REGENERATION IN DEFOLIATED AND THINNED HARDWOOD STANDS OF NORTH-CENTRAL WEST VIRGINIA

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Abstract: Overstory species regeneration was examined in 1989, prior to gypsy moth defoliation and thinnings, on 16 stands in the West Virginia University Forest. Three stands were thinned and defoliated while five were thinned only and three were defoliated only. Five stands were neither thinned nor defoliated. Data were collected from these stands for three years subsequent to the disturbances. The general response to defoliation was similar in number of seedlings irrespective of thinning, i.e., there was an initial depression of regeneration, although it was more noticeable in stands that were not thinned. Total seedling production increased significantly on thinned stands two years following thinning, but differences disappeared by third year after treatment. For both defoliated and undefoliated stands, any effect of thinning on total seedling abundance was lost by 1992. Oak regeneration was greatest on control stands and stands that were thinned but not defoliated. Defoliation alone was detrimental to oak regeneration, while thinning moderated the defoliation effect. Red maple seedlings dominated numerically, but black cherry was the most abundant species in the larger size classes in all stands irrespective of treatment, and is likely to dominate the next generation of overstory trees in this area.

INTRODUCTION

A relatively thorough literature exists explaining the effects of gypsy moth defoliation on overstory species composition (Campbell and Sloan 1977, Feicht and others 1993, Herrick and Gansner 1988, Stephens and Hill 1971, Twery 1990, among others). Less is known, however, about understory vegetation and woody species regeneration responses to gypsy moth defoliation. Such knowledge is critical in predicting species replacement and determining appropriate management techniques for post defoliated stands as well as in advance of defoliation.

As silvicultural methods are employed with greater frequency in attempts to reduce susceptibility and vulnerability to gypsy moth (Gottschalk 1993), the understory responses to such treatments should be an important consideration. In many ways, defoliation resembles thinning and as such is likely to produce comparable effects, particularly in creating canopy openings, and increasing light penetration. In areas that have been thinned and defoliated, the potential for dramatic changes in species composition is great. With this study, we examine the effects of both defoliation and thinning on woody species regeneration.

Oaks (*Quercus* spp.) represent the most favored host of gypsy moth. Declining oak dominance from the potential of extreme oak mortality is exacerbated by oak regeneration problems which appear to be common throughout Eastern forests (Loftis and McGee 1993). Competition from intolerant and intermediate species contribute to regeneration problems. For example, red maple (*Acer rubrum* L.) is one of the more abundant regenerating species in many oak-dominated forests in the Midwest (Host and others 1987, Johnson 1992) and the Northeast (Lorimer 1984). In the Ridge and Valley Province in Pennsylvania, Nowacki and Abrams (1992) found that maple, cherry (*Prunus)*, and/or birch (*Betula*) are slowly replacing oak and that maple and beech (*Fagus grandifolia* Ehrh.*)* are dominating historically white oak (*Quercus alba* L.) dominated areas. Studies by Allen and Bowersox (1989), Ehrenfeld (1980), Fosbroke and others (1991), and Hix and others (1991) have examined regeneration following gypsy moth

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defoliation. Results of the previous research consistently indicate a reduced regeneration of previously dominant overstory species.

This study examines woody species regeneration, particularly focusing on oak, in mixed hardwood stands of the central Appalachians. Specifically, the study assesses the impact of silvicultural techniques used to minimize gypsy moth defoliation damage in addition to the effect of gypsy moth defoliation and mortality on woody regeneration.

METHODS

The study area is the West Virginia University Forest in north central West Virginia. The forest is located in Preston and Monongalia Counties, within the general boundaries of the mixed mesophytic forest region (*sensu* Braun 1950) in the slightly folded region of the Appalachian Plateau. The forest is generally considered a mixed hardwood forest, although is purported to have been heavily dominated by white oak at one time (Carvell and others 1978). Elevation of the study area ranges from 1800 to approximately 2300 feet, and Dekalb series represent the most abundant soil type.

Since the late 18th century the area has been heavily disturbed. Charcoal manufacture for the iron industry accounted for early use of the timber resource, followed by specialty wood products such as railroad ties and whiskey barrels. Nearly all of the Forest was eventually clearcut and much of it burned by the early 1930's (Carvell and others 1978).

For the current study, sixteen stands (eight pairs), ranging from 19.3 to 31.2 acres and accounting for a total of 408 acres were selected in 1989. A pair represents two adjacent stands of similar species composition and size structure, and reflects comparable suitability as host for the gypsy moth. One of each pair (hereafter referred to as "stands"), was thinned in Fall, 1989 or early Spring 1990. The objective of thinning was to reduce stand susceptibility or vulnerability (Gottschalk 1993) prior to potential gypsy moth defoliation. Defoliation followed in six stands in 1990 and in 1991. Each of the six stands incurred over 50% defoliation of preferred (Twery 1990) species and over 40% defoliation of all species for two years. Defoliation on the other stands, i.e. background defoliation level, was less than 15% of all species, including preferred. Using the random (defoliation) and fixed (thinning) treatments, the stands were classified as **C** (control), unthinned and undefoliated, **T** - thinned and undefoliated, **D** - defoliated but unthinned, and **DT** - defoliated and thinned. The **C** and **T** groupings are paired, and the **D** and **DT** groups are paired, e.g. **C1** and **T1** represent one pair of stands, as do **D1** and **DT1.**

Species composition in all structural layers was determined in 1989 prior to any treatment, and was remeasured in 1990, 1991, and 1992. Nomenclature follows Little (1979). Twenty 0.1 acre (0.04 ha) plots were established for overstory sampling and within each of these plots three, systematically located, 113 ft^2 (10.5 m) circular plots were sampled for woody seedling regeneration. Regeneration in the control stands (**C**), however, was not measured in 1990. Species were identified and categorized by the following size classification:

Size class 1:	all woody plants to 1 ft tall
Size class 2	1 to 5 ft tall
Size class 3	Greater than 5 ft tall, but less than 2.49 inches dbh
Overstory	Greater than 2.49 inches dbh

We used repeated measures analysis of variance to determine temporal trends in regeneration and to examine treatment effects. The data from 1989 were used as contrasts to determine significance over time. Analysis of covariance, using the pre-treatment data as covariates, was used to examine individual treatment effects.

RESULTS

Overstory Species Composition

Generally a mixed hardwood forest with a substantial component of oak, the basal area of much of the West Virginia University Forest was dominated by yellow-poplar (*Liriodendron tulipifera* L.) in 1989 (Table 1). In stands dominated by oak there were fewer overstory species overall compared to stands dominated by yellow- poplar. Although considered the dominant species in the West Virginia University Forest at one time, white oak accounted for only a small proportion of total basal area on all stands. The red maple component ranged from 4 to 17% of total stand basal area initially.

Significant decreases in overstory basal area occurred in all but the control stands (Table 1). Although stand basal areas were reduced substantially in the thinned stands, the relative contribution of the important overstory species remained somewhat constant. One of the objectives of the thinning was to reduce the overstory oak component, but this proved difficult in practice because of the actual distribution of trees. In **D** and **DT** stands, red maple proportion in the overstory increased to as much as 47% in some stands. Black cherry (*Prunus serotina*) increased substantially on one defoliated stand (**D2**).

Initial Regeneration

Table 2 includes only those species likely to attain overstory size in the 16 stands. Some non-overstory woody species were also plentiful. For example, blueberry (*Vaccinium* spp.) was the third most abundant woody species across all sixteen stands. Maple-leaf viburnum (*Viburnum acerifolium* L.), spicebush (*Lindera benzoin* (L) Blume.), and blueberry accounted for a total of 12% of all individuals sampled. By contrast, red oak (*Quercus rubra* L.), the most abundant oak species, accounted for only 4% of all individuals sampled in 1989. Oak regeneration in general was minimal and was most apparent on those stands with a strong oak component, **D1, D2** and **T5**. Red oak regeneration occurs most abundantly in stands with a considerable red oak overstory, but in stands with the greatest oak component in the overstory, the understory was dominated by black cherry (**D2** and **DT2**) and red maple (**D3** and **DT3**). *Vaccinium* also was a major component in the understory in those four stands. Numerically, black cherry and red maple dominated the regeneration overall. Overstory species, present but excluded from the table, due to small numbers include elm (*Ulmus rubra*), beech, black locust (*Robinia pseudoacacia*), basswood (*Tilia americana*), sugar maple (*Acer saccharum*), and American chestnut (*Castanea dentata*).

Effect of Treatments on Total Number of Seedlings

Throughout the four year period, there were slightly more seedlings on the undefoliated than on defoliated stands. Over the four years, number of seedlings on thinned, defoliated stands did not change, but thinning contributed to a significant increase in the total number of seedlings on defoliated stands in 1990 and 1991 when compared with unthinned stands. By 1992, there was no significant difference due to thinning, and seedling abundances for that year were nearly identical for all stand types. The 1992 values were similar to the 1989 values (Fig. 1). On stands that were undefoliated, thinning significantly increased seedlings in 1991, but there was no effect by 1992 (Fig. 2). Thinning did not result in an increase in total number of seedlings; rather, differences arose primarily because of a decrease in seedling numbers in unthinned stands.

Repeated measures analysis of variance indicates no general change in total number of seedlings (all species) from 1989 to 1992; however, there was a significant treatment effect in 1990 ($P<0.001$), and 1991 ($P<0.001$). The treatment effect was lost by 1992. There is a significant treatment by time interaction, suggesting that the pattern is not the same for all treatments.

Table 1. Relative overstory composition of study stands based on stems $\geq$2.5 inches dbh. Basal area represents the total basal area of each stand and the percent each of the major species contributes to total for 1989 (pre-treatment), and for 1992.

Stand	Basal Area (ft^2/ac) year - total	Red oak %	White oak %	Chest-nut oak %	Other oaks* %	Red maple %	Yellow-poplar %	Black cherry %
C1	1989 - 133.4	10.4	1.8	14.5	5.1	8.7	40.5	0.5
	1992 - 137.6	10.9	1.9	13.5	3.1	9.4	39.2	0.6
C2	1989 - 134.3	25.5	3.5	9.3	4.6	16.3	28.1	2.3
	1992 - 140.6	24.0	3.4	9.4	4.7	16.5	28.5	2.3
C3	1989 - 136.0	12.1	5.1	9.5	8.3	8.7	40.6	0.6
	1992 - 140.3	12.4	5.0	9.7	8.4	9.3	41.2	0.4
C4	1989 - 133.5	31.5	3.0	13.3	0.9	16.4	8.0	14.7
	1992 - 142.3	31.3	3.0	13.4	0.8	16.6	8.2	14.8
C5	1989 - 122.6	35.6	1.7	9.1	2.0	16.4	21.7	4.7
	1992 - 127.8	37.5	1.5	9.2	2.0	16.8	22.1	4.4
T1	1989 - 147.5	20.8	2.3	13.3	4.3	12.2	30.8	1.9
	1992 - 107.4	21.2	1.4	7.1	4.9	14.7	36.3	0.6
T2	1989 - 149.0	18.3	1.6	15.6	3.7	13.8	37.2	3.0
	1992 - 114.4	18.3	2.0	10.9	1.6	18.2	41.0	3.9
T3	1989 - 144.1	10.4	0	0.3	1.3	3.9	64.8	2.7
	1992 - 103.0	10.8	0	0.1	1.9	5.5	68.0	1.4
T4	1989 - 132.7	42.3	3.5	5.1	1.4	14.0	7.6	14.4
	1992 - 88.4	47.1	4.0	1.5	0.5	16.9	6.0	11.7
T5	1989 - 125.9	28.8	6.7	13.2	5.9	14.6	22.1	3.2
	1992 - 86.6	32.4	5.1	12.0	3.8	17.5	20.0	3.9
D1	1989 - 110.7	43.8	4.0	5.1	0.1	17.3	8.6	1.5
	1992 - 75.0	22.6	1.5	1.5	0	29.3	14.2	2.8
D2	1989 - 120.5	53.4	5.2	17.0	4.2	6.5	0.6	12.3
	1992 - 49.8	30.5	1.2	15.2	0.7	18.1	0	30.6
D3	1989 - 129.5	51.3	6.4	12.4	5.7	15.7	0.7	1.7
	1992 - 52.6	38.2	0.1	0.5	0	46.1	1.8	4.4
DT1	1989 - 130.8	34.2	1.9	4.0	2.0	12.5	27.0	0.9
	1992 - 84.4	11.4	0	0.3	0	22.0	44.9	1.9
DT2	1989 - 125.7	62.3	3.6	6.6	8.6	7.4	0	9.6
	1992 - 69.1	63.0	0.8	3.1	7.8	14.0	0	9.7
DT3	1989 - 127.8	40.6	11.6	7.9	6.2	16.8	0	0.4
	1992 - 38.0	18.3	0	3.6	0.6	47.4	13.4	1.9

Table 2. Overstory species regeneration prior to treatments. Values represent number of seedlings per acre of each species. All size classes are combined.

Stand	red maple	black cherry	sassa-fras	yellow poplar	red oak	black gum	chest-nut oak	white oak	sweet birch	hick-ory	sour-wood	mag-nolia	ash	black oak	scarlet oak
C1	25167	957	3000	2544	334	546	373	109	129	103	193	39	77	6	6
C2	8982	8725	1818	1298	495	777	135	77	251	19	0	45	13	0	0
C3	12734	6001	8397	1022	771	244	752	964	0	71	283	51	39	39	13
C4	3155	15330	835	874	430	6	84	6	315	13	0	0	6	0	0
C5	6624	13486	1047	3347	1092	141	180	141	77	32	0	0	308	0	0
T1	13730	1561	2339	777	655	996	668	173	180	244	148	26	6	6	0
T2	8886	8956	1144	2634	482	315	238	77	45	0	0	6	6	6	0
T3	1606	3225	5872	3540	437	6	13	13	45	64	0	6	0	39	0
T4	3553	12092	398	970	578	0	64	186	302	13	0	0	0	13	0
T5	7408	9278	1471	4446	1632	77	116	116	0	77	0	411	0	13	0
D1	13171	411	341	732	1574	167	64	90	39	13	0	0	0	6	0
D2	4106	14116	463	26	1375	6	353	58	51	0	0	0	0	32	0
D3	6772	617	141	6	1092	720	334	109	199	0	26	0	0	13	6
DT1	9638	263	1092	2872	1812	443	71	0	418	13	0	0	0	0	0
DT2	3386	11944	328	0	2050	13	135	334	32	45	0	0	0	19	0
DT3	7993	649	1439	0	572	58	32	206	334	0	0	0	0	0	13

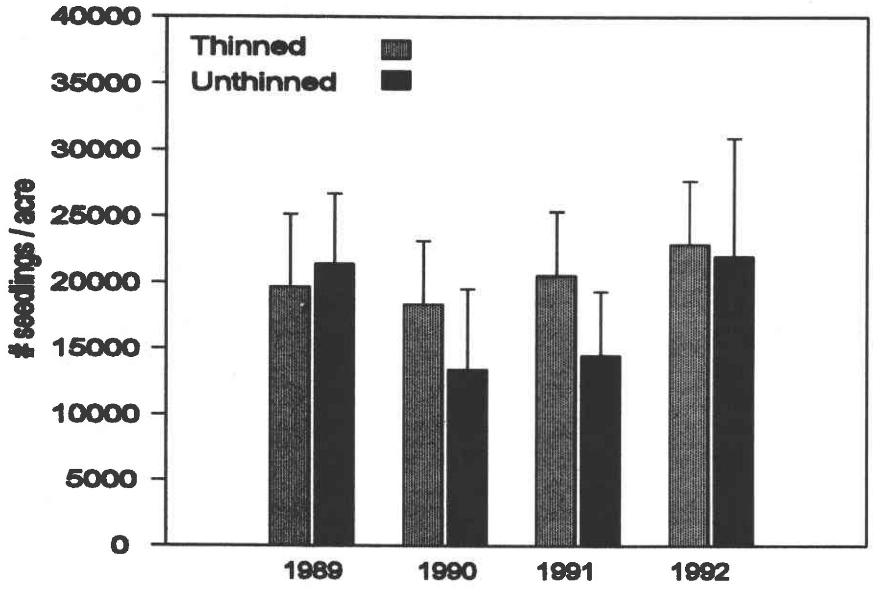

Figure 1. Average seedling abundance (all species) in defoliated stands.

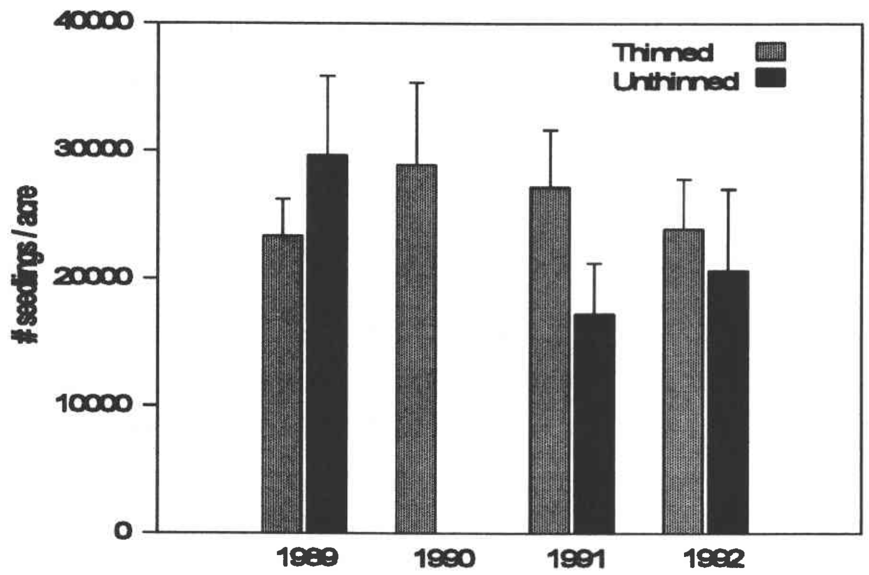

Figure 2. Average seedling abundance (all species) in undefoliated stands. Data were not collected for unthinned stands in 1990.

Oak Regeneration

The number of oak seedlings on defoliated stands (both **D** and **DT**) diminished over time (Figure 3). The decrease was greatest between 1989 and 1990 on **DT** stands; **D** stands dropped further, but after another year. Oak seedling abundance increased in both **T** and **C** stands, although, thinning increased production of oak seedling to a slightly greater extent. With time, in defoliated stands, irrespective of thinning, oak contributed less in successive years, as a consequence of both fewer oak seedlings and an increase in non-oak reproduction. This was confirmed through a significant time effect ($P<0.0001$), and a significant time by treatment effect ($P<0.001$), but no significant treatment effect ($P=0.21$).

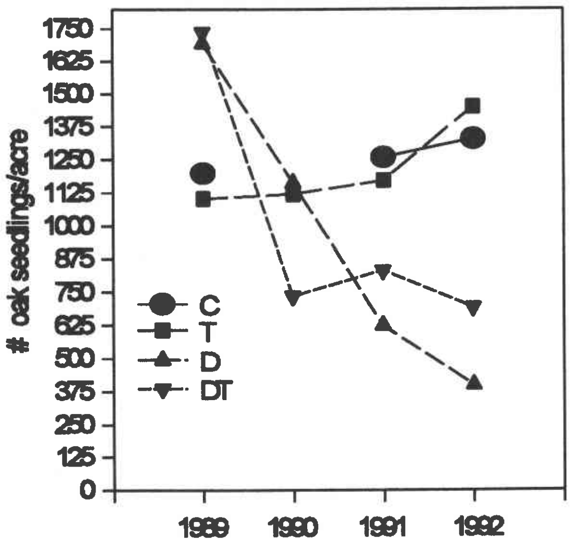

Figure 3. Oak regeneration from 1989 to 1992 for each treatment type. Regeneration was not sampled for control stands in 1990.

Treatment effects are not always consistent when individual stands are examined, and even control stands exhibit wide variation in production of oak seedlings. Figure 4 illustrates the change in oak seedlings as a percentage of original number (1989) of oak seedlings in each stand. With the exception of one stand (**T5**), thinning alone enhanced oak seedling production. Generally, thinning increased oak seedling production relative to no treatment in undefoliated stands, but one pair (**C1, T1**) did not follow the pattern of the other undefoliated stands. Defoliation, and thinning in conjunction with defoliation clearly reduced the oak component in the understory. Unthinned defoliated stands lost slightly more oak seedlings than **DT** stands in terms of absolute numbers and relative percentage of 1989 seedling numbers.

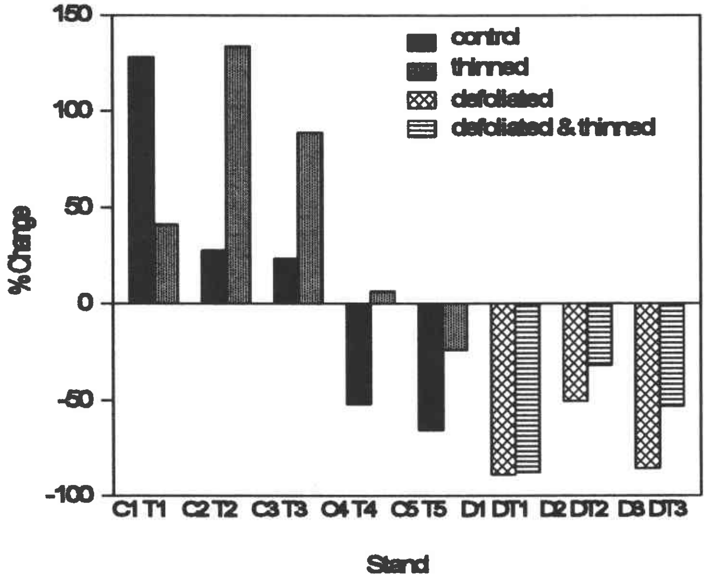

Figure 4. Percent change in oak seedlings from 1989 to 1992 for each stand. Values represent the number of oak seedlings in 1992 as a percentage of 1989 oak seedlings.

In all but one of the defoliated stands the amount that oak contributed to the regeneration decreased each year (Table 3). Pre-treatment (1989) regeneration values were not always comparable in the paired stands, and in no case was oak regeneration a very dominant group among seedlings despite the fact that some of these stands had over 70% basal area in oak originally. Oak contribution to regeneration was greatest prior to disturbance and immediately following initial disturbance (Table 3).

Regeneration Species Composition

Individual species responded differentially to the treatments (Table 4.) Over the four year period, red maple's contribution to total seedlings decreased under all treatments. With thinning alone this decrease was most dramatic. Black cherry increased only slightly in the control stands, but decreased both in raw numbers and as a percent of total seedlings in the other three treatments. Sassafras (*Sassafras albidum*), sweet birch (*Betula lenta*), and yellow-poplar increased in all treatments, but thinning, regardless of defoliation, increased sassafras and sweet birch production dramatically. Red oak increased as a proportion of total seedlings and in actual total number of seedlings in both **T** and **C** stands, while white oak decreased. In both types of defoliated stands, red and white oak diminished over the four years. Other increases in oak species were from 37 to 56 seedlings in **DT** stands for chestnut oak and from 171 to 223 in **T** stands; however, this only represents increases of 0.1%, and 0.3% of all seedlings, respectively . In **C** stands, chestnut oak increased by 1.1%.

Non-overstory woody species can account for considerable competition for regenerating species (Table 4). Of particular note is the abundance of *Vaccinium* spp. (blueberry) in defoliated stands. The presence of this species is not a function of disturbance as much as a reflection of site characteristics. Nonetheless, blueberry abundance is likely deleterious for regeneration, and it appears that thinning helps to reduce blueberry when compared to non-thinned defoliated stands.

Table 3. Oak reproduction in all stands. Each value represents the percentage of oak contribution to total regeneration. Total regeneration includes all species, irrespective of potential to exist in the overstory.

	1989	1990	1991	1992
Stand	%	%	%	%
DT - 1	10.4	1.8	1.1	0.9
D - 1	10.0	4.2	2.4	1.5
DT - 2	9.8	11.7	11.0	10.0
D - 2	6.6	5.9	5.4	3.9
DT - 3	5.4	3.6	1.2	1.5
D - 3	8.1	5.7	4.1	0.7
C-1	2.2	*	7.6	8.4
T-1	6.0	3.8	5.9	7.3
C-2	2.9	*	6.6	5.0
T-2	3.2	4.8	4.6	7.9
C-3	7.7	*	12.7	10.1
T-3	2.3	1.6	2.8	3.8
C-4	2.2	*	2.8	1.5
T-4	4.3	6.0	4.3	4.8
C-5	4.8	*	4.0	3.3
T-5	7.2	4.5	4.3	6.2

* - no data collected for control stands in 1990

Table 4. Percentage of total individuals represented by selected species for 1989 and 1992, by treatment.

	CONTROL		THINNED		DEFOLIATED		DEFOL. & THIN.	
species	1989	1992	1989	1992	1989	1992	1989	1992
red maple	38.2	27.2	30.1	17.8	37.4	35.6	35.7	28.2
black cherry	30.0	31.7	30.0	19.8	23.6	11.9	21.8	10.9
sassafras	10.2	12.1	9.6	22.2	1.5	5.4	4.8	21.7
yellow-poplar	6.1	9.0	10.6	16.4	1.2	5.8	4.9	11.7
red oak	2.1	3.2	3.2	3.9	6.3	1.5	7.5	2.7
sweet birch	0.5	4.7	0.5	6.2	0.5	2.9	1.3	8.9
white oak	0.9	0.9	0.5	0.5	0.4	0.1	0.9	0.1
scarlet oak	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
chestnut oak	1.0	2.1	0.9	1.2	1.2	0.4	0.4	0.5
black oak	0.0	0.2	0.1	0.1	0.1	0.0	0.0	0.1
blueberry	1.2	1.3	1.9	1.3	25.2	32.8	19.3	12.8
black gum	1.2	1.1	1.2	0.6	1.4	1.7	0.9	0.7
viburnum	4.2	2.8	3.8	1.8	0.0	0.0	0.0	0.0
spicebush	0.4	0.8	3.5	4.2	0.4	0.8	0.6	0.6

Effects of Defoliation and Thinning on Size Structure

For those seedlings most likely to reach the overstory, i.e. size class three, treatments had little effect over the four year period (Table 5). Red oak recruitment into the larger size classes was only significant in the thinned stands, with a total of 273 moving into size class 2, a group that had only 33 individuals four years previous. First year seedlings of chestnut oak (*Quercus prinus*) increased in **C, T** and **DT** stands. Black and scarlet oak (*Quercus velutina* and *Q. coccinea*) also increased in 1992 in the size classes under five-feet tall in undefoliated stands. White oak showed the poorest response among the oaks.

Certain species responded in a manner characteristic of their early successional nature. Black cherry increased in most size classes everywhere but **C** stands. Sweet birch increased in size class one in all treatment types, and in size class two, everywhere but **C** stands. Yellow-poplar followed a similar pattern, but growth of this species was evident only in **T** and **DT**. Sassafras increased in size classes under five feet in all but the **C** stands also. Thinning treatments (**T** and **DT**) appear to accelerate sassafras growth dramatically, giving rise to an abundance in the 1-5 ft size class during in the four year period.

DISCUSSION

Among studies examining regeneration as affected by gypsy moth defoliation, Allen and Bowersox (1989) sampled forests in both the Allegheny Mts. and Ridge and Valley provinces. The most abundant woody regeneration in many stands in both areas was red maple, accounting for up to 90% of all commercial regeneration in the Allegheny Mountains and 49% in the Ridge and Valley provinces. Birch was a major constituent of regeneration in the Ridge and Valley. The values for red maple in studies by Allen and Bowersox (1989), and Hix and others (1991) surpassed the quantities found at the West Virginia University Forest. Stands on the West Virginia University Forest exhibit greater species richness in regeneration than the previously mentioned studies, for black cherry and yellow poplar were commonly found, in addition to sweet birch and red mapels. Yellow-poplar seedlings ranged from 1259 (**D**) to 2585 (**DT**) seedling/acre at the West Virginia University Forest, while they were not even noteworthy in the previous work. Also, black cherry seedlings surpassed all but red maple in our study and were not noted by Allen and Bowersox (1989). Hix and others (1991) found 2333 black cherry seedlings/acre, a value comparable to the number found at the West Virginia University Forest. Sassafras averaged 1776 seedlings/acre in Allen and Bowersox's study, and 1138/acre in the **D** stands and 4567 seedlings/acre in **DT** stands. Some differences among the studies may be attribuable to sampling time, because we sampled immediately after defoliation, while the other research was no fewer than five years following defoliation.

The abundance of yellow-poplar seedlings likely reflects high site productivity (Ostaff and others 1982), and yellow-poplar regeneration may aggravate problems of oak regeneration (O'Hara 1986). This species is likely to dominate certain areas if disturbance is severe (Beck and Hooper 1986). Loftis (1983) found that any canopy opening is likely to promote yellow-poplar and lead to its dominance on good sites in the southern Appalachians. In the current study, the most abundant 1-5 feet regeneration of yellow-poplar occurs on thinned stands and thinned/defoliated stands. However, our data suggest that recruitment into the larger size classes for this species (Table 5) has been minimal. This species has increased relative to total basal area, in the overstory on two of the three **DT** stands, but increased only slightly elsewhere (Table 1) during the four year period. The increase in overstory corresponds to oak mortality in the highly disturbed stands.

In this study, black cherry seem to be assuming a role analogous to yellow-poplar in the southern Appalachians. Although total numbers of black cherry seedlings decreased over the four years of the study, the decreases were apparent in the smallest size classes. The seedlings in size class 3 increased significantly in the three disturbed treatments (Table 5). Black cherry is relatively intolerant of shade and will respond favorably when the canopy has been opened (Marquis 1990). A substantial cohort of black cherry was established pre-defoliation and pre-thinning

Table 5. Total number of seedlings per acre in three size classes. Size class 1:<1 ft. tall.; Size class 2: 1 -5 ft. tall; Size class 3: >5ft. tall, but less than 2.49 in dbh.

species	size class	control 1989	control 1992	thinned 1989	thinned 1992	defoliated 1989	defoliated 1992	defoliated & thinned 1989	defoliated & thinned 1992
red	1	10490	5037	6665	3736	7887	7673	6789	6066
maple	2	688	441	258	431	11	21	43	98
	3	128	123	97	73	34	28	160	81
sweet	1	92	917	37	1168	83	525	194	1592
birch	2	40	31	58	297	4	51	60	179
	3	22	21	19	19	9	9	6	4
yellow	1	1804	1846	2458	3812	253	1259	940	2553
poplar	2	9	4	9	97	0	0	11	32
	3	0	0	1	1	0	0	0	0
black	1	249	172	215	88	253	324	160	138
gum	2	54	32	37	45	13	6	0	6
	3	40	32	26	15	30	23	11	0
black	1	6595	4776	4628	2104	3704	898	3038	727
cherry	2	2155	1605	2199	2176	1249	1153	1111	1089
	3	129	153	179	455	62	357	109	506
white	1	242	182	97	82	81	14	170	18
oak	2	17	13	15	29	0	0	6	2
	3	0	0	0	0	4	4	2	0
scarlet /	1	13	31	15	34	19	2	10	20
black oak	2	0	4	0	75	0	0	0	2
	3	0	0	0	3	0	0	0	0
chestnut	1	263	405	208	228	238	66	77	88
oak	2	37	32	12	56	2	4	0	13
	3	4	3	0	1	9	6	2	2
red oak	1	604	645	718	656	1304	275	1460	466
	2	18	9	33	273	21	19	6	81
	3	1	4	4	8	13	6	2	0
sassafras	1	2846	2383	2023	4419	311	1087	898	4235
	2	167	101	217	881	2	51	49	332
	3	0	0	0	6	0	0	0	0

and the disturbance provided the opportunity for increased growth of this regeneration. Dominance in the overstory of the post-disturbance stand is a likely consequence of vegetation present at the time of disturbance. This concept of initial floristics has been used widely to characterize forest succession (Drury and Nisbet 1973, Egler 1954, Oliver and Larson 1990) as well as describe post-defoliation succession (Ehrenfeld 1980) and oak regeneration problems (Loftis 1983, Ross and others 1986).

In disturbed stands, red maple and birch are also expected to maintain importance in the overstory because of increases in the number of seedlings, and their comparable, but rather low, mortality rates as understory trees (Lorimer 1981) and ability to exploit conditions caused by defoliation (Collins 1961). Given repeated disturbance, the **T**, **D**, and **DT** stands are likely to be dominated by red maple and black cherry, with a component of birch.

Oak seedling abundance, both previous and subsequent to disturbance, was somewhat low relative to other studies. The range of total oak regeneration in 1989 was from 501 (Stand **T3**) to 2538 seedlings/acre (Stands **C3** and **DT2**). In 1992 the range was 193 (Stand **D1**) to 3122 (Stand **C3**) seedlings/acre. In Ridge and Valley Forests of southern Virginia, Ross and others (1986) found over 8,000 oak seedlings/acre in mixed oak types and 5059 oak seedlings/acre in mixed hardwood types. After clearcutting in those forests, however, values dropped to 1309 and 26 seedlings/acre respectively. In relatively undisturbed oak dominated ecosystems in Michigan, Johnson (1992) found a range of 5261 to 11152 oak seedlings/acre. Allen and Bowersox (1989) found 707 seedlings/acre of red oak in post defoliated stands in the Allegheny Mountains and Hix and others (1991) 1363 seedlings/acre, while we sampled 300 seedlings/acre in **D** stands and 547 in **DT** stands. Abundance of white oak seedlings was 458 and 2002 seedlings/acre, respectively for the previous studies, and we found fewer than twenty seedlings/acre in defoliated stands.

Red oak seedlings were generally taller on the thinned stands versus unthinned stands, a finding similar to Ward (1992). When compared with stands that had been defoliated only, **DT** stands had greater numbers of scarlet/black oak and chestnut oak seedlings. In **DT** stands in 1992, there were no white oak seedlings in size class 3, and only two in size class 2, whereas red oak seedlings increased from 6 to 81 in size class 2. Thinning, followed by defoliation provided suitable microclimatic conditions for growth enhancement of red oak, but not new reproduction. The increased growth phenomenon did not occur in stands that were defoliated only, but may be a function of severity of defoliation, as the extent of defoliation and mortality was not uniform throughout the stands. The decrease in total number of oak seedlings in both **D** and **DT** stands may in part be due to seedling defoliation by the gypsy moth (Hicks and others 1993) or by a decrease in acorn production due to defoliation (Gottschalk 1989).

Small size and low numbers of oak advance regeneration are primary causes of oak regeneration failure. Based on the scarcity of oak in the larger size classes (Table 5), it seems unlikely that oak will remain as large a component in the overstory as it currently is. The percentage of red oak in the overstory did not decrease in **DT2** from 1989 to 1992 (Table 1), so defoliation and thinning would appear to be less important than pre-disturbance species composition and site factors. In contrast, for all three **DT** stands, red maple increased substantially as a proportion of basal area, and is likely more sensitive to disturbance than site. In **DT1** yellow-poplar showed a dramatic increase in proportion of overstory during those four years, but this was primarily due to pre-disturbance presence of that species. Black cherry, red maple and *Vaccinium* dominate the understory of all the defoliated stands and provide severe competition for oak regeneration.

In the control stands, oak basal area remained virtually the same over the four years. Given the seedling abundance on control stands, oak regeneration might be inadequate to contribute much to the overstory. Since the goal of thinning was to reduce gypsy moth host species abundance, oak basal area decreased. Thinning also provided an opportunity for growth of oak regeneration, assuring a presence, albeit not necessarily dominance, of oak in these stands. Similarly, Carvell and Tryon (1961) found that partial overstory removal enhanced oak production, and that oak regeneration decreased with increasing basal area. Defoliation alone, and in concert with thinning reduced oak basal area in most of the thinned and/or defoliated stands in this study, but in stand **DT2**, the red oak proportion of total basal area increased slightly.

Defoliation alone adversely affected oak regeneration to a greater extent than the defoliation and thinning combination. Silvicultural practices in advance of potential overstory defoliation is warranted for perpetuating the oak resource. In these stands, however, oak regeneration is inadequate in these stands for all treatment types, in accordance by recommendations by Sander and others (1984) for the central hardwoods. Despite a sufficient total number of seedlings, there are too few in the taller size classes to assure oak in the overstory.

CONCLUSIONS

Black cherry is likely to dominate the next generation of overstory trees in the stands in this study and in comparable areas in the Allegheny Plateau. Disturbance accelerates this transition, but the response of black cherry to defoliation and defoliation plus thinning was similar. Recruitment of black cherry into the taller size classes stands that were thinned only was slightly less than stands that were thinned and defoliated and defoliated only, underscoring the importance of disturbance for black cherry success.

Despite an abundance of shade intolerant species in the understory of these stands and an increase in the number of seedlings and saplings less than a foot tall, few of these will become canopy dominants. Recruitment into the larger size classes of these species has been minimal.

Defoliation reduced the growth and recruitment of oak, but thinning moderated the defoliation effect. Thinning, without defoliation, enhanced growth of oak seedlings. Even in undisturbed stands, however, oak regeneration over 5 feet tall was negligible after four years.

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