three-dimensional plots were prepared to illustrate the relationship among important response variables-by-habitat to light and elevation.

RESULTS

There were no significant differences in the percent of incident light or elevation between habitats (table 1).

Neither index of species diversity showed differences between the two habitat types when data were analyzed using t-tests; although the ANCOVA revealed that there was a habitat effect, an elevation effect, and an almost significant habitat x elevation interaction for species richness (table 2). Several plant species occurred only in canopy gaps, including fetterbush (*Lyonia lucida*), *Rumex* sp., spleenwort (*Asplenium platyneuron*), water ash (*Fraxinus caroliniana*), and persicaria (*Polygonum setaceum*). By contrast, American elm (*Ulmus americana*) and Virginia willow (*Itea virginica*) occurred only in non-gap habitats.

Laurel oak comprised 86 percent of the seedlings and 10 percent of the seedlings were red maple. Other tree species present but unimportant (< 4 percent total density) were water ash, green ash (*Fraxinus pennsylvanica*), water locust (*Gleditsia aquatica*), American holly (*Ilex opaca*), sweetgum,

Table I-Mean (and standard error) values for response variables in non-gap and gap habitats on the Coosawhatchie Bottomland Ecosystem Study site'

Variable	Non-gap habitat	Gap habitat
Species richness (no. of species)	9.6 (0.67)	9.0 (0.62)
Shannon-Weiner diversity index	1.3 (0.84)	1.2 (0.10)
Density of tree seedlings (# m^{-2})	141 (24.8)	102 (23.1)
Density of grasses (# m^{-2})	31 (6.1)	46 (10.7)
Density of forbs (# m^{-2})	84 (15.2)	95 (29.5)
Relative density of tree seedlings	.49 (0.04)	.42 (0.08)
Relative density of grass	.12 (0.02)a	.24 (0.04)b
Relative density of forbs	.38 (0.04)	.32 (0.05)
Cover of tree seedings[b]	4.02 (0.26)	2.99 (0.24)
Cover of grass[b]	1.93 (0.26)a	2.84 (0.32)b
Cover of forbs[b]	5.19 (0.51)	5.14 (0.60)
Relative cover of tree seedlings	.42 (0.02)a	.28 (0.02)b
Relative cover of grass	.14 (O.OI)a	.28 (0.03)b
Relative cover of forbs	.44 (0.02)	.44 (0.03)
Light (percent of incident)	.04 (0.01)	.06 (0.01)
Elevation (MSL)	4.5 (0.06)	4.4 (0.04)

[a] Values followed by different letters are significantly different ($p < 0.05$) based on t-tests.
[b] Categories were 0 = does not occur, 1 = > 0 to 5 percent, 2 = 6 to 20 percent, 3 = 21 to 40 percent, 4 = 41 to 60 percent, 5 = 61 to 60 percent, 6 = 61 to 100 percent, and 7 = > 100 percent.

Table P--Results (p values for each variable and covariate) of Analysis of Covariance on ground vegetation response variables using habitat (non-gap versus gap plots) as the major independent variable of interest and light and elevation as covariates

Source	Species richness	Shannon-Weiner Diversity Index	Relative density of tree seedlings	Relative density of grass	Relative density of forbs	Relative cover of tree seedlings	Relative cover of grass	Relative cover of forbs
Habitat	0.052	0.118	0.066	0.117	0.364	0.042	0.018	0.718
Light	.329	.580	.891	.619	.269	.380	.648	.256
Elevation	.023	.255	.893	.150	.851	.678	.207	.219
Habitat x light	.179	.137	.399	.968	.378	.218	.792	.318
Habitat x elevation	.065	.328	.085	.156	.359	.081	.038	.779

magnolia *(Magnolia grandiflora)*, blackgum (Nyssa *sylvatica* var. *sylvatica)*, swamp tupelo, spruce pine *(Pinus glabra)*, water elm *(Planera aquatica)*, overcup oak (Q. *lyrata)*, swamp chestnut oak (Q. *michauxii)*, water oak, baldcypress *(Taxodium distichum)*, and American elm.

There were no differences between habitats for plant density, or for the density of tree seedlings, grasses and sedges, and forbs (table 1). in both habitats, relative tree seedling density was greater than relative forb density, which was greater than relative grass density. Relative cover in the non-gap habitat was similar for tree seedlings and forbs, which were greater than for grass cover. in the gap habitats, relative forb cover was greater than relative tree or grass cover, which were similar in magnitude. Roth relative density and relative cover for grass were greater in the gap than in the non-gap habitat.

Analysis of covariance revealed no effects of light or interactions between light and habitat for any response variable. However, ANCOVA showed elevation effects and a habitat and elevation interaction for species richness, as well as habitat and elevation interactions for relative cover for grass, relative cover for tree seedlings, and relative density for tree seedlings (table 2).

The interaction between elevation and habitat was apparent when individual plot values for response variables were plotted along light and elevation gradients. High on the elevational gradient, species richness was highest in the non-gap habitat; but values were similar between habitats lower on the elevational gradient (fig. 3). Similar interactions were evident for relative density of tree seedlings (fig. 4). relative cover of tree seedlings (fig. 5), and relative cover of grass (fig. 6).

DISCUSSION

Previous studies have shown that canopy gaps can influence the community structure of ground vegetation via greater light levels (Platt and Strong 1989); however, the light environment did not differ between habitats in this study. Probably this was due to the small size of gaps-96 percent were substantially smaller than the estimated minimum diameter (30-m, or canopy height) needed to

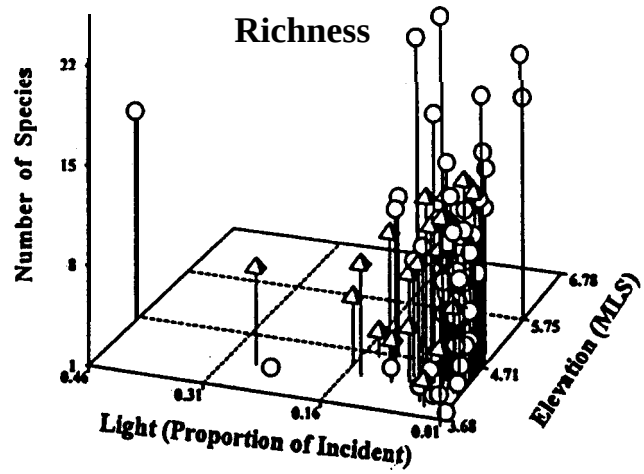

Figure3—Three-dimensional diagram of plant spades richness along elevation and light gradients in gap (pyramid) and non-gap (circle) plots.

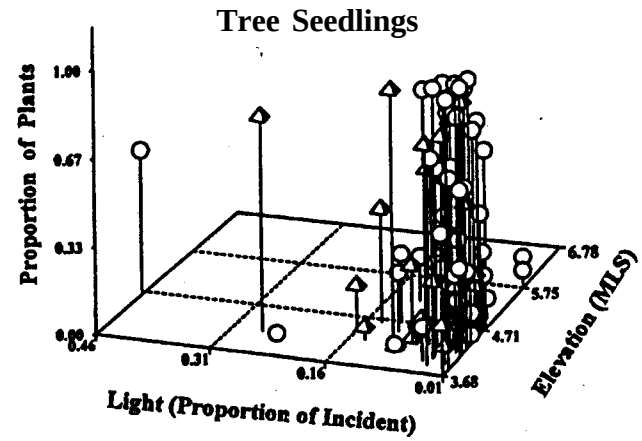

Figure4—Three-dimensional diagram of the relative density of tree seedlings along elevation and light gradients in gap (pyramid) and non-gap (circle) plots.

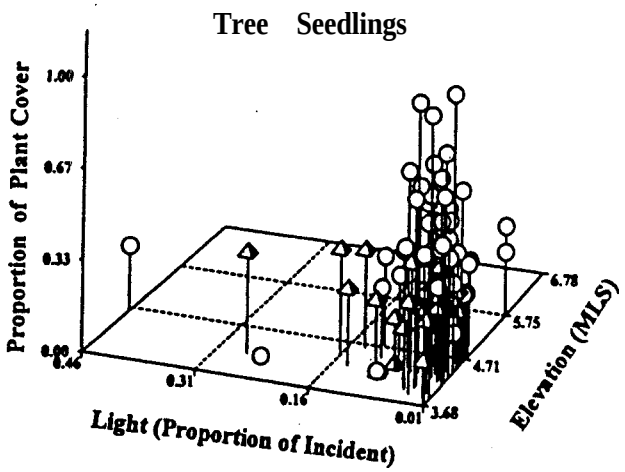

Figure 5—Three-dimensional diagram of the relative cover of tree seedlings along elevation and light gradients in gap (pyramid) and non-gap (circle) plots.

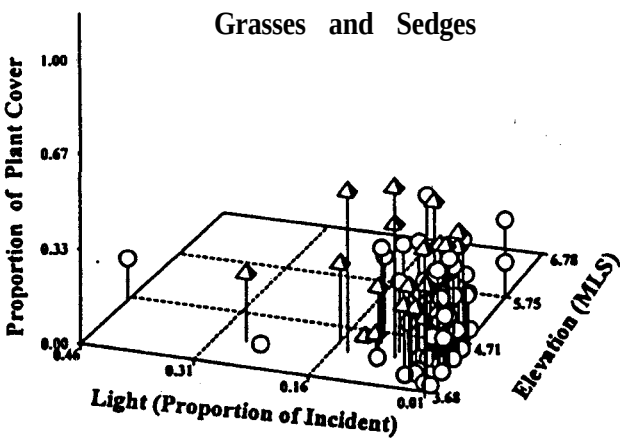

Figure 6—Three-dimensional diagram of the relative cover of grasses and sedges along elevation and light gradients in gap (pyramid) and non-gap (circle) plots.

stimulate tree seedling growth (Personal Communication. Beverly Collins. 1998. Ecologist, Savannah River Ecology Laboratory, Aiken, SC 29802). Single-tree gaps, with high canopy height-to-gap diameter ratios have little effect on understory light regimes, e.g., Canham and others 1990, and for this reason gap formation may not always prompt a strong growth response in bottomland hardwood community composition or improve tree seedling survival (Streng and others 1989).

Most ground vegetation species were not dependent on gaps. However, five species were found only in gap habitats, hence these species may be gap-phase species. The small gap size and low intensity of disturbance in gap formation (windthrow or mortality) probably provided a minimally diierent microenvironment, which is not typical in larger gaps. Generally, large gaps have more light, more extreme temperature and moisture regimes, and exposed mineral soil, all of which are necessary for the germination of plants more typical of gaps.

Burke and others (In press) noted the effect of elevation on species richness on the Coosawhatchie Bottomland Ecosystem Study site, but this study illustrated that habitat also affects species richness-non-gap habitat was more diverse than gap habitat. Two species were found only in non-gap habitats. However, non-gap plots were sampled more intensively (n = 63), so the study may have been biased toward identifying species that occurred in non-gaps.

Because tree seedlings were more important in the non-gap habitat and grasses were more important in the gap habitat, both might be responding to a flooding gradient in a similar way. Nonetheless, they appear to respond in a different way to canopy densities along the flooding gradient. Because we detected a habitat effect even after accounting for the covariates light and elevation, we concluded that something besides elevation or light level influenced the ground vegetation composition. Although the exact mechanism is not known, some possibilities include (1) grasses may more effectively use the small increase in light, which is characteristic of small gaps, (2) if gaps pm-date the oak regeneration, more acorns may have fallen in non-gap plots than in gap plots, where the gapmakers may have been oak trees, (3) the loss of the gap-makers removed root competition, thus liberating herbaceous plant roots from competition, and (4) windthrow exposed mineral soil in gaps, providing substrate more conducive to the germination of non-woody plant seeds. It is clear that differences between habitats could not be attributed to differences in plant communities, because elevations of the habitats were similar and elevation is the factor most important in structuring ground vegetation species composition at the site (Burke and others, In press). Nevertheless, the interaction effects between elevation and habitat suggest that further exploration of the nature and sources of this nonadditivity in the data is needed.

When tree seedling size was indexed using cover/density, tree seedlings were identical in size between habitats. This supports the finding by Streng and others (1989) that gap formation may not necessarily stimulate survival of tree seedlings. Instead, small canopy openings appear to increase the importance of other plant species that can compete for light and edaphic resources without improving conditions for growth of tree seedlings.

Not yet documented are the influence of greater light levels on growth and survival of individual tree seedlings, or the long-term significance of a thinned canopy on post-harvest tree seedling success.

ACKNOWLEDGMENTS

This study was conducted on land owned and managed by Westvaco Corporation as part of the Coosawhatchie Bottomland Ecosystem Study. The authors acknowledge the technical assistance of Cindy Bunton, Keshica Butler, Mark Eisenbies, and David Gartner; editorial assistance by Susan O'Ney, as well as the helpful discussions with Mike Aust, John Fauth, Sammy King, John Martin, Steve Meadows, and Paul Morino during study planning and in interpreting the data.

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