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Woody understory response to changes in overstory density: thinning in Allegheny hardwoods

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Abstract

Understanding the effects of silvicultural treatments on understory vegetation is important in predicting the consequences of such treatments, not only on regeneration but also on wildlife habitat, visual qualities, and recreation. We sought to develop an empirical model of understory response that could be generalized to other forest types. We analyzed understory populations of tree species for 15 years following thinning to different residual relative densities in 50- to 55-year-old Allegheny hardwoods. The average number of stems 1 ft (0.3 m) tall to 1 in (2.5 cm) dbh increased for 3 to 5 years after thinning and then leveled-off or decreased after 10 or 15 years. The greatest density of understory stems developed at low residual density. In stems 1 to 3 ft (0.3 to 0.9 m) tall, the densities of shade-tolerant species were unresponsive to thinning while the shade-intolerant were most responsive. The shade-intolerant and -intermediate species increased in importance over time in the more heavily thinned treatments. In the 3 ft (0.9 m) tall to 1 in (2.5 cm) dbh size class, shade-intolerant and -intermediate species were more responsive to thinning than tolerant species, but shade-tolerant species remained more important numerically throughout the study. Ingrowth to > 1 in diameter classes was greatest by shade-tolerant stems, increased over time, and was enhanced by thinning. We used repeated measures analysis of variance to model the number of stems in these three size classes and three shade-tolerance classes as a function of residual relative density at thinning and time since treatment. These models explained 0.08 to 0.80 of the variation in stem numbers, depending on the size and tolerance class. These descriptions might be improved by reference to prior conditions of the regeneration or interfering herbaceous competition, but a model that required this information would not be capable of predicting responses to future treatments. © 1998 Elsevier Science B.V.

Keywords: Regeneration; Model; Beech; Black cherry

1. Introduction

The effect of forest management on understory development has been studied mainly from the point of view of forest regeneration. For example, stocking guides give the numbers of seedlings per unit area required to stock a stand with commercially desirable species; shelterwood methods require an indication of overstory density required to best regenerate those species (Hannah, 1988). In addition to its role in forest regeneration, understory vegetation is also

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important to wildlife habitat, scenic beauty, and the recreational use of forests. To evaluate forest conditions for these non-timber resources requires a more general description of the response of understory plants to silvicultural treatments, including non-commercial species and treatments not especially intended to promote regeneration, such as thinning. We sought to develop a generalized model of understory response to silvicultural treatment, to be used in the Northeast Decision Model to support forest management decisions for a range of goals (Twery, 1994). Here, we present an analysis of a 15-year study following thinning in Allegheny hardwoods. Later, we will extend the application of this model to other forest types.

Thinning is common in even-aged hardwood forests managed for timber products. The choice of thinning as a silvicultural treatment and the design of the treatment usually are based on the anticipated effect on overstory trees (Smith, 1986). Removing competing overstory trees increases the site resources available to the residual trees, allowing them to grow faster (Heitzman and Nyland, 1991). Thinning also reduces mortality from competition and interference. Wildlife may benefit from thinning treatments, if mast production increases as a result of improved tree vigor. Thinning smaller stems may be prescribed for strictly aesthetic purposes, i.e., to improve the visibility of large stems.

In addition to affecting the current stand of canopy trees, thinning temporarily increases the amount of moisture, nutrients, and, most importantly, light available to understory vegetation. Differences in cutting intensity are likely to produce different understory responses, including the establishment of new stems and increased growth of established stems. These responses will also vary with the type of thinning. For example, low thinnings, in which most removals are from trees below the main crown canopy, will increase light levels at the forest floor much less than a crown thinning, in which most removals create openings in the main crown canopy. The vigor, density, and composition of the understory can have a profound influence on the future of the forest, changing the number and species of stems available for regenerating the stand. A dense shrub layer or midstory also supports additional species of birds (deCalesta, 1994) and provides more forage for herbivores (Beck, 1983) than an open, sparsely vegetated forest floor. Understory vegetation contributes to the scenic beauty of forest stands (Palmer and Sena, 1993), but reduces visual penetration as the understory develops in height.

Current simulators of forest growth for northeastern hardwoods do not treat regeneration adequately, partly because it is so difficult to predict. The composition of new stands that establish after major disturbance and the composition of understory stems in existing stands are highly variable due to variation in seed production and dispersal, site conditions, weather conditions, herbivory, and other factors (Monserud, 1987). Widely used empirical growth models such as SILVAH (Marquis and Ernst, 1992) and FIBER (Solomon et al., 1987, 1995) simulate the development of an existing stand until timber reaches maturity. Small stems are not simulated, and ingrowth functions may not adequately predict the nature of a new stand after a simulated regeneration treatment. In models driven by timber values, prediction beyond current financial maturity is not important. But to manage forests for long-term sustainability and non-timber resources, better information is needed on the dynamics of understory stems in existing stands and on the composition and growth of new forest stands.

Successful prediction of forest development beyond a stand-regenerating disturbance requires analysis of understory response to various types and intensities of disturbance. Our approach is to model the response over time of seedlings grouped by size and shade-tolerance to partial overstory removal. By limiting our analysis to factors that are common to many different forest types, such as shade-tolerance and broad size classes of stems, we hope to develop a model that works in many forest types but also has sufficient empirical basis to provide reasonably accurate estimates of understory response in Allegheny hardwoods.

We report results of our first efforts, modeling tree regeneration taller than 1 ft (0.3 m) following thinning across a range of residual densities in 50- to 55-year-old, even-aged Allegheny hardwood stands. Responses are reported as numbers of seedlings over time since treatment in three shade-tolerance classes and two size classes: small seedlings and large seedlings (less than and greater than 3 ft (0.9 m) tall). Ingrowth, or the number of seedlings entering the 1 in (2.5 cm) dbh size class in each 5-year period, also is modeled.

2. Methods

2.1. Study description

Data for this analysis are from a Forest Service thinning study in Allegheny hardwoods that primarily tested effects of residual relative density on overstory growth after thinning. We used data from two even-aged stands treated about 50 to 55 years after stand initiation. Primary overstory species were black cherry (*Prunus serotina* Ehrh.), sugar and red maple (*Acer saccharum* Marsh. and *A. rubrum* L.), and American beech (*Fagus grandifolia* Ehrh.), with minor components of both yellow and black birch (*Betula allegheniensis* Britt. and *B. lenta* L.), white ash (*Fraxinus americana* L.), tulip-poplar (*Liriodendron tulipifera* L.), and cucumbertree (*Magnolia acuminata* L.). Table 1 shows overstory stocking before and after treatment.

The study took place in northwestern Pennsylvania (latitude 41°35′ to 41°37′, longitude 78°45′ to 78°50′). Both stands extended across toposequences with soil associations representative of the unglaciated portion of the Allegheny Plateau. Soil series included Buchanan silt loam, Cookport channery loam (fine-loamy, mixed, mesic Aquic Fragiudults), Hartleton channery silt loam (loamy-skeletal, mixed, mesic Typic Hapludult), and Hazleton channery loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) (Soil Conservation Service, 1993). Annual precipitation averages 44 in (112 cm) per year, including about 4 in (10 cm) each month throughout the growing period. Details of the study design and overstory results are reported by Marquis (1986), Ernst (1987), and Marquis and Ernst (1991).

Thinning treatments followed guidelines by Roach (1977). Thinning was primarily from below, including both commercial and non-commercial removals. The thinning was a heavy low thinning (Smith, 1986), meaning that while most removals were of intermediate or overtopped trees, enough codominants were removed to create gaps in the main crown canopy. Stocking was controlled by relative density, a variant of traditional stocking guides that takes into account differences in species and tree size (Roach, 1977, Stout and Nyland, 1986). For example, the basal area in Allegheny hardwoods at 100% relative density can vary by as much as 50% depending upon the proportion in black cherry: stands with a high proportion of black cherry have higher basal areas than stands with low proportions. Controlling thinning with relative density instead of basal area accounts for this natural variation. The measure of relative density used to install the treatments (Roach, 1977) was based on two species groups, while the measure in current use in the Allegheny hardwood type (Marquis et al., 1992) is based on three. We used the current measure in our analyses.

Data were collected from two stands about 0.6 mile (1 km) apart, which were divided into 11 (Stand 1) or 10 (Stand 2) treatment areas, each 2 acres (0.8 ha) in size (Fig. 1). Two treatment areas in each stand were left uncut; the rest were thinned to residual relative densities of 37 to 82%. Stand 1 was treated in 1973; Stand 2 was treated in 1975. Because of this temporal difference (and possible effects associated with it, such as differences in weather patterns, seed supply, and browsing pressure over time) and because the thinning treatments were not applied evenly to each stand, the two stands cannot be treated as replicates. They were analyzed separately.

Eight 6 ft (1.8 m) radius plots were established in each treatment area. The plots in each treatment area were combined for analysis. Measurements were taken prior to thinning and 1, 3, 5, and 10 years following treatment in Stand 1 and 3, 5, 10, and 15 years following treatment in Stand 2. We recorded the number of stems of each species in each of two size classes: small seedlings, from 1 ft (0.3 m) to 3 ft (0.9 m) tall, and large seedlings, from 3 ft (0.9 m) tall to 1 in (2.5 cm) dbh. Ingrowth, or the number of seedlings entering the 1 in (2.5 cm) dbh size class in each 5-year time period, was also tallied. For analysis, we grouped the species into three shade-tolerance classes. Also available for each plot at each tally is an ocular estimate of percent coverage by ferns and grass.

Because ingrowth was rare, the number and species of trees growing into the overstory were taken from the overstory tallies. These tallies included the size and species of all stems > 1 in dbh in the central 0.6 acre (0.24 ha) of each treatment area at several times after treatment.

Table 1
Overstory stocking and basal area on treatment areas pre- and post-thinning

Area	Relative density (%)		Basal area (m^2/ha)					
			Total	Black cherry	Red maple	Sugar maple	Beech	Other
Stand 1								
1	Pre	99	28.0	12.2	3.9	10.7	1.1	0.0
	Post	43	14.0	8.0	1.8	4.1	0.1	0.0
2	Pre	98	30.7	17.3	1.2	10.3	0.4	1.6
	Post	70	23.0	13.2	0.9	7.3	0.3	1.3
3	Pre	99	29.2	16.1	2.1	3.3	6.7	1.1
	Post	82	25.3	14.8	2.0	2.8	4.7	0.9
4	Pre	95	29.1	16.7	0.7	9.8	1.6	0.4
	Post	93	28.7	16.6	0.7	9.3	1.6	0.3
5	Pre	98	31.7	18.7	0.5	10.6	1.2	0.7
	Post	60	20.7	12.5	0.9	6.4	0.7	0.3
6	Pre	95	30.3	11.1	8.2	8.8	1.3	0.8
	Post	49	18.3	9.2	4.5	3.7	0.3	0.6
7	Pre	92	25.8	8.2	2.5	12.1	3.0	0.0
	Post	64	19.0	6.4	2.4	8.3	1.9	0.0
8	Pre	92	24.3	5.6	0.4	16.4	1.4	0.6
	Post	75	20.4	5.2	0.4	13.3	1.1	0.5
9	Pre	88	23.6	6.4	1.0	14.4	1.3	0.5
	Post	88	23.6	6.2	1.0	14.5	1.4	0.4
10	Pre	99	25.0	3.5	0.0	21.0	0.2	0.3
	Post	37	10.3	2.5	0.0	7.4	0.1	0.3
11	Pre	93	26.9	9.7	0.6	15.5	0.5	0.6
	Post	56	17.7	7.2	0.5	9.1	0.3	0.5
Stand 2								
1	Pre	98	30.0	15.6	9.3	2.1	0.4	2.5
	Post	67	21.0	10.5	7.0	1.3	0.5	1.9
2	Pre	97	31.0	14.2	7.7	6.1	1.9	1.2
	Post	96	30.3	13.3	8.0	6.0	1.7	1.2
3	Pre	98	27.9	10.4	2.6	13.3	1.5	0.1
	Post	43	13.4	5.7	1.3	5.9	0.4	0.0
4	Pre	105	28.9	9.8	0.4	17.7	0.6	0.4
	Post	64	18.3	6.1	0.3	11.3	0.3	0.3
5	Pre	106	30.0	9.8	2.9	11.4	2.7	3.2
	Post	51	16.0	6.1	1.3	5.6	0.9	3.5
6	Pre	108	35.9	15.6	12.9	6.7	0.5	0.1
	Post	57	20.1	8.5	7.9	3.6	0.1	0.0
7	Pre	101	34.1	16.5	7.3	8.4	0.5	1.4
	Post	72	25.9	13.7	5.4	5.3	0.4	1.0
8	Pre	103	29.8	11.6	1.6	15.7	0.0	0.8
	Post	51	16.9	7.8	1.3	7.0	0.0	0.8
9	Pre	100	30.1	14.8	0.2	11.2	2.8	1.0
	Post	42	14.2	8.2	0.0	4.4	1.0	0.5
10	Pre	96	29.9	15.1	2.6	4.7	3.3	4.2
	Post	94	29.3	14.9	2.6	4.5	3.1	4.2

2.2. Statistics

In the first stage of analysis, we explored factors contributing to variation in the total numbers of understory stems. Independent variables were the residual density after thinning, the time since thinning, and the interaction of these two terms. A repeated-measures regression analysis was required because the same treatment areas were measured at each tally and are not independent observations. The degrees of freedom are reduced to the number of independent observations (treatment areas). The analysis was performed on the log of stem numbers.

In the second stage of analysis, we separated total stems into size classes and shade-tolerance classes. We used the same repeated-measures model to predict the log of stem numbers in each size and shade-tolerance class. In both analyses, we excluded

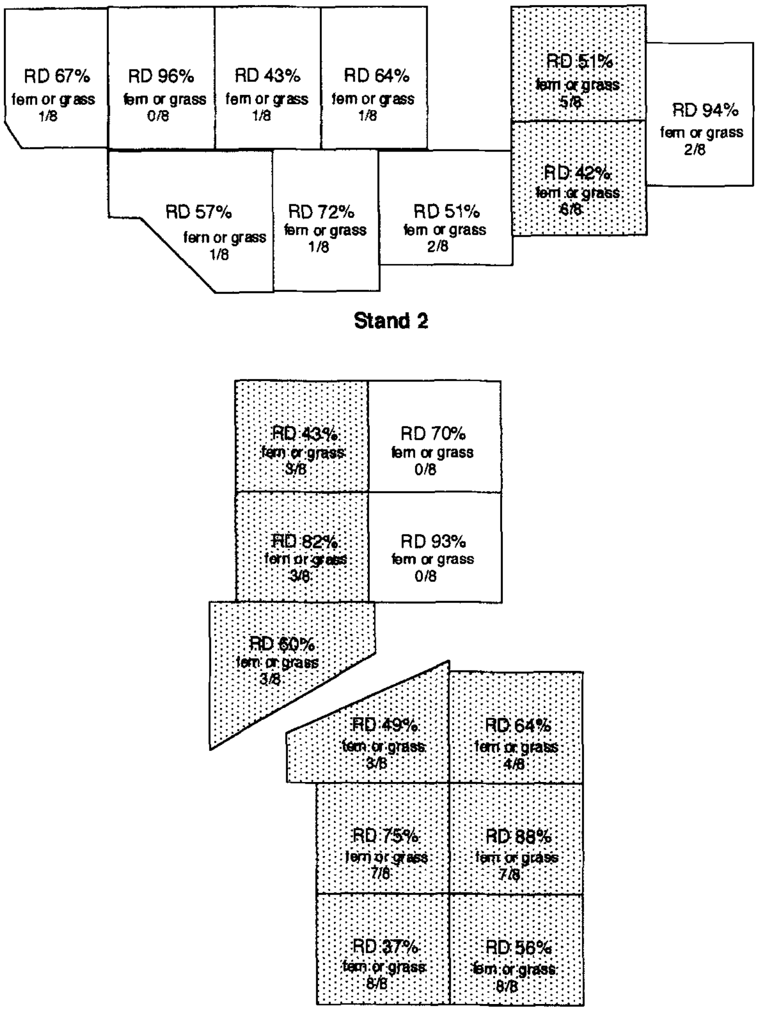

Fig. 1. Map of treatment areas showing residual relative density after thinning (RD) and the fraction of the eight plots in each treatment area with at least 30% cover of fern and grass at 5 years after treatment. Treatment areas with cover above the threshold considered to be interfering are shaded.

Table 2
Number of stems in each treatment area at 5 years after thinning by size and tolerance class

Residual density Species	Shade tolerance	Stand 1										
		37	43	49	56	60	64	70	75	82	88	93
		Thousands of stems/acre 1′–3′ tall										
Sugar maple	Tolerant	0.529	1.490	0.000	0.000	0.721	0.000	0.962	0.000	0.000	0.000	0.000
Beech	Tolerant	0.096	0.481	0.962	0.240	0.096	0.385	0.240	0.144	0.385	0.337	0.433
Striped maple	Tolerant	0.048	0.000	0.000	0.000	0.096	0.240	0.192	0.048	0.000	0.000	0.000
Red maple	Intermed.	0.048	3.654	8.221	0.048	0.096	0.048	0.192	0.000	1.010	0.000	0.000
Birch	Intermed.	0.192	0.048	1.058	0.000	0.096	0.048	0.000	0.000	0.000	0.000	0.000
Cucumbertree	Intermed.	0.000	0.192	0.288	0.000	0.096	0.000	0.288	0.000	0.000	0.000	0.000
Serviceberry	Intermed.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.048	0.000
Black cherry	Intolerant	10.481	19.183	7.115	3.990	1.394	1.538	0.433	0.337	0.048	0.000	0.000
Yellow poplar	Intolerant	0.769	0.000	0.048	0.000	0.096	0.000	0.000	0.000	0.000	0.000	0.000
Pin cherry	Intolerant	0.144	0.433	0.048	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		Thousands of stems/acre 3′ tall–1″ dbh										
Beech	Tolerant	0.000	0.096	0.577	0.048	0.048	0.240	0.096	0.000	0.337	0.048	0.337
Sugar maple	Tolerant	0.000	0.865	0.000	0.000	0.192	0.000	0.048	0.000	0.048	0.000	0.000
Striped maple	Tolerant	0.000	0.000	0.000	0.000	0.000	0.096	0.000	0.000	0.000	0.000	0.000
Birch	Intermed.	0.000	0.000	0.096	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cucumbertree	Intermed.	0.000	0.096	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Red maple	Intermed.	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Black cherry	Intolerant	0.288	0.096	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Yellow poplar	Intolerant	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		Thousands of new stems/acre > 1″ dbh										
Sugar maple	Tolerant	0.000	0.010	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.002	0.000
Beech	Tolerant	0.000	0.000	0.005	0.000	0.003	0.002	0.000	0.005	0.000	0.000	0.000
Red maple	Intermed.	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
		Stand 2										
Residual density		42	43	51	51	57	64	67	72	94	96	
		Thousands of stems/acre 1′–3′ tall										
Beech	Tolerant	0.721	0.817	0.962	0.096	0.721	0.048	1.490	0.625	0.577	0.817	
Striped maple	Tolerant	0.000	0.096	0.048	0.144	0.144	0.144	1.587	0.096	0.000	0.096	
Sugar maple	Tolerant	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Birch	Intermed.	1.635	2.500	0.385	0.096	0.529	0.048	0.529	0.096	0.000	0.000	
Red maple	Intermed.	0.240	0.817	0.096	0.096	0.096	0.048	0.000	0.000	0.000	0.000	
Cucumbertree	Intermed.	0.048	0.048	0.000	0.000	0.000	0.337	0.000	0.000	0.000	0.000	
Serviceberry	Intermed.	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000	0.000	0.000	
Black cherry	Intolerant	1.394	32.885	1.731	32.404	10.865	24.760	0.096	0.721	0.000	0.000	
Pin cherry	Intolerant	0.048	0.144	0.048	0.096	0.096	0.000	0.000	0.048	0.000	0.000	
		Thousands of stems/acre 3′ tall–1″ dbh										
Beech	Tolerant	0.625	0.144	0.288	0.000	0.048	0.096	0.192	0.000	0.048	0.048	
Striped maple	Tolerant	0.000	0.288	0.000	0.000	0.048	0.240	0.000	0.000	0.000	0.000	
Sugar maple	Tolerant	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Birch	Intermed.	0.048	0.192	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Red maple	Intermed.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Black cherry	Intolerant	0.096	0.817	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
		Thousands of new stems/acre > 1″ dbh										
Sugar maple	Tolerant	0.002	0.017	0.002	0.002	0.005	0.000	0.000	0.000	0.000	0.000	
Beech	Tolerant	0.007	0.000	0.005	0.013	0.012	0.027	0.002	0.008	0.000	0.000	
Striped maple	Tolerant	0.000	0.002	0.000	0.000	0.002	0.000	0.002	0.000	0.000	0.000	

the pretreatment ($t = 0$) stem numbers from the regression, because the residual densities with which they are identified had not yet been applied.

3. Results

Table 2 shows the number of stems of the 10 most frequently tallied species for the three size classes for each treatment area at 5 years after thinning. Details of species composition can be seen here; elsewhere we have grouped species into shade-tolerance classes as shown in the table. The untreated treatment areas had 88 and 93% residual relative density in Stand 1 and 94 and 96% residual relative density in Stand 2.

3.1. All seedlings combined

The average number of seedlings (small and large combined) increased for 3 to 5 years after thinning and then leveled off or decreased by 10 or 15 years (Fig. 2). Regeneration was greatest in treatment areas with low residual density; treatment areas with high density (including four that were not cut) were less responsive. The discrepancies in ranking of stem densities are associated with severe herbaceous competition. Treatment areas thinned to 42 and 51% have the greatest fern and grass cover in Stand 2 (Fig. 1), and they fall below the expected numbers of stems per acre (Fig. 2).

The repeated-measures analysis (Fig. 3; Table 3) showed that residual density at time of thinning had a significant effect on stem numbers in both stands (Stand 1 $P < 0.001$; Stand 2 $P = 0.016$). In Stand 1 there also was a significant effect of time since thinning ($P < 0.001$) and of the interaction between time since thinning and residual density at thinning ($P = 0.002$). In Stand 2 these were not significant, perhaps in part because post-treatment tallies in that stand began at year 3. By that time, much of the increase in stem density already had taken place. Also, there was more scatter around the regression lines for Stand 2. This is consistent with Fig. 2, which shows a clearer segregation of understory densities based on overstory residual densities in Stand 1.

Total stem numbers increase over time in the

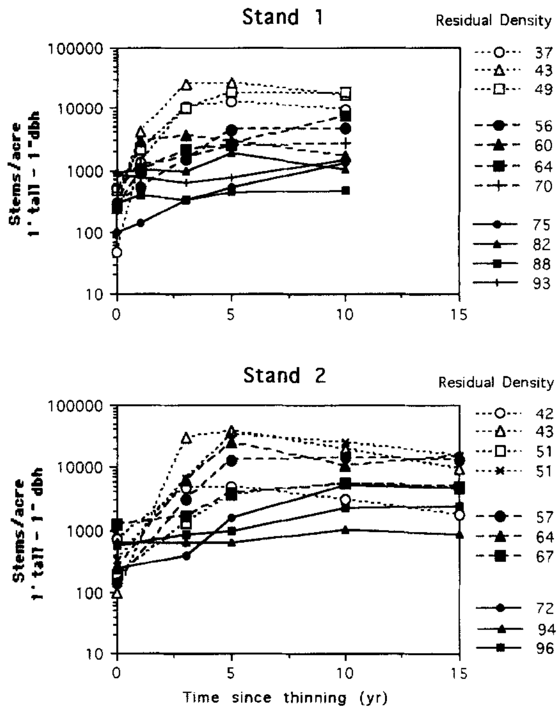

Fig. 2. Thousands of stems (1 ft tall to 1 in dbh) per acre over time in each treatment area (average of eight plots) in Stand 1 and Stand 2. Stand 1 was measured for 10 years; Stand 2 was measured for 15 years.

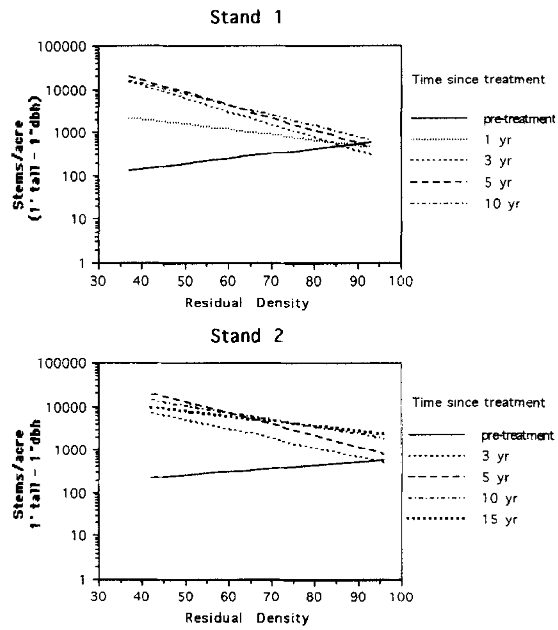

Fig. 3. Predicted number of stems (1 ft tall to 1 in dbh) per acre as a function of residual relative density from pretreatment to 10 years post-treatment in treatment areas in Stand 1 and Stand 2.

Table 3
Degrees of freedom, mean squares, and F- and P-values for the analysis of stems 1 ft tall to 1 in dbh, by stand

Source	df	MS	F	P
	Stand 1			
Residual density	1	7.95	30.1	< 0.001
error (between subjects)	9	0.264		
Time	3	0.409	12.0	< 0.001
Residual density * time	3	0.230	6.77	0.002
error (within subjects)	27	0.034		
	Stand 2			
Residual density	1	4.57	9.34	0.012
error (between subjects)	8	0.490		
Time	3	0.111	2.24	0.110
Residual density * time	3	0.124	2.50	0.084
error (within subjects)	24	0.050		

thinned treatment areas (Fig. 3), with most of the increase in the first 3 years after treatment, as was clear in Fig. 2. There was little change in the untreated areas. The relationship between stem numbers and residual relative density was strongest 5 years after thinning (the regression lines are steepest). This relationship flattens at 10 and 15 years as the overstory canopy closed, especially in Stand 2. Some of this change in slope is due to increased numbers of seedlings in the treatment areas with high residual density. Changes in numbers over time in the untreated areas are significant in the small seedling class (Stand 1 $P = 0.06$; Stand 2 $P = 0.04$) but cannot be attributed to thinning. The effect of resid-

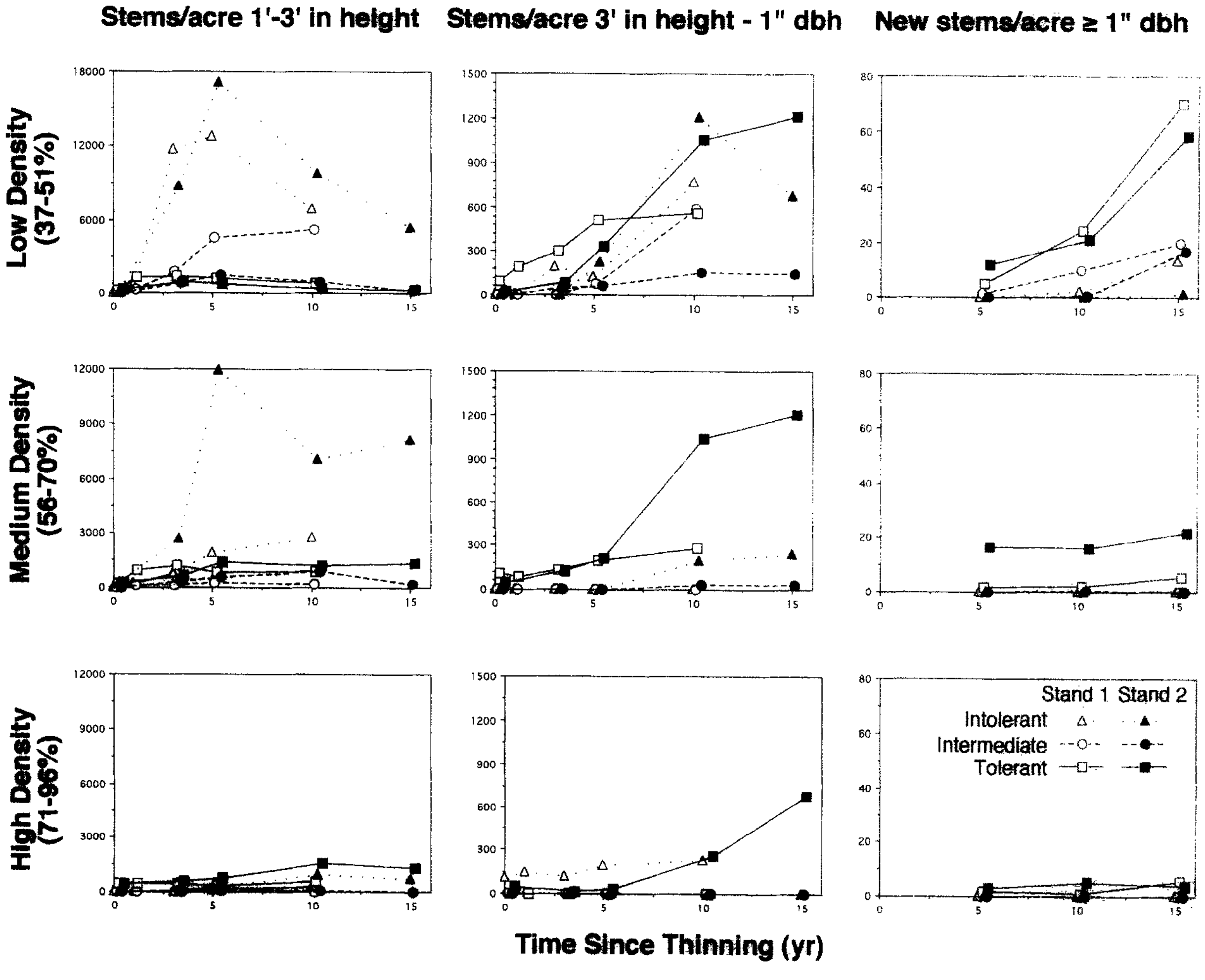

Fig. 4. Number of stems per acre 1 ft to 3 ft tall, 3 ft tall to 1 in dbh, and reaching 1 in dbh over time by shade-tolerance class and three classes of residual relative density. Note the change of scale for stems 1 to 3 ft tall at the lowest residual densities.

ual density on seedling numbers in the treatment areas before treatment was not significant, according to a one-way ANOVA (Stand 1 $P = 0.074$; Stand 2 $P = 0.213$).

3.2. Pattern over time, divided by tolerance class and residual-density class

Separating stems into size and shade-tolerance classes reveals important differences in the response over time of these groups to thinning (Fig. 4; Table 4). In the small seedlings, shade-intolerant stems increase dramatically in response to thinning. Note the change of scale in the graph of small stems at low residual density. These species account for the peak in total numbers in low- and medium-density plots at 3 to 5 years after thinning (Fig. 2). By contrast, the number of shade-intolerant stems in the high-density areas is lower than the number of shade-tolerant stems. Shade-tolerant species in the small size class did not respond to thinning.

Among the large seedlings, shade-intolerant stems do not consistently outnumber the -intermediate and -tolerant ones. In contrast to small seedlings, shade-tolerant stems in this size class were dominant even at low residual densities. The number of stems in this size class continued to increase over the 15 years of observation; the numbers of smaller stems peaked at 5 years and then declined.

The number of stems growing into the 1 in size class during each 5-year interval was small (note the change in scale in Fig. 4). In the medium- and high-density treatments, only tolerant trees grew into this size class. At low densities, a small number of intolerant and intermediate trees reached 1 in dbh, but they always were outnumbered by tolerant trees. In these heavily thinned treatments, recruitment into the 1 in class increased continuously over the 15 years of observation.

3.3. Regression: stems by size and tolerance class as a function of residual relative density

Fig. 5 shows stem numbers as a function of residual density by tolerance and size classes, graphed separately for each tally. In the small seedlings, the

Table 4
F- and *P*-values for the analysis of stems in each size and tolerance class, by stand

Size class	Effect	Tolerant		Intermediate		Intolerant	
		F	*P*	*F*	*P*	*F*	*P*
		Stand 1					
1′–3′ tall	Residual density	1.85	0.207	7.16	0.025	90.4	< 0.001
	Time	0.970	0.421	4.75	0.009	3.17	0.040
	R.D. * time	0.954	0.429	3.25	0.037	1.10	0.366
3′ tall–1″ dbh	Residual density	0.008	0.930	3.22	0.106	7.80	0.021
	Time	1.67	0.198	2.74	0.132	2.34	0.125
	R.D. * time	0.986	0.414	1.83	0.209	1.85	0.186
> 1″ dbh	Residual density	8.01	0.020	5.18	0.049[a]	3.50	0.094[b]
	Time	13.7	< 0.001	2.94	0.121[a]		
	R.D. * time	9.11	0.002	2.04	0.187[a]		
		Stand 2					
1′–3′ tall	Residual density	0.018	0.896	33.5	< 0.001	18.7	0.003
	Time	1.06	0.385	3.88	0.022	0.924	0.444
	R.D. * time	1.60	0.216	2.12	0.125	0.422	0.739
3′ tall–1″ dbh	Residual density	2.06	0.189	5.32	0.050	19.2	0.002
	Time	2.38	0.095	0.157	0.924	4.68	0.025
	R.D. * time	0.774	0.520	0.010	0.999	2.02	0.166
> 1″ dbh	Residual density	12.2	0.008	1.34	0.280[a]		
	Time	4.74	0.024	1.93	0.202[a]		
	R.D. * time	3.02	0.077	1.35	0.279[a]		

[a]Analysis based on year 5 to 10 and year 10 to 15 only.
[b]Analysis based on year 10 to 15 only.

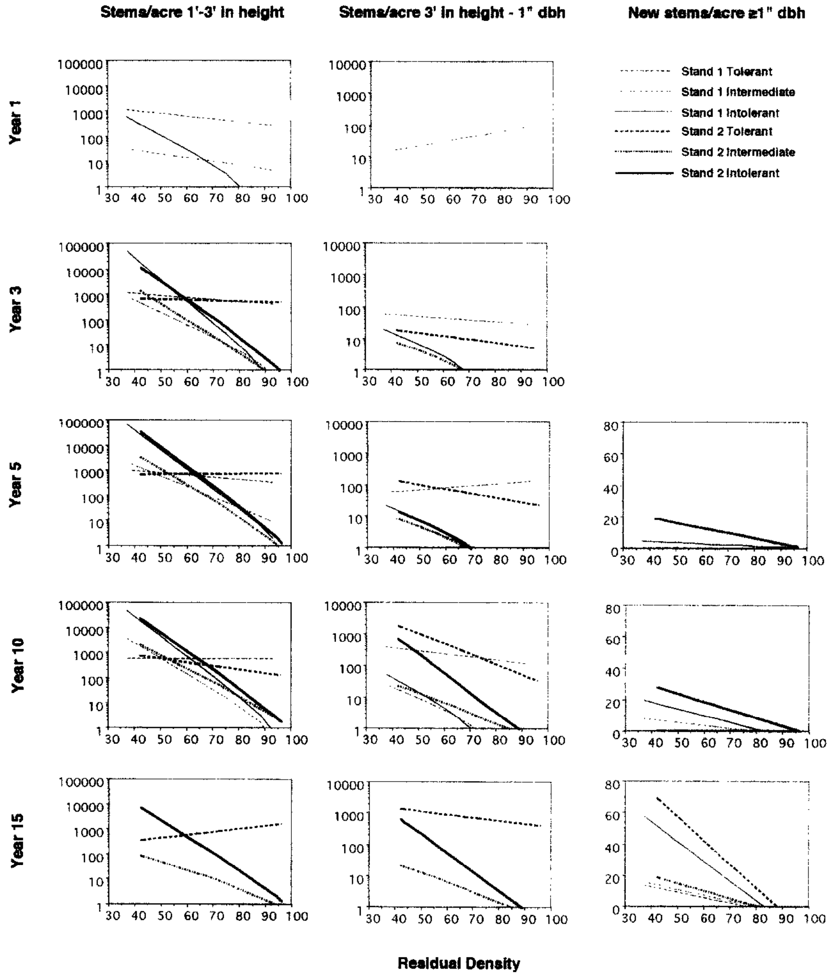

Fig. 5. Predicted numbers of stems per acre as a function of residual relative density for each combination of size class and time since treatment.

shade-tolerant species are unresponsive to thinning, while the shade-intolerant are the most responsive. Shade-intolerant and -intermediate stems increase in importance over time, especially in the most heavily thinned areas. The results of the repeated-measures analysis are summarized in Tables 3 and 4.

In the large seedlings, shade-intolerant and -intermediate species developed better at the lower densities and showed more residual density dependence than shade-tolerant species, but shade-tolerant species remained more abundant throughout the 15-year period. In Stand 2 there appears to be a response of tolerant species to thinning, though it is not statistically significant.

Ingrowth to 1 in dbh was greatest for tolerant stems. The rate of ingrowth increased over time and was enhanced by heavier thinning. This effect increased over time; that is, the difference between the ingrowth to > 1 in dbh from the most heavily thinned areas and lightly thinned or untreated areas was greater at the end of the period than early in the period.

4. Discussion

4.1. Numerical response

Thinning stimulated establishment and growth of seedlings and beech root suckers in the understory.

Total seedling numbers peaked by about the fifth year after treatment; the net increase persisted throughout the measurement period. The response was greatest in the most heavily thinned treatments, as observed in northern hardwoods in upper Michigan (Tubbs, 1968). Thinning increased regeneration of oaks in Connecticut (Ward, 1992) and West Virginia (Kirkham and Carvell, 1980). Similarly, selection and shelterwood cuts increased the growth of understory trees in northern hardwoods in Wisconsin (Metzger and Tubbs, 1971), New Hampshire (Leak and Solomon, 1975) and Vermont (Tubbs and Lamson, 1991). In natural canopy gaps, saplings grow faster in large than in small gaps, as documented in the southern Appalachians (Runkle and Yetter, 1987).

Shade-intolerant species were nearly absent from the understory before treatment but increased substantially after heavy thinning in the small seedling class. Similarly, in central Appalachian hardwoods, shade-intolerant species increased with degree of overstory removal (Trimble, 1973). The response of shade-intolerant species to light availability depends on germination cues (Auchmoody, 1979) and rapid growth rates (Canham and Marks, 1985). In natural forest disturbance, large canopy gaps favor shade-intolerant species, while small gaps are filled by shade-tolerant species and advance regeneneration (Runkle, 1982, McClure and Lee, 1993).

Although their numbers were less responsive to thinning than the shade-intolerant and -intermediate species, shade-tolerant species dominated the taller size classes and ingrowth to 1 in dbh. Most of these individuals probably were established before the disturbance (Tubbs, 1968, Metzger, 1980). This result illustrates an important aspect of the response to partial disturbances described by Oliver and Larson (1990): when disturbances are partial, existing stems tend to capture the resources liberated by the disturbance and grow more rapidly than newly established stems. Although shade-tolerant species are less plastic than early successional, shade-intolerant species (Bazzaz, 1979), they do respond to small increases in light in natural canopy gaps (Canham, 1988). Heavier cutting would be necessary to regenerate intolerant species, as is the case in the upland central hardwood forest (Sander and Clark, 1971) and northern hardwood forest (Leak and Wilson, 1958).

The number of seedlings increased through the 15-year period even in areas that received no treatment. This unexpected result is consistent with anecdotal evidence that Allegheny hardwood stands make the transition from the stem-exclusion to the understory-reinitiation stage of stand development (Oliver and Larson, 1990) during the development interval covered by these measurements (55 to 70 years).

4.2. Model approach

In this approach, survival and growth are not modeled explicitly; individuals are not followed over time. We describe the state of the understory at intervals following thinning independent of prior conditions, to ensure that such a model can predict the effect of treatments in future rotations. A more specific analysis could make use of prior conditions, such as advance regeneration and herbaceous competition. Herbivory by deer is another important factor in Allegheny hardwoods. The effect of herbivory is not a predictive variable in our analysis, but the presence of these herbivores is implicit in our parameter values. Finally, our approach does not predict the response of individual species. Each of these issues is explored in the following sections.

4.3. Initial conditions

Although the responses measured fit general expectations of stand development and response to partial disturbance, there is a great deal of unexplained variation in the data (time since treatment and residual overstory density explained from 8 to 80% of the variation, depending on the size and tolerance class). Some of this variation probably is due to microsite conditions, as was found for density of pin cherry and yellow birch following clearcutting in New Hampshire (Thurston et al., 1992) and in northern hardwoods and hemlock-hardwoods in Michigan and Wisconsin (Metzger, 1980). Another important source of variation is the presence of advance seedlings and sprouts (Wang and Nyland, 1993), especially for sugar maple and beech, as is common in other forest types in the region (Leak and Wilson, 1958, Trimble, 1973, Metzger, 1980, Thurston et al., 1992). The advance seedlings seem to ensure a good representation of these species in the emerging community. In our study, the pretreatment density of stems > 1 ft tall and less than 1 in dbh ranged from fewer than 100 to more than 1000 per acre. Well established advance regeneration also can prevent the survival of new seedlings that develop in response to partial disturbance (Tubbs, 1968, Trimble, 1973, Metzger, 1980, Stout, 1994). In our study, beech root suckers dominated the advance regeneration and they dominated ingrowth to > 1 in dbh despite the regeneration of shade-intolerant seedlings. In this area, deer browsing prevents stump sprouts from being an important part of understory response to thinning. A third important pretreatment difference was the degree of interference from fern and grass. Regeneration sample plots with at least

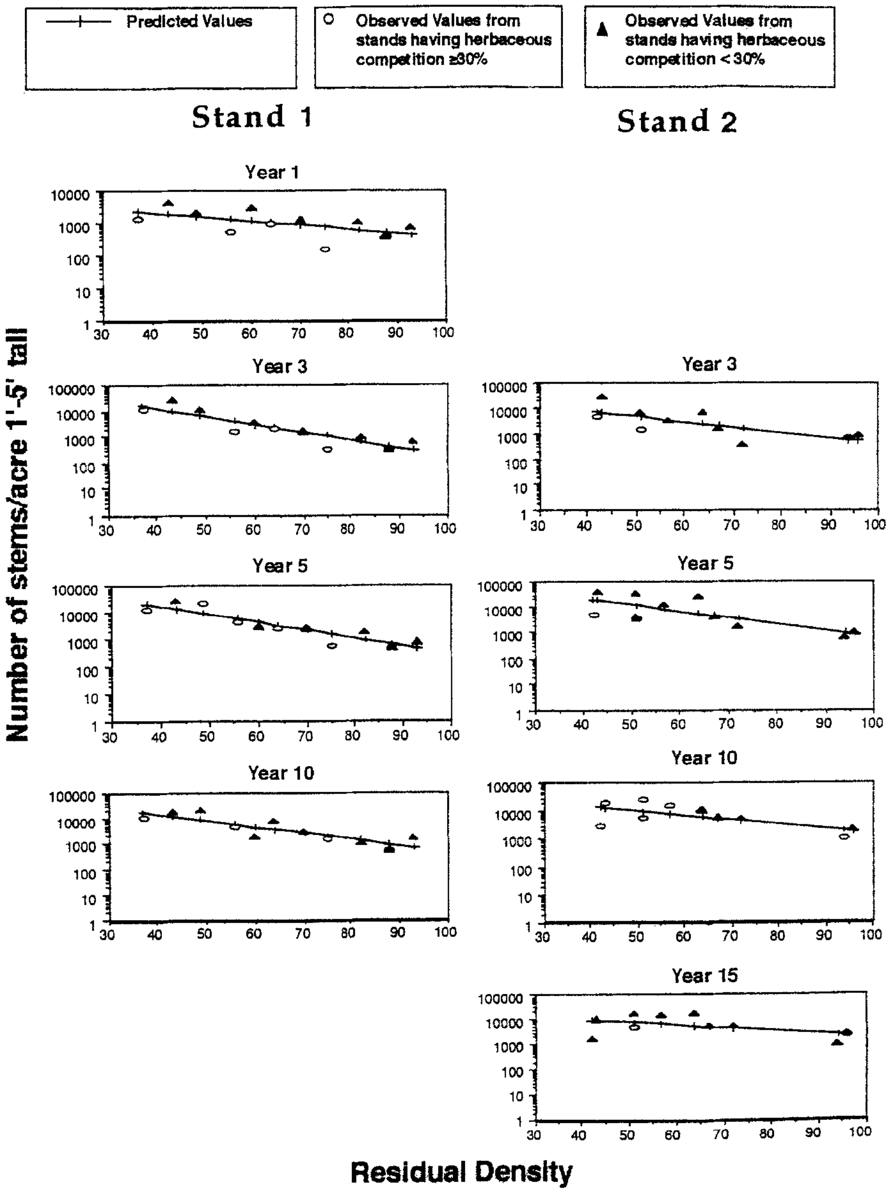

Fig. 6. Predicted and observed numbers of stems per acre in Stand 1 and Stand 2 showing which treatment areas had greater than 30% of plots with at least 30% cover of fern and grass.

30% fern cover (the threshold at which interfering plants are considered to be a problem; Marquis, 1982) ranged from none to all eight plots sampled within each treatment area (Fig. 1).

4.4. Advance regeneration

The outcome of regeneration treatments in Allegheny hardwoods depends on the presence of advance regeneration (Grisez and Peace, 1973, Marquis et al., 1992). Pretreatment conditions also affect understory response to partial cuttings (Stout, 1994). Regeneration treatments have been well studied in Allegheny hardwoods (Grisez and Peace, 1973, Marquis, 1973, Marquis and Bjorkbom, 1982, Horsley and Marquis, 1983, Stout, 1994). Existing regeneration guidelines (Marquis et al., 1992, Horsley et al., 1994) suggest that overstory removal in even-aged stands should only take place after large numbers of well distributed advance seedlings of desirable species have developed. Research has demonstrated the importance of deer browsing on advance regeneration (Marquis, 1981) and of ferns and grasses in preventing the establishment and growth of some species (Horsley and Marquis, 1983). Regeneration guidelines also suggest removing interfering plants when they cover 30% or more of the area in a stand (Horsley, 1991). Black and yellow birch and tulip-poplar are the only common overstory species in the Allegheny hardwood type that do not depend on advance regeneration for establishment.

4.5. Herbaceous competition

Fern cover interferes with the establishment and growth of important shade-intolerant and -intermediate species in this forest type (Horsley and Bjorkbom, 1983, Horsley, 1991). Similarly, fern and aster inhibit black cherry in central New York (Drew, 1990) and northern hardwoods can be inhibited by pin cherry (Heitzman and Nyland, 1994) or by *Rubus*, grasses, and sedges (Metzger and Tubbs, 1971). Similar effects have been shown for other forest types (Bowersox and McCormick, 1987).

The occurrence of fern and grass is shown in Fig. 1, with shading showing treatment areas in which three or more understory plots had at least 30% cover of fern and grass — the level considered to cause interference — at 5 years after thinning. The percentage of plots with more than 30% fern cover increased from 7% before treatment to 29% after 15 years (Nowak, pers. comm.). Stocking of grasses and sedges increased significantly only in the most heavily thinned areas (Nowak, pers. comm.). These interfering plants are correlated with lower numbers of stems in the plots in which they occur. Fig. 6 shows the residual variation in the number of stems predicted by residual density and time since treatment for the 1- to 5-ft size class (all species combined). The numbers of stems in areas with high herbaceous competition generally were overpredicted by the model while those in areas with lesser competition were underpredicted. In areas where the degree of herbaceous competition is known, understory development might be predicted with greater certainty than our more general model formulation allows.

4.6. Herbivory

Deer are a controlling factor in this forest type in that they alter the relative success of species by selectively browsing the more palatable species (Kittredge and Ashton, 1995). In addition, some species are more resilient to browsing than others (Tilghman, 1989).

Browsing pressure depends on both the density of deer and the availability of alternate food sources. The region has relatively little agricultural land, which, if present, serves as an important food source. Average density of deer in the Allegheny National Forest is about 30 deer per square mile, or about 50% more than the goal for the region established by the Pennsylvania Game Commission. Because of this high deer impact, unpalatable species such as beech and striped maple dominate understory species composition, and stump sprouts do not play an important role.

4.7. Disaggregating shade-tolerance groups to species

We chose to predict understory composition by shade-tolerance, a general approach that should apply to diverse forest types. Grouping species into functional groups reduces the variation that needs to be explained by a model. Shade-tolerance is one of many possible characteristics by which species could be grouped; we chose it because light is the factor most affected by thinning in these forest types. For some purposes, it is important to identify the individual species present. For example, to supply ingrowth to an overstory simulator, species are required; species composition is important to the future development of the forest and to its management.

The species composition of regeneration reflects the species composition of the overstory (Metzger, 1980, Kittredge and Ashton, 1990, Wang and Nyland, 1993) and will be most similar when the harvest method used is the same as that used to generate the existing stand (Trimble, 1973). Overstory species can be augmented by small seeded species that blow in over long distances and by species that germinate from buried seed (Wang and Nyland, 1993).

In this data set, black cherry seedlings dominated the shade-intolerant group and birch the shade-intermediate group (Table 2). The shade-tolerant group generally is dominated by beech, but in several treatment areas, striped maple and sugar maple are as important as beech. This distinction has important economic and ecological implications. Sugar maple has the greatest commercial value; striped maple has none, and beech will be damaged by beech bark disease. Beech produces the best mast of the three. Striped maple has a much shorter life and rarely reaches the diameter or height of the other two. Chosing silvicultural treatments for their effect on understory development cannot be based on shade-tolerance class without knowledge of the locally important species.

5. Conclusions

5.1. The modeling process

We modeled numbers of stems in three shade-tolerance classes and three size classes as a function of time since thinning and the relative residual density at the time of treatment. This simple model predicted a median of 40% of the observed variation in stem numbers. The model would have described understory characteristics more precisely had it included factors such as the presence of advance regeneration at the time of treatment, the interference of herbaceous competition, and variation in site conditions. We did not include these factors because we wanted a form of model that would be readily generalized to other forest types and that could be used in supporting decisions about the management of future stands, for which pretreatment information is unavailable. Prediction of understory characteristics beyond the time scale of observation cannot be extrapolated from these equations but should be based on expert judgement when data are not available. The disaggregation of shade-tolerance classes to individual species may be important in some forest types and could be included in a second stage of analysis.

5.2. Understory response to thinning

The effect of thinning on understory vegetation has implications for scenic beauty, wildlife habitat, and forest regeneration. Heavy thinning of the overstory creates a midstory of trees that blocks visual penetration and provides nesting sites for many species of birds. Thinning also promotes the growth of shade-tolerant species into the overstory. The heaviest thinnings reported here were insufficient to allow the recruitment of shade-intolerant or -intermediate species into the overstory. This outcome was influenced by the effect of deer on advance regeneration and would be different if deer impact were lessened. The presence of this shade-tolerant midstory could change the silvicultural options available for regeneration and the future trajectory of the stand. Although thinning is not practiced for its effect on the understory, the importance of changes in understory composition to the future of the stand suggests that the effect of thinning on the understory merits greater attention.

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