DEVELOPMENT OF REGENERATION FOLLOWING GYPSY MOTH DEFOLIATION OF APPALACHIAN PLATEAU AND RIDGE & VALLEY HARDWOOD STANDS[1,2]

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Abstract: The effects of gypsy moth defoliation and subsequent overstory mortality on regeneration were examined in 26 stands in Pennsylvania and Maryland. The Pennsylvania stands were located in the Appalachian Plateau physiographic province, and the Maryland stands were located in the Ridge & Valley province. Pre–defoliation data (1984-1986) were compared with post–defoliation data (1989) from the same 315 six-foot–radius plots. Seedlings of all woody vegetation were counted by species and height class. Separate matched pair t-tests were used to test for differences in pre- and post–defoliation regeneration counts for the most common species in each province. In the Appalachian Plateau, the total numbers of white oak, chestnut oak, and northern red oak decreased while the numbers of less desirable species (red maple, blueberries, raspberries, and greenbriers) increased following defoliation. In the Ridge & Valley, the total number of white oak also decreased; however there was an increase in the number of chestnut oak and northern red oak. The number of less desirable species increased as well, specifically red maple, black cherry, serviceberry, blueberries, and raspberries. In both provinces, there were fewer than 165 oak seedlings per acre in the greater-than-3-foot-height class following defoliation. Therefore, it appears that adequate oak regeneration had not become established in these stands at the time of our study.

INTRODUCTION

The impact of gypsy moth (*Lymantria dispar* L.) defoliation and subsequent overstory mortality on regeneration is of concern to forest managers interested in regenerating oak stands, yet little is known about this impact. It has been reported that some species of

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advance regeneration beneath a defoliated oak canopy (e.g., red maple (*Acer rubrum* L.)) may benefit from the increased light intensity and nutrients in the insect frass (Collins 1961). In a mature oak forest in New Jersey, Ehrenfeld (1980) found that 7-year-old gaps caused by the gypsy moth were dominated by the red maple, American beech (*Fagus grandifolia* Ehrh.), and black birch (*Betula lenta* L.) that had become established in them at or before the time of defoliation. Very little new establishment of plants had occurred; tree reproduction was apparently inhibited or excluded. In 1985, Gansner observed that after 10 years a particular heavily-defoliated oak--hickory stand in northeastern Pennsylvania had very little regeneration of commercial species. Blueberries (*Vaccinium* spp.), witch-hazel (*Hamamelis virginiana* L.), raspberries (*Rubus* spp.), and several species of ferns dominated the understory, along with some tree seedlings that had been heavily browsed by deer. More recently, Allen and Bowersox (1989) found that defoliated oak stands in the Allegheny Mountains and the Ridge & Valley Provinces had understories dominated by red maple, birch, and non--commercial species. Only 4-16% of the stems were northern red oak (*Quercus rubra* L.) or white oak (*Q. alba* L.). In all these studies, the stands were examined several years after defoliation, and their pre--defoliation understory compositions were unknown.

Our study benefitted by the availability of pre--defoliation data, so we were able to compare prior understory compositions with the regeneration that existed after defoliation. The purpose of this paper is to examine the effects of gypsy moth infestation on the development of hardwood stand regeneration in the Appalachian Plateau and Ridge & Valley physiographic provinces.

METHODS

A total of 26 stands were sampled in this study. Seventeen stands were located in the Appalachian Plateau physiographic province in Somerset County, Pennsylvania (Figure 1). These stands are on tracts managed by either the Pennsylvania Game Commission, Westvaco Company, or a private landowner. Topography of the stands ranged from relatively flat, elevated plateaus at 2,250 feet above sea level to rugged, mountainous terrain with many short ridges and steep coves. The average site index for northern red oak was 55 feet (range 32-91). Stands were primarily of pole- and small sawtimber-size and of mixed-oak composition (oaks averaged of 74 percent of the basal area). In general, these stands were moderately defoliated in 1985, severely defoliated in 1986, lightly defoliated in 1987, and virtually undefoliated in 1988 and 1989. The average reduction in percent stocking over the five-year period was 28%. A more detailed description of these Appalachian Plateau stands including their defoliation and mortality histories can be found in Fosbroke and Hicks (1989).

Nine more stands were located in the Ridge & Valley province of western Maryland (Figure 1). All Ridge & Valley stands used in the study are on Green Ridge State Forest in Allegany County, Maryland. Elevations range from 475 to 2,309 feet above sea level. The primary forest type of this area is mixed-oak (oaks averaged 66 percent of the basal area). The average site index was 56 feet (range 34-76). In general, these stands were moderately defoliated in 1985 and 1986. The study stands received little defoliation in 1987, 1988, or

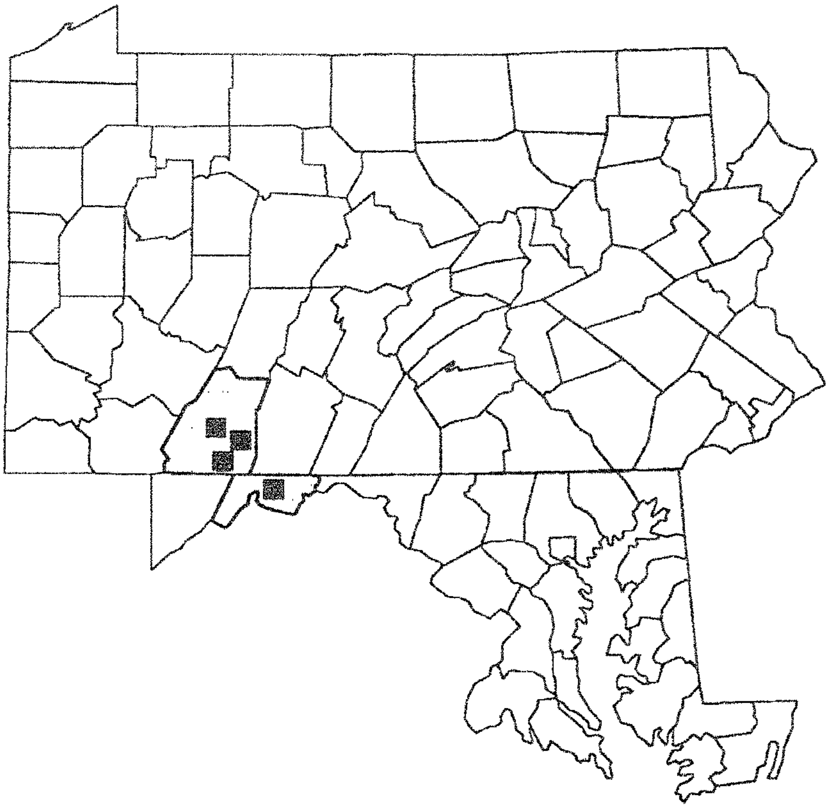

Figure 1. Regeneration plots were located in Pennsylvania and Maryland. The Pennsylvania stands were located in the Appalachian Plateau physiographic province, and the Maryland stands were located in the Ridge and Valley province.

1989. The average reduction in stocking was 14 percent. Though portions of Green Ridge State Forest were defoliated by a looper complex in 1981, none of the stands used in this study were involved in this previous defoliation event. Crow and Hicks (1990) provide a more complete description of the Ridge & Valley stands.

Within each stand, the understory vegetation was surveyed on a series of 6-foot–radius plots. The number of plots per stand ranged from five to thirty. All woody vegetation was tallied by species and height class (< 1.0 ft, 1.0-3.0 ft, and > 3.0 ft but less than 2.9 in. dbh). From 1984 to 1986, 315 plots (194 in PA, 121 in MD) were inventoried prior to gypsy moth defoliation. These same plots were again inventoried following defoliation in 1989.

Analysis of variance indicated that many of the most abundant species differed between physiographic provinces in their response to gypsy moth defoliation and subsequent mortality

(Fosbroke, unpublished data). Therefore, the development of regeneration in each province was analyzed separately.

Since the same plots were measured pre- and post-defoliation, matched pair t-tests were used to determine if there was a significant change in the number of understory stems per acre following gypsy moth defoliation and subsequent tree mortality. A separate test was done for each of the 13 most abundant species (chestnut oak (*Quercus prinus* L.), northern red oak, white oak, red maple, sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), black birch, witch-hazel, downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern.), dogwoods (*Cornus* spp.), blueberries, raspberries, and greenbriers (*Smilax* spp.)). Separate tests were also done for each height class of white oak, northern red oak, chestnut oak, red maple, sugar maple, black cherry, and black birch. Only plots which had a given species either before or following defoliation were included in the test for that species. Therefore, the means reported in Tables 1 and 2 represent the average number of stems per acre for those plots in each province where each species was present. These means do not represent the average number of stems of each species for the entire province.

Each of the species was then placed into one or more of four broad groups for additional testing. The commercial tree species group consisted of red maple, sugar maple, northern red oak, white oak, chestnut oak, black oak (*Quercus velutina* Lam., scarlet oak (*Q. coccinea* Muenchh.), black birch, black cherry, American beech, yellow-poplar (*Liriodendron tulipifera* L., hickories (*Carya* spp.), butternut (*Juglans cinerea* L.), cucumbertree (*Magnolia acuminata* L.), eastern white pine (*Pinus strobus* L.), table-mountain pine (*P. pungens* Lamb.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). An all oak group contained northern red oak, scarlet oak, black oak, white oak, and chestnut oak. Non-commercial tree species included black locust (*Robinia pseudoacacia* L.), American elm (*Ulmus americana* L.), slippery elm (*U. rubra* Muhl.), sassafras (*Sassafras albidum* (Nutt.) Nees), pin cherry (*Prunus pensylvanica* L.), and black gum (*Nyssa sylvatica* Marsh.). The final group includes shrubs, vines and small trees which are usually restricted to the understory and considered competing vegetation. The species that make up this "all other woody plants" group are blueberries, raspberries, greenbriers, dogwoods, witch-hazel, downy serviceberry, mulberries (*Morus* spp.), crabapples (*Crataegus* spp.), minniebush (*Menziesia pilosa* (Michx.) Juss.), spicebush (*Lindera benzoin* (L.) Blume), eastern redbud (*Cercis canadensis* L.), azaleas (*Azalea* spp.), American chestnut (*Castanea dentata* (Marsh.) Borkh.), honeysuckles (*Lonicera* spp.), currants (*Ribes* spp.), boxelder (*Acer negundo* L.), striped maple (*A. pensylvanicum* L.), grapes (*Vitis* spp.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), poison ivy (*Toxicodendron radicans* (L.) Kuentze), mountain laurel (*Kalmia latifolia* L.), roses (*Rosa* spp.), devil's walkingstick (*Aralia spinosa* L.), American hornbeam (*Carpinus caroliniana* Walt.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch). Comparisons were made for the total number of stems and for each height class for each of these four species groups.

RESULTS

Appalachian Plateau Province

For many tree species, the matched pair t—tests indicated that the average pre-defoliation numbers of stems per acre of various height classes were significantly different from the post-defoliation numbers (Table 1). For instance, prior to defoliation the most common commercial tree species was red maple (5038 stems/acre). The total number of red maple significantly increased ($P < 0.001$) to 10,763 following defoliation. Other commercial tree species that increased in total number following defoliation were black cherry and black birch, while sugar maple decreased (Table 1). However, these changes were not significant ($P > 0.1$). It is interesting to note that the number of stems in the 1-3—foot height class of each of these four species increased following defoliation, although only two of these increases were significant at the 10% level (Table 1). The trend for the all commercial tree species group was similar with significant increases ($P < 0.001$) in all height classes except the greater-than-3-foot class (Table 2).

Numbers of chestnut oak, northern red oak, and white oak of most height classes significant decreased ($P < 0.1$) in numbers after defoliation, with the exception of the 1-3-foot classes (Table 1). But, the increases in the 1—3—foot class for all three major oak species were not significant ($P > 0.2$). However, there was a significant increase ($P < 0.01$) in this height class for the species group that includes all oaks (Table 2). Otherwise, the total number of all oaks and the 0-1—foot class of all oaks significantly decreased ($P < 0.03$) following defoliation. Following defoliation, an average of only 162 oak stems per acre greater than 3 feet tall were present (Table 2).

As a group, the total number of non-commercial tree species increased from 2282 to 2729 stems per acre following defoliation (Table 2). This increase was not significant at the 10% level.

The overall increase in density following defoliation was primarily the result of the large significant increase ($P < 0.001$) in total number of the all other woody plants species group (Table 2). Most of these stems were less than 1 foot tall (Table 2). The two most common species groups following defoliation were blueberries and raspberries, numbering approximately 41,000 and 19,000 stems per acre, respectively (Figure 2). Greenbriers also increased significantly ($P < 0.04$) after defoliation, although by a lesser amount (Figure 2). The total numbers of witch-hazel and serviceberry increased significantly ($P < 0.06$) following defoliation, while there was a significant decrease ($P < 0.02$) in the total number of dogwoods (Figure 2).

Table 1.--Average numbers of stems per acre of the major tree species by height class and paired t-test significance levels for hardwood stands before and after gypsy moth defoliation in the Appalachian Plateau and Ridge & Valley provinces.

Species	Height class (feet)	Appalachian Plateau			Ridge & Valley		
		Pre-	Post-	P > t	Pre-	Post-	P > t
Chestnut oak							
	0-1	1491	856	0.050	3326	6411	0.009
	1-3	372	440	0.412	754	987	0.365
	> 3	122	77	0.032	192	128	0.132
	All	1985	1373	0.086	4172	7526	0.010
Northern red oak							
	0-1	1825	959	0.004	1045	1537	0.049
	1-3	262	363	0.203	175	434	0.004
	> 3	79	41	0.023	8	19	0.181
	All	2166	1363	0.007	1228	1991	0.010
White oak							
	0-1	1981	1438	0.014	4355	3043	0.004
	1-3	420	426	0.959	347	323	0.777
	> 3	144	137	0.742	185	81	0.033
	All	2545	2002	0.056	4888	3447	0.003
Red maple							
	0-1	4143	9807	0.0001	1749	7463	0.001
	1-3	580	756	0.078	821	927	0.340
	> 3	314	199	0.015	271	208	0.219
	All	5038	10763	0.0001	2842	8599	0.001
Sugar maple							
	0-1	1699	1586	0.729	544	1269	0.326
	1-3	498	634	0.235	476	227	0.531
	> 3	709	498	0.076	90	45	0.332
	All	2908	2719	0.583	1110	1540	0.665
Black cherry							
	0-1	1544	1243	0.254	650	5135	0.004
	1-3	385	1010	0.0001	333	465	0.168
	> 3	84	80	0.867	40	160	0.028
	All	2013	2333	0.128	1023	5761	0.002
Black birch							
	0-1	1528	1023	0.250	--[a]	--	--
	1-3	657	1193	0.167	--	--	--
	> 3	549	751	0.320	--	--	--
	All	2734	2968	0.707	--	--	--

[a]In the Ridge & Valley province, black birch was found on only one plot prior to defoliation, and it was not found on any plots following defoliation.

Table 2.--Average numbers of stems per acre of species groups by height class and paired t-test significance levels for hardwood stands before and after gypsy moth defoliation in the Appalachian Plateau and Ridge & Valley provinces.

Species	Height class (feet)	Appalachian Plateau			Ridge & Valley		
		Pre-	Post-	P > t	Pre-	Post-	P > t
All oaks							
	0-1	3195	2163	0.001	6267	6375	0.864
	1-3	594	934	0.001	953	1067	0.427
	> 3	195	162	0.108	222	124	0.011
	All	3984	3259	0.027	7442	7566	0.854
All commercial trees							
	0-1	8138	12052	0.0001	8620	16956	0.0001
	1-3	1703	2909	0.0001	2298	2521	0.319
	> 3	889	782	0.256	729	551	0.028
	All	10730	15743	0.0001	11647	20028	0.0001
All non-commercial trees							
	0-1	1900	1864	0.907	2116	1921	0.441
	1-3	300	751	0.008	997	820	0.071
	> 3	82	114	0.259	172	131	0.431
	All	2282	2729	0.262	3285	2873	0.149
All other woody plants							
	0-1	22405	35700	0.0001	19945	30233	0.0001
	1-3	5688	8988	0.0001	5077	8120	0.0001
	> 3	1503	972	0.0004	2200	1264	0.0001
	All	29595	45660	0.0001	27222	39617	0.0001
All of the above							
	0-1	31519	48577	0.0001	30125	48539	0.0001
	1-3	7566	12277	0.0001	8231	11217	0.0002
	> 3	2456	1811	0.0002	3247	1907	0.0001
	All	41541	62665	0.0001	41603	61663	0.0001

[a]Species groups are defined in the Methods section.

Ridge & Valley Province

As was true in the Appalachian Plateau province, the matched pair t—tests indicated that the average pre-defoliation numbers of stems per acre of various height classes of many tree species were significantly different from the post-defoliation numbers (Table 1). Prior to

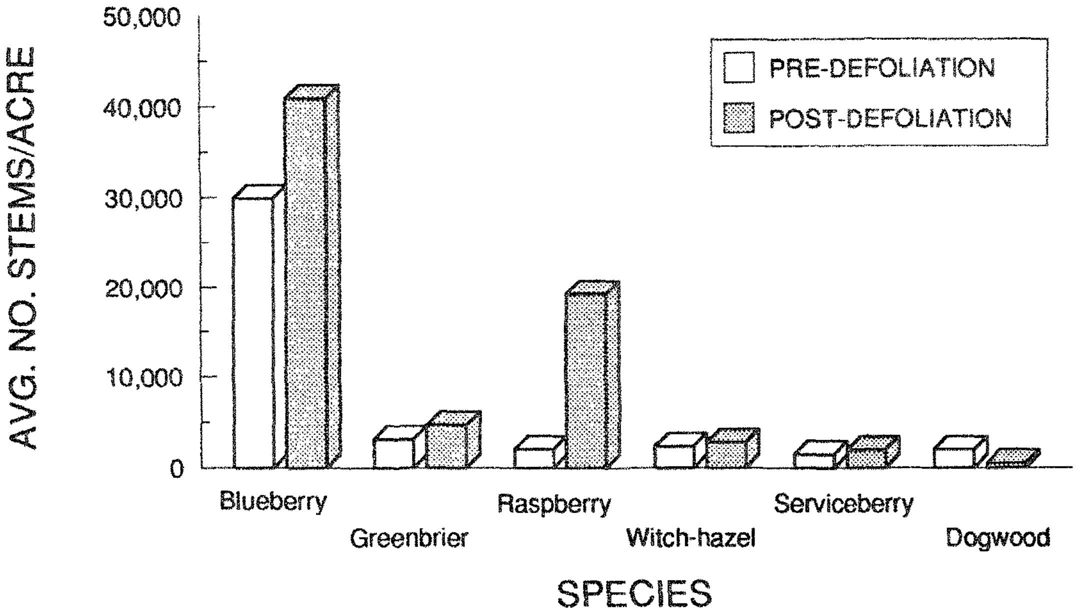

Figure 2. Histograms of the average numbers of stems per acre of the major species of competing vegetation before and after gypsy moth defoliation on the Appalachian Plateau province. All differences between the pre- and post–defoliation numbers were significant at the 10% level.

defoliation, the most common commercial tree species were white oak and chestnut oak (4888 and 4172 stems/acre, respectively). These two oak species reacted differently following defoliation; chestnut oak significantly increased ($P = 0.01$) to 7526 stems per acre while white oak significantly decreased ($P < 0.01$) to 3447 stems per acre. The vast majority of the oak stems were still less than 1 foot tall in 1989. Following defoliation, red maple was again the most common commercial tree species with 8599 stems per acre. Two other commercial tree species that significantly increased ($P < 0.011$) in total number following defoliation were northern red oak and black cherry (Table 1). Sugar maple also increased following defoliation but not significantly ($P > 0.6$). As a group, all commercial tree species approximately doubled with significant increases ($P < 0.001$) in both total number and in the 0-1-foot height class (Table 2). The greater-than-3-foot class significantly decreased ($P < 0.03$) following defoliation.

The only significant change ($P = 0.011$) in any height class for the all oaks species group was a 44% decrease in the greater-than-3-foot class (Table 2). Following defoliation, an average of only 124 oak stems per acre greater than 3 feet tall were present (Table 2).

Each height class of the all non-commercial tree species group decreased following defoliation (Table 2), but only the decrease in the 1-3-foot height class was significant (P < 0.1).

Following defoliation, there was a large significant increase (P < 0.001) in total number and in the 0-1-foot-height class of the all other woody plants species group (Table 2). Blueberries were still the most common species group following defoliation, with about 16,000 stems per acre present (Figure 3). Raspberries also increased significantly (P < 0.02) after defoliation (Figure 3). The total number of serviceberry increased significantly (P = 0.01) following defoliation, while there was a significant decrease (P < 0.001) in the total number of dogwoods (Figure 3). The total numbers of witch-hazel and greenbriers did not significantly change (P > 0.7) after defoliation (Figure 3).

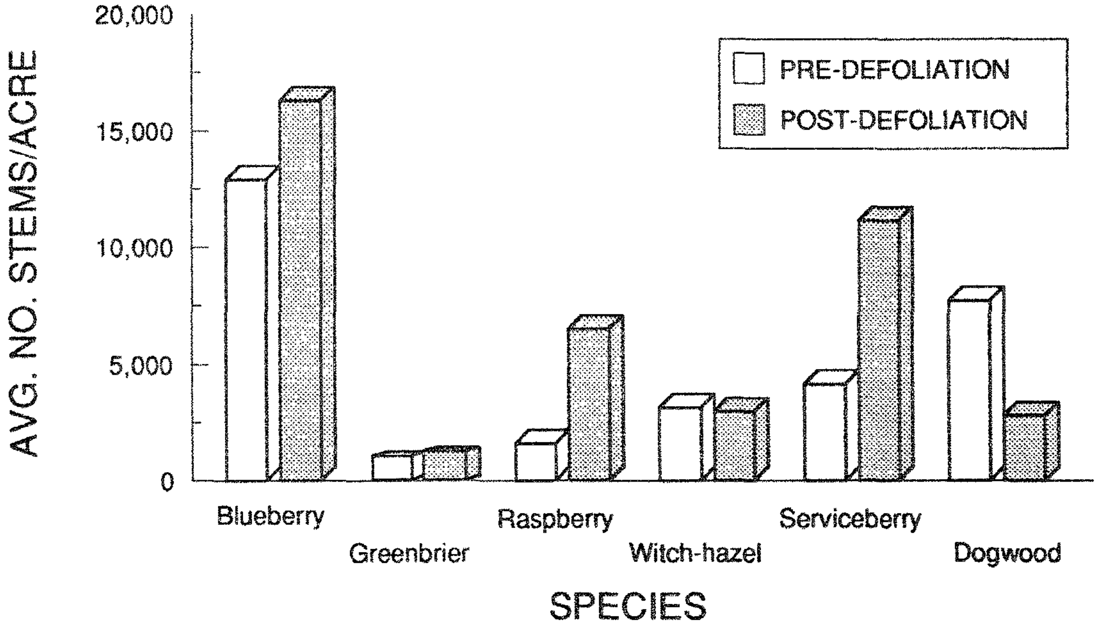

Figure 3. Histograms of the average numbers of stems per acre of the major species of competing vegetation before and after gypsy moth defoliation on the Ridge & Valley province. Differences between the pre- and post-defoliation numbers for blueberry, raspberry, serviceberry, and dogwood were significant at the 10% level.

The total densities, before and after defoliation, were very similar between the two provinces (Table 2). The changes in the number of stems per acre in each height class were also very similar in magnitude and direction (Table 2). All of these changes were highly significant

($P < 0.001$). It is interesting to note that the only decreases were in the greater–than-3–foot-height class.

DISCUSSION

Comparisons of the Results with Other Studies

Tree mortality in gypsy moth-defoliated stands is often patchy, and the result is a mosaic of gaps interspersed within an otherwise continuous forest canopy. Ehrenfeld (1980) studied these kinds of gaps in a New Jersey oak forest seven years following gypsy moth defoliation, and found that their understory composition contrasted sharply with the surrounding "recovered forest". Allen and Bowersox (1989) examined the understories of Pennsylvania stands which had suffered at least a thirty percent volume reduction of the overstory due to gypsy moth-induced mortality. Their regeneration counts were made six to seven years following mortality. They concluded that although commercial tree species were adequately regenerating, lower-value species were still much more common than the oaks. The results from the current study provide additional information about the change in regeneration occurring over a short period of time following defoliation and subsequent overstory mortality. Our data come from stands which experienced a range of defoliation levels and suffered various degrees of tree mortality. In stands where mortality was moderate to severe, trees began dying by the summer of 1986. Therefore, these data represent a point in time 2-3 years following the initiation of tree mortality, and it remains to be seen how the regeneration will develop in these stands in the future.

A lack of an increase in species richness led Ehrenfeld (1980) to suggest that new species are not recruited following gypsy moth-induced tree mortality. Those species which were already present on the site expanded to fill canopy gaps. We also did not find new species establishing 1-3 years following tree mortality. In fact, prior information about the number of stems of a given species prior to defoliation is highly significant in determining the importance of that species in the understory following defoliation (Fosbroke unpublished data).

This paper does not attempt to describe differences in the response of understory vegetation to gypsy moth under varying levels of defoliation, mortality, and site quality. However, it is expected that the higher the level of defoliation and subsequent mortality, the greater the understory response. Results of analysis of variance tests by Fosbroke (unpublished data) indicate that overstory mortality, site index, and physiographic province are all important factors related to the differences between pre- and post-defoliation regeneration.

There seems to be a consensus among forest managers who have seen the effects of gypsy moth defoliation that the understories in defoliated stands are dominated by low-value species. Results from earlier studies suggest that this is usually the case (Ehrenfeld 1980, Allen and Bowersox 1989). The results of our study also indicate a profusion of seedlings of species which will either not become a part of the overstory or will be of low value. In ours and other studies, red maple, black birch, blueberries, and raspberries were often the species which increased the most following defoliation. There is also an increase in the total density from about 42,000 to 62,000 stems per acre in both provinces, as a result of the additional light, nutrients, and moisture reaching the forest floor.

In both provinces, the dogwood genus reacted differently than the other major species of competing vegetation. There were significant decreases in the total numbers of dogwoods (primarily *Cornus florida* L.) following defoliation. This is in contrast to the stands studied by Ehrenfeld (1980) where flowering dogwood became the most common species in the understory following defoliation. Perhaps this difference between the two studies is due to site or geographical factors, or it may indicate the increased incidence of the lethal disease dogwood anthracnose (Hibben and Daughtrey 1988) in forests of the study area.

Differences in Regeneration Between Provinces

Though we did not test for differences in regeneration counts between provinces as did Allen and Bowersox (1989), some comparisons can be made between their results and ours. The Allegheny Mountains are a subregion of the Appalachian Plateau physiographic province. Plots located there by Allen and Bowersox were geographically near our study areas. In comparing post-defoliation densities between the two studies, both studies show a similar trend for red maple with respect to province: the Ridge & Valley province had fewer red maples per acre in the understory following defoliation than the Appalachian Plateau province. However, Allen and Bowersox found roughly twice as many red maple per acre in both provinces as we did. In contrast, Allen and Bowersox found less than half as many birch stems per acre in the understories of Allegheny Mountain stands following defoliation than we did on the Appalachian Plateau. The greatest difference between the two post-defoliation regeneration tallies was that we found virtually no birch in the Ridge & Valley province compared with the 7,986 stems per acre found by Allen and Bowersox. Differences are expected between the means of any two regeneration studies of this type due to random variability and to the unequal amounts of time following defoliation. Regardless, in both studies red maple and black birch appear to be thriving in post-defoliation understories and are likely to become serious competitors with the more valuable species for growing space, nutrients, moisture, and light.

Other forms of ground vegetation besides tree seedlings are very important restrictors of the future establishment and growth of desirable regeneration. Allen and Bowersox (1989) found ferns and blueberries to be the most common species in the ground cover. Ferns occupied an average of 38 percent of the ground in the Allegheny Mountains and 6 percent in the Ridge & Valley province. Blueberries covered 14 percent of the Allegheny Mountain sites and 21 percent of the plots in the Ridge & Valley province. Although we did not determine the coverage of ferns, there is no doubt that blueberries and raspberries are also important competitors in the stands we studied. In the Appalachian Plateau province, we found approximately 35,000 stems per acre of these two species prior to defoliation. Following defoliation, the number increased to 65,000. In the Ridge & Valley province, both the pre- and the post-defoliation number of these species were somewhat lower, 15,000 and 23,000 stems per acre, respectively.

Future Development of Oak Stands in These Provinces

The problem of regenerating oaks on good sites is a serious concern of forest managers throughout most of the eastern United States (Lorimer 1989). In this study, white oaks of all height classes consistently declined in numbers following gypsy moth defoliation. Northern red oak and chestnut oak also decreased in total number in the Appalachian Plateau province, but increased in the Ridge & Valley province. The majority of the increases were in numbers of stems less than 3 feet tall. Interestingly, there was even an increase in the numbers of these two oak species in the 1-3—foot height class for the Appalachian Plateau province. Oak seedlings were generally more common in the Ridge & Valley province than in the Appalachian Plateau province. Allen and Bowersox (1989) also found more oak seedlings in the Ridge & Valley.

It appears that the existing advance regeneration of oaks is responding to defoliation by increasing in height. However, only about 125-165 oak stems per acre are presently tall enough (greater than 3 feet) to have a chance of successfully competing with other faster-growing species like black cherry, black birch, and red maple. It is unknown precisely how many oak seedlings (and of what size) should be established in a stand before it is regenerated. Sander *et al.* (1976) concluded that at least 430 seedlings at least 4.5 feet tall would be needed to ensure a pole-size stand containing 30% oaks. In our stands, regeneration is currently insufficient to meet this criterion. The oak component in future stands will depend to a great degree on how many of the small oak seedlings (0-1 foot tall) survive and grow. Because of the influx of competing vegetation (e.g., red maple, blueberries, and raspberries), we speculate there may be a reduced oak component of gypsy moth—defoliated stands in the future. Because of this shift in composition and the increased species diversity of stands, the future impact of the gypsy moth may be diminished in these provinces.

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