

Effects of Gypsy Moth Defoliation on Acorn Production and
Viability, Litterfall, and Litter Layer Depth and Biomass
in North-central Virginia and Western Maryland

Steven P. McConnell

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE in FORESTRY

Approved:

Thomas J. Nichols

David Wm. Smith

Richard G. Oderwald

F. William Ravlin

Caleb L. Morris, Adjunct

May, 1988
Blacksburg, Virginia

Effects of Gypsy Moth Defoliation on Acorn Production and
Viability, Litterfall, and Litter Layer Depth and Biomass in
North-Central Virginia and Western Maryland

by

Steven P. McConnell

(Abstract)

The effects of gypsy moth defoliation on acorn production (the seed source for oak regeneration), and the forest floor regeneration environment were investigated. Parameters measured included: acorn quantity, weight, development, and viability; litterfall; and forest floor depth and biomass. Nineteen plots in north-central Virginia and western Maryland on which trees suffered heavy, moderate, or no defoliation were monitored over a two-year period.

Almost no developed acorns were produced on heavily defoliated trees. Moderately defoliated trees produced developed acorns, but the quantity was less than from trees which were not defoliated, and a higher percentage of them were rotten. More partially developed acorns were produced by moderately defoliated trees than on trees with no defoliation. Heavy defoliation caused abortion of the acorn crop before acorns could develop. Almost all acorns from heavily defoliated trees had dropped by mid-September and almost all were undeveloped. The effects of defoliation on acorn production may be evident in the growing season following defoliation as well; trees not defoliated in the second year of the study but defoliated the year

before had much lower production of acorns than trees which suffered no recent defoliation.

The timing of litterfall was changed substantially by heavy defoliation. Most foliar biomass fell from heavily defoliated trees during the early summer, most foliage drop from nondefoliated trees occurred in the fall. Similar trends in the timing of drop were observed for woody biomass.

Forest floor depth and biomass were not changed by gypsy moth defoliation. The forest floor regeneration environment, as measured by these factors, therefore, was unchanged by gypsy moth defoliation. Increased solar insolation, temperatures, and possible altered moisture content and nutrient availability may have effects on the regeneration environment that are not quantified by this study, however.

ACKNOWLEDGEMENTS

This thesis is dedicated to my grandfather, _____, who taught me how to drive a tractor, how not to cook eggs, and has made the lives of people around him better for 95 years.

I would like to thank the members of my graduate committee for their contributions. Each of them had valuable suggestions that added to the quality of this work. In particular I would like to thank Dr. Tom Nichols, my Major Advisor, for his enthusiastic interest in all phases of this project. The final editing, and suggestions on ways to present data more clearly by Dr. Dave Smith and Dr. Rich Oderwald substantially improved the final thesis product and was greatly appreciated.

I would also like to thank the amigos I have made in Blacksburg who directly or indirectly helped with this work. _____ provided conscientious help with data collection and plot establishment. _____ learnt her expertise to helping me prepare for seminars and presentations at scientific meetings, and helped edit portions of my thesis. _____ helped me fight paperwork battles and almost never got mad about the procedures I forgot to follow. _____ (Winchester amigo) provided invaluable assistance with Figures and Tables.

Funding for this project was provided by the National Park Service under _____, _____, and _____. The Park Service also allowed the placement of research plots on Park Service land and provided living accommodations and storage facilities required

to sustain this research effort. _____ of the Maryland Department of Natural Resources allowed the use of State Forest land for placement of research plots and use of State facilities to accommodate data collection. _____ and _____ of the Maryland Department of Agriculture helped identify areas meeting study criteria for plot establishment and provided information on stand defoliation history.

_____, _____, and _____ of West Virginia University generously shared site information on common research plots in the Green Ridge State Forest in Maryland.

_____, _____, _____, and _____ allowed use of their private land for placement of research plots. The contribution of each of these individuals and organizations is gratefully acknowledged.

- Director, Department of Planning, _____ - County Administrator, and _____ - Director, Department of Personnel in Frederick County, Virginia allowed me to adjust my work schedule so that I could continue work on my thesis during my tenure as the Gypsy Moth Coordinator in Frederick County. I am indebted to Frederick County, and to these individuals in particular, for their interest and support.

_____ provided me with a place to stay on my weekends, and occasionally weeks, in Blacksburg while I battled the thesis and gypsy moth coordinating simultaneously. The importance of having a quiet place to come and go to as I chose in the limited time I had in Blacksburg during this period can not be overstated. Thanks also are due _____ roommates and associates: _____.

, , and . Each of them put up with me with only minor complaints, became new friends, and gave me subtle and direct encouragement as needed.

, , and helped with field work. These individuals, along with , , and

provided even more important help by their occasional visits, letters, phone calls, and encouragement to pursue science vigorously (and get back to the West!).

Last but by no means least I would like to thank my family. The constant support and enthusiasm of my parents, and

, and my sister (, ?) were important factors in sustaining my drive to complete this work. My cousins

and also encouraged me along the way, and many times took me to, or picked me up from the airport at times that were not always all that reasonable.

TABLE OF CONTENTS

	page
	<hr style="width: 50px; margin-left: auto; margin-right: 0;"/>
ACKNOWLEDGEMENTS	iv
I. INTRODUCTION1
A. Justification1
II. LITERATURE REVIEW5
A. Gypsy Moth Life Cycle5
B. Characteristics of Stands Susceptible to Defoliation by the Gypsy Moth.7
C. Oak Regeneration Patterns in Upland Oak Forests8
1. Site quality.8
2. Oak regeneration sources: seedling sprouts, stump sprouts, and seedlings.9
D. Effects of Gypsy Moth Defoliation on Forest Trees	10
1. Refoliation and loss of carbohydrate reserves	10
2. Reduced growth of trees	11
3. Tree mortality.	12
E. Effects of Gypsy Moth Defoliation on Changing the Tree Species Composition of Forest Stands	15
F. Characteristics of Acorn Production and Survival in Upland Oak Forests18
G. Wildlife Utilization of Acorn Crops	20
H. Effects of Gypsy Moth Defoliation on Acorn Production	21
I. Effects of Forest Floor Litter on Seed Survival and the Germination Environment	25
J. Effects of Gypsy Moth Defoliation on Forest Floor Depth and Biomass	27
III. METHODS AND MATERIALS	31
A. Description of Study Plots	31
B. Sample Stand Characteristics.	31
C. Study Design	33
D. Plot Design	38
1. Plot configuration	38
2. Acorn trap design	40
3. Litter trap design.	42
E. Sampling Times	42
F. Data Collection for Individual Objectives	43
1. Field methods	43
a) Acorn, foliar, and woody biomass collection.	43
b) Forest floor biomass accumulation - "duff samples"	45
c) Forest floor biomass accumulation - depth measurements.	47
2. Laboratory methods	47
a) Acorn, foliar, and woody biomass collection.	47
b) Forest floor biomass accumulation - "duff samples"	48
c) Acorn quantity, weight, viability, and development	48

TABLE OF CONTENTS
(cont.)

	page
G. Analysis	51
1. General	51
2. Foliar and woody biomass collection	52
3. Forest floor depth and biomass accumulation	52
4. Acorn collection	53
IV. RESULTS and DISCUSSION	55
A. Effects of Defoliation on Foliar and Woody Biomass Collection	55
B. Effects of Defoliation on Forest Floor Biomass.	61
C. Effects of Defoliation on Acorn Quantity, Weight, Viability, and Development.	65
1. Quantity, weight (stand basis), and development of acorns.	65
2. Acorn viability	72
3. Acorn production the year after defoliation	75
V. SUMMARY AND CONCLUSIONS	79
VI. LITERATURE CITED	82
VII. APPENDICES	90
Appendix A. Plot Location Maps.	90
Appendix B. Trap Comparison Study	97
1. Introduction and Justification.	97
2. Analysis.	97
a) Acorn collection	97
b) Foliar and woody biomass collection.	98
3. Results and Discussion.	100
a) Acorn collection	100
b) Foliar and woody biomass collection.	107
4. Summary and Conclusions	110
Appendix C. Effects of Defoliation on Forest Floor Depth.	112
1. Introduction and Justification.	112
2. Analysis.	112
3. Results and Discussion.	113
4. Summary and Conclusions	114
Appendix D. Forest Floor Depth vs. Biomass Correlation	
1. Introduction and Justification.	118
2. Analysis.	118
3. Results and Discussion.	119
4. Summary and Conclusions	120
VITA.	124

LIST OF TABLES

Table	page
1 - Study plot characteristics. Plots are grouped where similarities exist between stands. Characteristics by which plots are grouped include location, defoliation history, basal area of the overstory, and species composition of the overstory	34
2 - Sample plot groupings by defoliation level and year. . .	37
3 - Sample collection dates and sampling intensity	44
4 - Mean foliar biomass collection by defoliation level and year. Includes all materials produced and aborted on an annual basis (excluding fruits) such as flower parts, leaves, frass, and leaf petioles.	56
5 - Mean woody biomass collection by defoliation level and year. Includes all materials produced over more than one growing season (excluding fruits)	57
6 - Mean forest floor biomass (1000 kg/ha) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.	62
7 - Mean forest floor biomass (1000 kg/ha) by sample collection trip # (season), and plot	64
8 - Mean number of acorns collected by sample period, year, and defoliation level; separated by stage of development.	66
9 - Mean biomass of sound acorns, and of all developed acorns, by year and defoliation level; separated by stage of development.	70
10 - Mean number of fully-developed acorns by sample period, year, and defoliation level; separated by viability category	73
11 - Mean number of partially-developed acorns by sample period, year, and defoliation level; separated by viability category	74
12 - Mean number of acorns from plots not defoliated in the sample year but with differing defoliation histories; separated by stage of development. Includes acorns in all viability categories (sound, unsound insect-damaged, unsound rotten, unsound animal-damaged).	76

LIST OF TABLES
(cont.)

<u>Table</u>	<u>page</u>
B1 - Acorn collection from acorn and litter traps101
B2 - Acorn and acorn cap collection from acorn and litter traps	102
B3 - Foliar biomass collection from acorn and litter traps.	.108
B4 - Woody biomass collection from acorn and litter traps .	.109
C1 - Mean forest floor depth (cm) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986	114
C2 - Mean forest floor depth (cm) by sample collection trip # (season), and plot.116

LIST OF FIGURES

Figure	page
1. Study plot locations in the Green Ridge State Forest in Maryland, the Billmeyer Wildlife Management Area in Maryland, privately owned land in Northern Virginia, and the Shenandoah National Park	32
2. Sample plot configuration.	39
3. Acorn trap specifications and design	41
4. Forest floor biomass collection locations for each sample collection date	46
5. Mean forest floor biomass (kg/ha) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.	63
A1. Plots 3 and 6, high elevation Maryland plots, not defoliated in either 1985 or 1986, located in the Billmeyer wildlife Management area near Flintstone, Maryland.	90
A2. Plots 1,2,4, and 5, low elevation Maryland plots, moderately defoliated in 1985 and not defoliated in 1986, located in the Green Ridge State Forest near Flintstone, Maryland	91
A3. Plot 11, heavily defoliated in 1985, equipment removed from plot in spring of 1986, located on privately owned land on Short Hill Mountain one mile north of Hillsboro, Virginia.	92
A4. Plot 12, heavily defoliated in 1985, not defoliated in 1986 (treated with Dimilin), located on privately owned land 2 miles north of Snickers Gap (on Route 7) near Bluemont, Virginia	93
A5. Plot 19, established in spring of 1986, heavily defoliated in 1986, located on privately owned land near Paris, Virginia	94
A6. Plots 7,8,16,17,18. Plots 7 and 8 were not defoliated in 1985 and heavily defoliated in 1986. Plots 16 and 17 were established in 1986; Plots 16 and 17 were heavily defoliated but all acorn traps were destroyed by bears for one collection period, Plot 18 was moderately defoliated. Plots are located in the Shenandoah National Park	95

LIST OF FIGURES
(cont.)

Figure	page
A7. Plots 9,10,13,14,15. Plots 9 and 10 were not defoliated in 1985 or 1986. Plots 13, and 15 were heavily defoliated, Plot 14 was moderately defoliated. Plots are located in the Shenandoah National Park. . . .	96
C1. Mean forest floor depth (cm) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.	115
D1. Dummy variable regression coefficients, by sample collection date (season).	121
D2. Coefficients of dummy variable regression incorporating plot, and defoliation level	122

I. INTRODUCTION

A. Justification

The gypsy moth (Lymantria dispar L.) has become a major forest pest in the eastern United States since its accidental introduction from Europe to Massachusetts in 1869. Since that time the majority of gypsy moth related research efforts have been concentrated on identifying the life cycle and preferred hosts of the gypsy moth, methods of control, and describing the effects of defoliation on growth and mortality of forest trees. Very little research has gone into determining what effects the gypsy moth may have on future forest stands by the disturbance it creates, or what effect it may have on wildlife or the habitat for wildlife in susceptible forests. Since control measures have proven largely ineffective in preventing the spread of the gypsy moth and continued expansion of its range appears inevitable (McManus and McIntyre 1981), land managers are interested in knowing what effects the gypsy moth may have on their resource base.

The upland hardwood stands of north-central Virginia and western Maryland that the gypsy moth is presently invading are in the Blue Ridge and Ridge-and-Valley physiographic provinces. The forests in each of these provinces are dominated by oak trees (Quercus sp.). Both provinces have considerable forest tree species diversity and were once dominated by the American chestnut (Castanea dentata (Marsh.) Borkh.). The climax species in these forests following the demise of the chestnut are still not certain in many areas. In both provinces, the low site quality areas (site index less than 15 m - base age 50 for oaks) and medium site quality (site index 15 to 20)

areas dominated by oaks usually regenerate to oak naturally. In the higher site quality areas (site index greater than 20), oak regeneration is often lacking and often requires silvicultural manipulation to obtain (Beck and Hooper 1986, Hannah 1987).

Silvicultural systems for managing upland oak stands have been a subject of many recent research efforts and are beginning to be established (Hannah 1987), however, the problem of regenerating oak forests to oak remains a persistent problem for foresters. One fundamental tenet of oak regeneration is that oaks will regenerate into forest stands in proportion to their presence in the stand at the time of harvest (Clark and Watt 1971, Sander 1979). This tenet may also be applied to other disturbances causing mortality to the overstory such as fire and wind (Hannah 1987). Stump sprouts, and seedling sprouts with well established root systems can successfully compete with woody vegetation (Clark and Watt 1971, Sander 1979). If advance regeneration meeting this criterion are not present in a stand at the time of disturbance, it is unlikely that a stand will regenerate to oak.

There is evidence that forest stands dominated by oaks are not regenerating to oak following defoliation by the gypsy moth (Gottschalk 1984). This may be because stump sprouts and seedling sprouts may die, or may sprout with insufficient vigor to compete with shrub and unaffected tree species following defoliation (Frank 1982, Gottschalk 1983). The potential for regeneration to develop may be reduced following defoliation because there is evidence that seed production is reduced following insect defoliation (Crawley 1985,

Fedde 1962, Rockwood 1973, and Torrent 1956). Evidence indicates that defoliation may accelerate decomposition on the forest floor (Gosz 1984, Schowalter et al. 1986) which may reduce the depth and biomass of the forest floor. Researchers have identified forest floor depth as one of the most critical factors affecting the germination of oak seeds (Korstian 1927, Barrett 1931, Minckler and Jensen 1959). Reduced forest floor depths have been shown to favor germination and establishment of lighter seeded species (Minckler and Jensen 1959). The combination of reduced seed source and decreased suitability of the germination environment, combined with loss of advance regeneration, may indicate that initial shifts in species composition resulting from mortality may not quickly return to domination by oak.

Decreased acorn production may affect not only the seed source for regeneration but can also substantially affect wildlife. Acorns are the principal food source for a large variety of wildlife species during the fall and winter months when other sources of food are limited (Goodrum et al. 1971, Korschgen 1962). Acorn crops may have a }
regulatory influence on reproductive success, survival, size of }
population, or body condition of wildlife (Goodrum et al. 1971).

Humans are affected indirectly when mast crops fail by having decreased size and numbers of animals to hunt and view, and increased deer damage to agricultural crops and forestry plantations caused by limited alternate food sources (Goodrum et al. 1971). Decreased acorn production in the year gypsy moth defoliation occurs, or longer term loss in acorn production resulting from mortality in the oak component of the stand, could have serious impacts on wildlife populations and

wildlife management considerations.

Present management plans in Virginia for the Jefferson National Forest, the George Washington National Forest, and the Shenandoah National Park (SNP) call for direct control of the gypsy moth using chemical insecticides or the Bacillus thuriengensis (Berliner) bacterium, only in special areas such as campgrounds and historic areas. Areas not designated as being "special" have the potential for outbreak level gypsy moth populations. The National Forests provide forest products as well as other amenities such as game for hunters, while SNP provides a forested area of scenic beauty and a place where wildlife may be easily seen. Changes in forest tree species composition over time as a result of gypsy moth defoliation, and temporary or permanent effects on wildlife habitat (especially from altered mast production), are key concerns of land managers. This research effort was designed to determine the changes to mast production resulting from gypsy moth defoliation, and determine the effects to the forest floor regeneration environment (measured by forest floor depth and biomass). To further this goal the following specific objectives were addressed in oak dominated forest stands in north-central Virginia and western Maryland:

- 1) Quantify gypsy moth defoliation effects on timing and quantity of foliar and woody biomass drop.
- 2) quantify gypsy moth defoliation effects on litter layer accumulation and decomposition.
- 3) Determine gypsy moth defoliation effects on quantity, weight, viability, and development of acorns produced.

II. LITERATURE REVIEW

A. Gypsy Moth Life Cycle*

The gypsy moth overwinters as eggs which are usually laid in bark flaps, under limbs, in cracks in the bark, or other protected places including forest floor litter. Upon hatching in mid-May the larvae ascend a tree or other vertical object and disperse. At this stage they are about 3 mm long and very "hairy" (long setae), making them ideally suited for transport by the wind. "Ballooning" is the process by which the larvae ascend the tree to the branch tips, attach themselves by a single strand of silk they spin and let the wind carry them away. Ballooning is the most critical stage in the spread of the gypsy moth, and the most significant means of natural spread of the main front of the gypsy moth. The larvae may be carried 15 miles in this manner and greater distances have been reported (Collins 1915, Leonard 1971). Most larvae (99%) are deposited within 1 km of their source area in non-mountainous terrain, and within 3 km of their source area in mountainous terrain (Mason and McManus 1981). Taylor and Reling (1986) suggest that only 0.3% of the larval population travel as far as 19 km but consider this quantity sufficient to account for the rapid expansion of gypsy moth populations into new areas.

* Much of the information in this section was synthesized from: Leonard, D. E. 1981. Bioecology of the gypsy moth. IN: The gypsy moth: Research towards Integrated Pest Management. USDA Forest Service Tech. Bull. 1584. pp. 9-29.

After dispersing, larvae begin to feed on new leaves. When gypsy moth populations are at low levels, male moths typically go through five instar stages while females have six instars. Larvae normally remain on the leaves day and night through the first several instars. During the last two or three instars they feed at night, climbing down the tree to hide during the day. When gypsy moth population levels are high, feeding continues day and night, and larvae do not move up and down the trees. The number of instars may increase when population levels are high (Leonard 1968).

Typically, gypsy moth larvae hide in bark flaps, holes where limbs have broken off, or the litter layer if it is well developed. Their choice of a hiding place can have significant impact on their survival, especially in sparse populations. When gypsy moth larvae rest in the litter layer they are subject to predation by small mammals (Campbell and Sloan 1977a, Campbell and Sloan 1977b, Smith 1985). By the end of the final larval instar gypsy moths are from 50 mm to 90 mm long and have consumed about 1 m^2 of foliage (Leonard 1981). The larval stages last from about early-May to the end of June in Virginia and western Maryland. Exact length of any of these stages is weather dependent, varying year-to-year depending on climatic conditions. Because climatic conditions change with elevation, elevation is an important determinant of the exact time period of larval activity.

Gypsy moth larvae usually use the same resting spots that they used for hiding and molting as the site for pupation. The pupal stage lasts about two weeks. On average males emerge several days before

female moths. After emergence female moths, which are incapable of flight, begin emitting pheromones that attract male moths for mating. Once mating is completed the female oviposits, usually within several feet of the pupation site. The number of eggs varies and is related to the status of the population. When population levels are increasing egg masses can contain up to 1000 eggs. When populations are declining there may be as few as 100 eggs per egg mass. Larvae emerge from eggs after overwintering (8 or 9 months later) and the life cycle begins again.

B. Characteristics of Stands Susceptible to Defoliation by the Gypsy Moth

The forest cover types that gypsy moths usually attack first, and in which their populations increase, have been identified (Bess et al. 1947, Houston 1979, Houston and Valentine 1977). These stands have a large component of oak, (Quercus sp.) which is a favored food source for the gypsy moth. Often chestnut oak (Quercus prinus L.) is the dominant species. Chestnut oak is frequently found on ridgetops or other sites of lower quality, and usually has abundant hiding places for the gypsy moth such as bark flaps, under broken limbs, and in fissures in the bark. Ridgetop chestnut oak sites are often somewhat open. The conditions found on susceptible sites are frequently a reflection of harsh growing conditions and are a distinct contrast from higher quality oak sites dominated by species such as northern red oak (Quercus rubra L.) which have smoother boles and less mechanical damage on the trees.

Abundant hiding locations situated off the forest floor in dark, dry

places on or near trees that are favorable food sources (characteristic of low site quality chestnut oak stands), have a significant impact on the increase of gypsy moth populations. Predation from small mammals maintains gypsy moth populations at innocuous levels where a large percentage of the hiding places available to the gypsy moth are in the litter layer. Typically there are no alternative hiding places to the litter layer in higher site quality stands, and wildlife predation can maintain gypsy moth populations at low levels (Campbell and Sloan 1977a, Campbell and Sloan 1977b, Smith 1985). Where gypsy moth populations have reached outbreak proportions though, wildlife are ineffective in controlling the gypsy moth.

C. Oak Regeneration Patterns in Upland Oak Forests

1. Site quality

Ecological characteristics between high site quality and low site quality stands are much different. In the Appalachian Hardwood Subregion, the poorest sites are dominated by the chestnut oak-scarlet oak type group have site indices of 15 (m at base age 50) and less (Smith and Linnartz 1980). The white oak-black oak type group, which represents the fair sites in this region, has site indices ranging from 16 to 20. The sugar maple-red oak type group has site indices of 20 to 24, and the yellow poplar-mixed hardwood type group has site indices of 25 and above. The first two types mentioned usually regenerate to oak naturally, while in the latter two types special silvicultural manipulations are usually required to obtain adequate oak regeneration (Smith and Linnartz 1980). Lower quality sites will

perpetuate in oak because advance regeneration accumulates in the understory of these sites. Following disturbance stump sprouts can provide a significant portion of the regeneration on these sites.

Ross et al. (1986) found that in mixed oak forest types with upland oak site index values of less than 14, advance regeneration and stump sprouts were significant contributors to restocking following clear felling. In contrast, mixed oak forest types with site indices greater than 20 had only small numbers of stump sprouts and scattered stems of advance regeneration to maintain a continued presence of oak on the site. More intense competition from other species on high quality sites limits the establishment of advance regeneration and makes its occupation of the site difficult. Silvicultural manipulations to promote advance regeneration must be undertaken to ensure the dominance of oaks on higher site quality areas (Arend and Gysel 1952, Clark and Watt 1971, Ross et al. 1986, Weitzman and Trimble 1957).

2. Oak regeneration sources: seedling sprouts, stump sprouts, and seedlings.

Advance regeneration developing in bumper acorn crop years accumulates in the understory (Carvell and Tryon 1961). This is possible because oak seedlings are somewhat shade tolerant. Additionally, new seedlings possess a large number of rudimentary buds at the base of the stem that form a reservoir for repeated resprouting of shoots (Olson and Boyce 1971, Watt 1979). When the top of a seedling is destroyed by browsing, fire, insect damage, or unfavorable microclimatic conditions, the seedling often resprouts (termed a

"seedling sprout") from one or more of these buds (Olson and Boyce 1971, Watt 1979). Seedling sprouts typically die back and resprout repeatedly while in the understory (Merz and Boyce 1956, Liming and Johnston 1944). The roots of almost all advance regeneration are older than the shoots (Liming and Johnston 1944, Merz and Boyce 1956).

When a forest canopy is opened by a disturbance such as timber harvest, advance regeneration is able to establish itself quickly on the site since it has a large carbohydrate reserve built up, and a well established root system. Similarly, in uncut stands, oak stems killed back by disturbances such as fire (including many of the overstory oaks) are able to resprout and dominate the site. Following a timber harvest, the advance regeneration, as well as stump sprouts from the harvested trees, usually make up the oak component in the new stand (Ross et al. 1986).

Reproduction from seed disseminated after a disturbance, or from seedlings germinating just before the disturbance, is unable to compete effectively with shrub and other tree species and is not an important means of reestablishment of oaks after a disturbance (McQuilkin 1975, Ross et al. 1986, Sander 1979). Seedlings do not have stored reserves and are incapable of the rapid growth required to compete for a position in the canopy (McQuilkin 1975).

D. Effects of Gypsy Moth Defoliation on Forest Trees

1. Refoliation and loss of carbohydrate reserves

Gypsy moth larval development and host tree leaf phenology occur such that larval hatch and initiation of annual leaf development nearly coincide. As a result, defoliation begins shortly after leaves

develop each year. This is significant because defoliation occurring early in the growing season has a more severe impact on tree survival and growth than defoliation occurring later in the year (Heichel and Turner 1976). Defoliation deprives trees of their leaves, directly decreasing photosynthesis. Trees defoliated greater than 60% will generally refoliate that growing season (Campbell and Sloan 1977c).

The combination of decreased photosynthesis and refoliation causes a decline in tree carbohydrate reserves. Much of a trees' reserves are stored in tree roots. Successive defoliations over several years caused a decrease in food reserves that could be extracted from tree roots (Parker 1981). Decreased food reserve levels indicate that a tree has less carbohydrate to allocate to refoliation and to fight invasion of secondary organisms that often cause mortality in weakened trees. Trees defoliated early in the season (May and June) which subsequently refoliate, suffer a more severe decline in food reserves than trees defoliated later in the season (Parker 1981).

2. Reduced growth of trees

Both diameter and height growth are affected by defoliation. Energy that normally would have been allocated to growth is instead allocated to leaf production. Diameter growth is affected to a greater extent by progressively more severe defoliation, and by repeated defoliations over several years (Baker 1941, Brown et al. 1979, Minott and Gould 1925, Nichols 1961). Loss of radial increment in both the year of defoliation and the year following defoliation have consistently been reported (Baker 1941, Brown et al. 1979, Turner 1963). Recovery of radial increment following the cessation of defoliation is slow.

Radial growth remains low for a period of at least a period of several years. In the year following two years of heavy defoliation and one year of moderate defoliation Brown et al. (1979) reported growth rates that were 66% of pre-defoliation levels. Turner (1963) reported oaks growing at 93% the rate of comparable controls 5 years after 1 heavy defoliation. Campbell and Sloan (1977c) reported oaks heavily defoliated just once take more than ten years to return to full growth.

Height growth is also significantly reduced by defoliation (Wargo 1977). White oaks (Quercus alba L.) and black oaks (Quercus velutina Lam.) that were artificially defoliated (100%) in June had only 18% and 20%, respectively, of normal terminal growth after three years of defoliation. Two years later after no further defoliation, terminal growth improved only to 29% and 54% of controls. The reduction in both radial and terminal growth is an indication of the adjustments trees make as they respond to the stress of defoliation. The reduction in terminal growth could have ecological significance if oaks were overtopped by trees not susceptible to gypsy moth defoliation. This is likely not a problem in mature stands where canopy dominance has been established. In young stands, however, nonsusceptible trees overtopping oaks following defoliation could lead to a permanent changes in canopy position (Wargo 1977), leading to changes in species composition of forest stands.

3. Tree mortality

Gypsy moth defoliation has also been shown to be associated with mortality of trees. The initial invasion of the gypsy moth usually

has the most severe impact, causing greater mortality than subsequent infestations (Bess et al. 1947, Stephens 1981). In virtually all cases the actual mortality is attributed to the action of secondary organisms, particularly the two-lined chestnut borer (Agrilus bilineatus (Weber)), and to a lesser extent the shoestring fungus (Armillaria mellea (Vahl.) Quel.) (Anderson and Gould 1974, Cote 1976, Dunbar and Stephens 1975, Stalter and Serrao 1983). Defoliation causes stress which predispose trees to increased susceptibility and vulnerability to the action of these organisms. One defoliation will rarely result in mortality of an affected tree in the common deciduous host species of the gypsy moth, (Baker 1941, Nichols 1968, Stephens 1971). Repeated defoliations, however, will often have a dramatic impact on increasing tree mortality (Campbell and Sloan 1977c, Kegg 1971, Kegg 1973, Stephens and Hill 1971).

Since preferred host species are commonly the species subjected to repeated defoliation, mortality is usually highest among these species (Anderson and Gould 1974, Gansner et al. 1983, Kegg 1971, Nichols 1968). Less preferred species usually will be heavily defoliated only after foliage on the preferred species has been stripped and may be untouched while preferred species around them are heavily defoliated (Bess et al. 1947). When less preferred coniferous species, such as eastern hemlock (Tsuga canadensis (L.) Carr.) are defoliated, mortality will usually be greater in the conifers than in the preferred hardwood species which suffer defoliation more frequently (Campbell and Sloan 1977c, Turner 1963). Eastern white pine (Pinus strobus L.) appears to be an exception to this. Mortality of white

pine is similar to that of susceptible oak species (Turner 1963).

The physiological condition of trees prior to defoliation is an important determinant to the chances of tree survival. Trees in poor physiological condition suffer the greatest mortality from gypsy moth defoliation (Stalter and Serrao 1983). This is true whether the condition is induced by crown position, drought, overmaturity, or other factors. Trees already stressed from conditions such as drought or frost have been shown to be especially vulnerable to mortality when subjected to gypsy moth defoliation (Baker 1941, Kegg 1973, Nichols 1968, Stalter and Serrao 1983). Trees suffering the greatest mortality following gypsy moth defoliation are usually either in the lower crown positions (Campbell and Sloan 1977c), or are over-mature and physiologically weak dominants (Stalter and Serrao 1983).

Mortality is usually greater on moist or mesic, higher quality sites than on lower site quality dry ridges, sandy soils, or poorly drained wet sites, when the areas are attacked and the defoliation severity the same for each (Stalter and Serrao 1983, Campbell and Sloan 1977c, Hicks and Fosbroke 1987). The more moist, high quality sites, however, are usually less susceptible to attack by the gypsy moth, and are attacked less frequently than lower site quality areas (Bess et al. 1947). Higher mortality on high quality sites may be a result of a better habitat for the shoestring fungus on the more mesic sites (Hicks and Fosbroke 1987). It may also be that more vulnerable tree species grow on the more mesic sites (Hicks and Fosbroke 1987). A third possibility is that trees growing on mesic sites do not develop as extensive a root system as trees growing where conditions are

harsher. Greater competition for light on higher quality sites and greater ease of attaining water may favor allocation of resources to height growth rather than root development. The result may be that trees on higher sites have less stored reserves than trees on lower quality sites with which they may respond to the stress of defoliation.

E. Effects of Gypsy Moth Defoliation on Changing the Tree Species

Composition of Forest Stands

Short term declines in density of the overstory result from mortality, and conversion of forest stands to less preferred species has resulted from proportionately higher mortality of preferred species (Bess et al. 1947, Campbell and Sloan 1977c, Kegg 1973, Nichols 1961, Stephens 1971). Frequently the decline in overstory density is similar to a thinning from below (Campbell 1979). The change to forest stands that results from mortality of understory and weakened trees is similar to changes that occur with the natural process of succession; gypsy moth defoliation hastens this process (Gottschalk, in press). The resulting species compositions of forest stands are usually less susceptible to gypsy moth attack because they have a lower proportion of oak (Houston and Valentine 1977), and canopy trees of different species increase in importance. On some lower site quality stands suffering heavy mortality, however, succession is set back to a shrub stage. Almost all oak regeneration is overtopped and for the most part eliminated from the stand (Gansner 1985).

In addition to the loss of overstory oaks causing an immediate

change in forest stand species composition, there is evidence that oak regeneration on these sites is reduced because of gypsy moth defoliation. Sprouts from stumps are often the only reliable form of regeneration on many sites (Gottschalk 1982, Gottschalk 1983). When trees die following defoliation by the gypsy moth there is evidence that oaks will not resprout, or sprout with insufficient vigor to compete against shrub and unaffected tree species (Frank 1982, Gottschalk 1982). Gypsy moth defoliation early in the growing season induces trees to re-leaf that growing season causing a significant drain on carbohydrate reserves. The loss of carbohydrate reserves leads to enhanced tree susceptibility to attack from secondary insect and fungal organisms such as the two-lined chestnut borer and the shoestring fungus (Cote 1976, Dunbar and Stephens 1975, Wargo 1977). Mortality frequently results and resprouting will not occur because of the prolonged carbohydrate drain (Gottschalk 1982). Deer browsing has contributed to the loss of vigor of sprouts in many areas, and the shoestring fungus has killed sprouts (Gottschalk 1983).

Seedling sprouts are defoliated by the gypsy moth but the extent to which their ability to compete for a place in the canopy is affected is currently unknown. Loss of stump sprouts and seedling sprouts, the two important sources of oak regeneration, could contribute to a substantial degree to the reduction in oak observed on defoliated sites. Research investigating the effect of gypsy moth defoliation on advance regeneration is currently underway (Gottschalk 1984).

In Pennsylvania, Marquis et al. (1976) attributed regeneration failure following defoliation to destruction of acorns by insects,

consumption of acorns by rodents, inadequate acorn crops, and browsing by the unusually large deer herds found in Pennsylvania. Except for the possibility of a reduced acorn crop resulting from gypsy moth defoliation, the problems described by Marquis et al. (1976) are all typical problems to oak regeneration. The stands involved in Marquis' study had little regeneration in the understory before gypsy moth defoliation occurred. Attempts to promote advance regeneration with shelterwood cuts or planting were unsuccessful. The problem was exacerbated by a reduced seed source because of overstory mortality. Because the forest stands studied by Marquis et al. lacked advance regeneration it is unknown whether the gypsy moth adversely effects advance regeneration.

The understory can also be changed by gypsy moth attack. Openings, either short term for the period between defoliation and refoliation during one season, or long term openings resulting from mortality in the overstory, decrease the competition for light, moisture, and nutrients, and can substantially change the microenvironment on the forest floor. Likely results of this type of stand opening are 1) the existing understory not damaged or consumed by the gypsy moth shows a positive response to competition release because light penetration and available moisture and nutrients increases photosynthetic activity and growth, and 2) new seedlings or other understory vegetation are established.

Whether response of existing understory vegetation, or establishment of new seedlings will predominate depends on the makeup of the understory (Ehrenfield 1980). Gaps in the canopy resulting from

mortality showed effects of response from both groups with a greater tendency towards domination by the existing understory (Ehrenfield 1980). Ehrenfield found dogwood (Cornus florida L.) was the major beneficiary of gypsy moth defoliation in northern New Jersey, increasing in importance and inhibiting or excluding canopy-tree reproduction. Short term responses by red maple (Acer rubrum L.) were observed by Collins (1961). Understory red maple responded vigorously to increased sunlight in the time period in which the overstory oaks were defoliated until they refoliated. The effect temporary openings created by defoliation have on seedling germination and early survival, and the effects to survival and growth of advance regeneration, are still largely unanswered questions, but are the subject of current research (Gottschalk 1984).

F. Characteristics of Acorn Production and Survival in Upland Oak Forests

Factors that have been shown to affect acorn production include tree age, crown vigor, site quality, exposure, and weather (Gysel 1956, Sharp and Sprague 1967). Acorn production varies year to year, between species, and even within species (Gysel 1958). Acorn production is an innate characteristic of individual trees; some trees will produce acorns copiously nearly every year, while other trees of the same species will never produce acorns or produce only light crops (Sharp and Sprague 1967).

Acorns produced each year are subject to mortality and damage from a wide variety of sources. Acorns are consumed by birds, animals, insects, and microorganisms (Korstian 1927). In all but bumper crop

years nearly all acorns produced are consumed by wildlife (Watt 1979). Where wildlife were excluded, insects still caused up to 82% mortality of acorns, and all but 1% were left completely undamaged (Watt 1979). In years of poor acorn crops the percentage of acorns suffering mortality to animal predators is significantly greater than in years of good or bumper acorn crops (Olson and Boyce 1971).

Acorns left available for regeneration suffer additional mortality from environmental factors. Acorns are particularly susceptible to freezing and desiccation, and a covering of forest litter is critical to protect acorns against environmental extremes (Barrett 1931, Korstian 1927). The moisture percentage of acorns must not get below 30 to 50% for white oaks, or 20 to 30% for red oaks (Korstian 1927) if they are to remain viable. The moisture requirements of oaks are distinctly different from the requirements of other commercial forest species such as the maples (Acer sp.), and the pines (Pinus sp.) which are dried to 10 to 15%, and 5 to 10% moisture content, respectively for storage purposes, and retain optimal germination at these moisture levels (USDA 1974). Damage to acorns from desiccation and freezing has been great in years of poor acorn crops, and relatively unimportant in years of bumper crops (Olson and Boyce 1971).

Oak seeds rarely store in a viable condition on the forest floor for more than one year, unlike many other commercial forest species. Generally, the acorns of the white oak group (subgenus Leucobalanus) are non-dormant and will germinate almost immediately after falling. Acorns in the red oak group (subgenus Erythrobalanus) are dormant in the fall, and germinate the following spring. Acorns from both groups

have been stored successfully in a viable condition for more than one year in controlled conditions, but it is unlikely that acorns from either group could do so in a natural setting.

Even if acorns could remain viable in the forest floor for more than one year, it is doubtful this would occur because of the many factors which cause damage or mortality to acorns. Acorn weevils (Curculio sp.) are responsible for a loss in viability of a large number of acorns (Marquis et al. 1976, Myers 1978). Wildlife is usually the most important factor controlling the number of acorns available for regeneration. Nearly all acorns produced each year are normally consumed by wildlife except during bumper crop years (Burns et al. 1954, Shaw 1968, Watt 1919).

G. Wildlife Utilization of Acorn Crops

In addition to their importance as a seed source for development of advance regeneration, acorns are a highly desirable food for wildlife. Acorns are relatively high in fat and carbohydrates, and contain proteins, vitamins, calcium, and phosphorus (Goodrum et al. 1971). These characteristics make acorns a highly desirable food source. Acorns are used to some degree by a long list of wildlife including the most common big game species in upland oak forests: black bear (Ursus americana), white-tailed deer (Odocoileus virginianus), and turkey (Meleagris gallopavo). Pekins and Mautz (1987) showed that acorns are sought in preference to other food sources by white-tailed deer in southern New Hampshire. Similar preference has been observed in other regions of the country (Pekins and Mautz 1987). Cottam et al. (1939) report acorns to be the most abundant food item of black

bears in the early winter in the mountains of Virginia.

Other wildlife species that utilize acorns for at least a portion of their diet include squirrels (Scirius sp.), rabbits (Sylvilagus sp.), bobwhite quail (Colinus virginianus), crows (Corvus brachyrhynchos), jays (Cyanocitta aristata), woodpeckers (Melanerpes sp., Dendrocopos sp.), raccons (Procyon lotor), and gray foxes' (Urocyon cinereoargenteus) (Goodrum et al. 1971). In addition domestic animals - hogs, goats, and cattle have been shown to consume acorns in southern forests and compete with wildlife for the acorn crop.

Acorn crops have been shown to have a regulatory influence on reproductive success, survival, size of population, and body condition of squirrels and deer (Goodrum et al. 1971). Condition of wild hogs is also apparently tied to acorn availability. Defoliation by the elm spanworm (Ennomos subsignarius (Hbn.)) was probably the cause of reduced acorn production in Tennessee in 1960 and 1961 (Fedde 1962, Henry and Conley 1972, Matschke 1964). Wild hog (Sus scopa) populations were forced to subsist on an energy deficient diet which produced an anestrus condition in sows (Henry and Conley 1972, Matschke 1964). When acorns were again available in 1963 the sows returned to an estrus condition (Matschke 1964).

Acorns are the principal food source for a large variety of wildlife species during the fall and winter months when other sources of food are limited (Goodrum et al. 1971, Lay 1965). Increased damage to forest regeneration and agricultural crops has been shown to occur in years of mast crop failure (Goodrum et al. 1971).

H. Effects of Gypsy Moth Defoliation on Acorn Production

The effect that gypsy moth defoliation may have on acorn production is not known but it may affect it in three ways: 1) directly - by consuming flowers and immature acorns along with leaves as the larvae feed, 2) indirectly - by causing decreased tree vigor resulting in increased premature abscission of acorns, decreased acorn size, or decreased viability of acorns, and 3) indirectly - by causing decreased tree vigor and inducing tree to produce a stress related bumper crop of seeds.

No studies were found in the literature documenting the fate of oak flowers during defoliation by the gypsy moth. Crawley (1985) reported no difference in the number of female flowers produced by nondefoliated pedunculate oaks (Quercus robur L.) trees, and trees that were partially defoliated (<12%) by low levels of oak tortrix (Tortrix viridana L.), Operophtera brumata L., and many less important Lepidoptera (but not the gypsy moth). There was, however, a decrease in acorn production which he suggested was a result of an increased number of aborted peduncles from the defoliated trees. There was no evidence of flowers being consumed directly in his study. Defoliation levels were very small, ranging from 3 to 11.5%, levels usually thought to be below a no-effect level (Bray and Gorham 1964, Gosz 1984).

Rockwood (1973) hand defoliated (100% defoliation) six different species of tropical trees. Seed production on defoliated trees was significantly lower for every comparison made in which both control trees and test trees produced some fruit. Over 80% of the defoliated trees produced no fruit at all (gypsy moth defoliation of oaks differs

from defoliation of the trees in this study in that Rockwoods trees were defoliated before development of the seed crop had begun, while gypsy moth defoliation occurs after seed crop development began). The lack of seed production observed was attributed to a "reduction of fitness" of trees experiencing defoliation.

Torrent (1956) observed that where oak tortrix defoliation had occurred there was almost no acorn production in groves of holm oak (Quercus ilex L.), but when insecticidal control measures were taken to prevent defoliation production ranged from 400 to 1000 kg/ha/year. Liscinsky (1985) observed that in years of gypsy moth defoliation production of sound acorns ranged from 0.0 to 5.6 kg/ha/year. Very low acorn crops (15.2, 8.7, and 1.1 kg/ha/year) were reported in three other years when trees were not defoliated by the gypsy moth, however. The high yields from the research site was 540 kg/ha/year. Average yields were 283 kg/ha/year. Fedde (1962) reported mast crop failures for several successive years in the southern Appalachian Mountains during an elm spanworm outbreak. The mast crop failure was attributed to elm spanworm defoliation. "Failure" was not defined quantitatively by Fedde.

None of these authors (Fedde 1962, Liscinsky 1985, or Torrent 1956) categorized acorns into viability or development categories. The acorn crop reduction they reported was apparently a reduction in the number of sound acorns, though only Liscinsky (1985) stated this. All of them were probably referring to fully developed acorns only, though none of them mentioned this specifically. While these data strongly indicate that there is likely a reduction in the number of sound

acorns following defoliation, they do not address relationships such as whether defoliation may change the total number of acorns produced each year (developed and undeveloped), change the proportion of sound and unsound acorns produced, or show quantitatively the effect moderate levels of defoliation may have on acorn production.

Torrent (1956) reports the possibility that oak tortrix may destroy some of the pistillate flowers and cause a reduction of the acorn crop. Crawley (1985) did not find evidence of oak tortrix destroying pistillate flowers. It is not known conclusively whether the gypsy moth or elm spanworm may consume oak flowers. Forbush and Fernald (1896) discussed instances where in extreme outbreaks of gypsy moth populations, larvae reportedly ate not only the flowers of oak trees but attempted to eat the acorn. These observations were not documented in scientific studies, however, so the extent to which gypsy moth larvae may consume oak flowers at varying population levels is still unknown.

Physiological effects were also discussed by Forbush and Fernald (1896). Apple trees which were heavily defoliated were reported to produce a reduced percentage of their normal apple yield. Accounts were given of fruit trees defoliated by the gypsy moth aborting their fruit, developing immature fruit, or developing fruit so late in the year that it was damaged by frost, apparently caused by the stress of defoliation. The work by Crawley (1985) and Rockwood (1973) corroborate Forbush and Fernalds' (1896) suggestion that reduction of the fruit crop was a result of trees aborting the fruit crop in response to physiological stress. Delayed development or immature

development of fruit crops were not observed in the studies by Crawley (1985) or Rockwood (1973).

Some trees subjected to stress have produced bumper seed crops often called "stress crops" (Kozlowski 1971). If the gypsy moth does not directly consume flowers and remove the possibility of a fruit crop, it is possible that defoliated oaks may respond in this manner and produce a larger than normal crop. There is no indication that this occurs following defoliation from the limited information available, however. It is possible that defoliation may affect production of acorn crops differently in the red oak group and the white oak group. Red oak group acorn production may be affected for both the year of defoliation and the year following defoliation since acorns representing each years' crop will be on the tree at the time of defoliation.

I. Effects of Forest Floor Litter on Seed Survival and the Germination Environment

Korstian (1927) found that leaf litter cover was the most critical factor in producing an environment most suitable for acorn germination and early survival of seedlings. He attributed his findings of much higher germination and survival rates of oaks where covered by leaf litter to the influence leaf litter has on reducing water loss, equalizing temperatures, and facilitating root penetration. Minckler and Jensen (1959) found that one inch litter depths were desirable for oak germination, while depths greater than one inch caused a slight decline in successful germination. Similarly, Barrett (1931) found that litter layer depths of one to two inches were optimal for acorn

germination and early survival. Survival decreased gradually above that depth due to the effects of etiolation, and increased below one inch due to desiccation. Tryon and Carvell (1958) found differential survival rates among red and white oak acorns in West Virginia: white oak acorns survived at a rate of 5 to 1 over red oaks. They attributed differing survival rates to the smaller white oak acorns being covered more easily by the leaf litter and thus more protected from damage. White oaks also germinate and establish roots in the fall. An established taproot may help white oaks avoid mortality resulting from desiccation to a greater degree than red oaks which do not germinate until spring (Tryon and Carvell 1958).

The importance of the presence of a litter layer to oak regeneration is evident. Perhaps equally important to the question of regeneration in the understory is the response of other species to a diminished litter layer. Minckler and Jensen (1959) found that litter depths of one inch or greater effectively prevented the establishment of tulip-poplar and other light-seeded species. Koroleff (1954) made a similar observation. The presence of a thick litter layer that had been allowed to build in a mixed conifer-hardwood stand as a result of preferential logging of the spruce component of the forest effectively prevented regeneration of spruce.

Oak forests are apparently able to regenerate to oak partially because of the presence of a litter layer that both favors their establishment and inhibits the establishment of other species. Removal of this litter layer and excessive opening of the stand may select against oaks in favor of species that thrive where the litter

layer is minimal or absent. Downs and McQuilkin (1944) and Sander (1979) warned against opening a stand too much when attempting to create openings for the development of understory oaks because of the possibility that an environment that would select against oaks might be inadvertently created. Gypsy moth defoliation opens the forest canopy, but the effect that this has on forest floor regeneration is an unanswered question.

J. Effects of Gypsy Moth Defoliation on Forest Floor Depth and Biomass

Gypsy moth removal of a portion of, or all of, a forest canopy affects forest ecosystems by its influence on ecosystem processes. The decomposition rate of organic matter on the forest floor has been shown to be significantly affected by: 1) temperature, 2) moisture status, 3) quality (nutrient content) of organic matter, 4) the physical characteristics of the organic matter, and 5) the quantity and type of microflora and fauna present (Waring and Schlesinger 1985).

Decreased canopy allows for increased throughfall of moisture, wind circulation, and light incidence (and concomitant greater temperatures) on the forest floor. Increased temperatures can increase other parameters related to decomposition such as nitrogen (N) mineralization. In the 5 to 35 °C range there is a Q_{10} of 2 for N mineralization (Stanford et al. 1973). Q_{10} values are the rate at which biologic processes increase with every 10 °C increase in temperature. Where the Q_{10} is 2, every 10 °C increase in temperature results in a doubling of the decomposition rate. This relationship is

true where moisture is adequate since there is a highly significant interaction between temperature and moisture in N mineralization (Cassaman and Munns 1980).

Gypsy moth defoliation may increase soil moisture because throughfall is greater where canopy is diminished. Higher soil and organic layer moisture contents occur because defoliated trees lose the driving force (leaves) for the transpirational process (Cowan 1965) and transpire at a much lower rate than nondefoliated trees (Schowalter et al. 1986). In a protracted dry spell, however, the organic component of the forest floor may dry out because losses from evaporation are likely to be greater on defoliated sites, which will decrease the rate of decomposition.

Nutrient rich frass and the nutrients contained within insect bodies provide a substantial input of high quality organic material, as compared to stands with no defoliation (Gosz 1984). Higher litter quality results because gypsy moth defoliation occurs early in the growing season when nitrogen (N) levels in leaves are high (Carlisle et al. 1966, Grace 1986). When trees are defoliated by the gypsy moth they are unable to translocate N back into the tree as they do prior to leaf abscission in the normal seasonal pattern. Decomposition rates increase with increases in the N content of organic matter (Merrill and Cowling 1966). Gosz (1984) found that nutrient-rich litter not only decomposed rapidly but also increased the rate of decomposition of lower quality organic matter it came in contact with. Because many of the nutrients supplied to trees are provided by mass-flow, short-term nutrient uptake is decreased when transpiration

slows, also serving to increase litter quality (Gosz 1984, Mattson and Addy 1975).

Defoliation by the gypsy moth directly affects the physical characteristics of organic matter. Leaf material is reduced to frass, or to leaf cuttings which are not consumed. The physical size and surface area of the material is greatly reduced and less energy is required to break it down. The net result is a more rapid decomposition rate (Gosz 1984, Schowalter et al. 1986).

The activity and number of micro-flora and fauna increases where temperature, litter quality, or moisture conditions increase; or physical size of litter decreases. Because gypsy moth defoliation can be expected to positively change the environment for microflora and fauna, it can be anticipated their number will increase and they will have an influence on increasing the rates of decomposition in defoliated stands.

Forest floor depth and biomass may be decreased in defoliated stands because of all of these factors increasing forest floor decomposition rates. Depth may also be decreased more directly by the physical conversion of leaves to less voluminous frass. A further reduction of forest floor depth and biomass may occur because refoliated trees have significantly less leaf biomass than the original spring growth (Heichel and Turner 1976) so Autumn leaf fall is decreased. Primary leaves the following spring are smaller and fewer after previous year defoliation (Heichel and Turner 1976). Reduced leaf development in the year following defoliation may contribute to decreased depths and biomass of the forest floor into the growing season following

defoliation. Oak reproduction from seed may be adversely affected by the diminished protective leaf cover required for successful germination and early survival.

III. METHODS AND MATERIALS

A. Description of Study Plots

Study plots were located in the Green Ridge State Forest in Western Maryland, privately owned land in Northern Virginia, and SNP in North-central Virginia (Figure 1). Western Maryland is in the Ridge and Valley Physiographic Province, SNP and Northern Virginia are in the Blue Ridge Province (Fenneman 1938). All of the plots are within the Oak-Chestnut Forest Region (Braun 1950). Soils throughout the study area are typically shallow, stony, medium to low in fertility, medium to strongly acidic, and low in available water capacity. The climate for all of the plots is continental but is modified by elevation. The growing season ranges from 178 days in Northern Virginia to 146 days in the higher elevations of SNP. Annual precipitation averages from 91 cm in Western Maryland to 101 cm in SNP (US Department of Commerce 1985).

B. Sample Stand Characteristics

Study plots selected were judged to be susceptible to gypsy moth attack based on criteria established for identification of susceptible stands by Bess et al. (1947), Houston and Valentine (1977), and Houston (1979). These stands contained oaks (Quercus sp.) as a major component and had full canopy closure. The stands selected in 1985 were known to have gypsy moth populations meeting the criteria established, as well as susceptibility to attack, based on the observations of local forestry officials and egg mass observations made in the late summer of 1985. Plot selection in 1986 was made shortly after peak defoliation so that defoliation levels meeting the

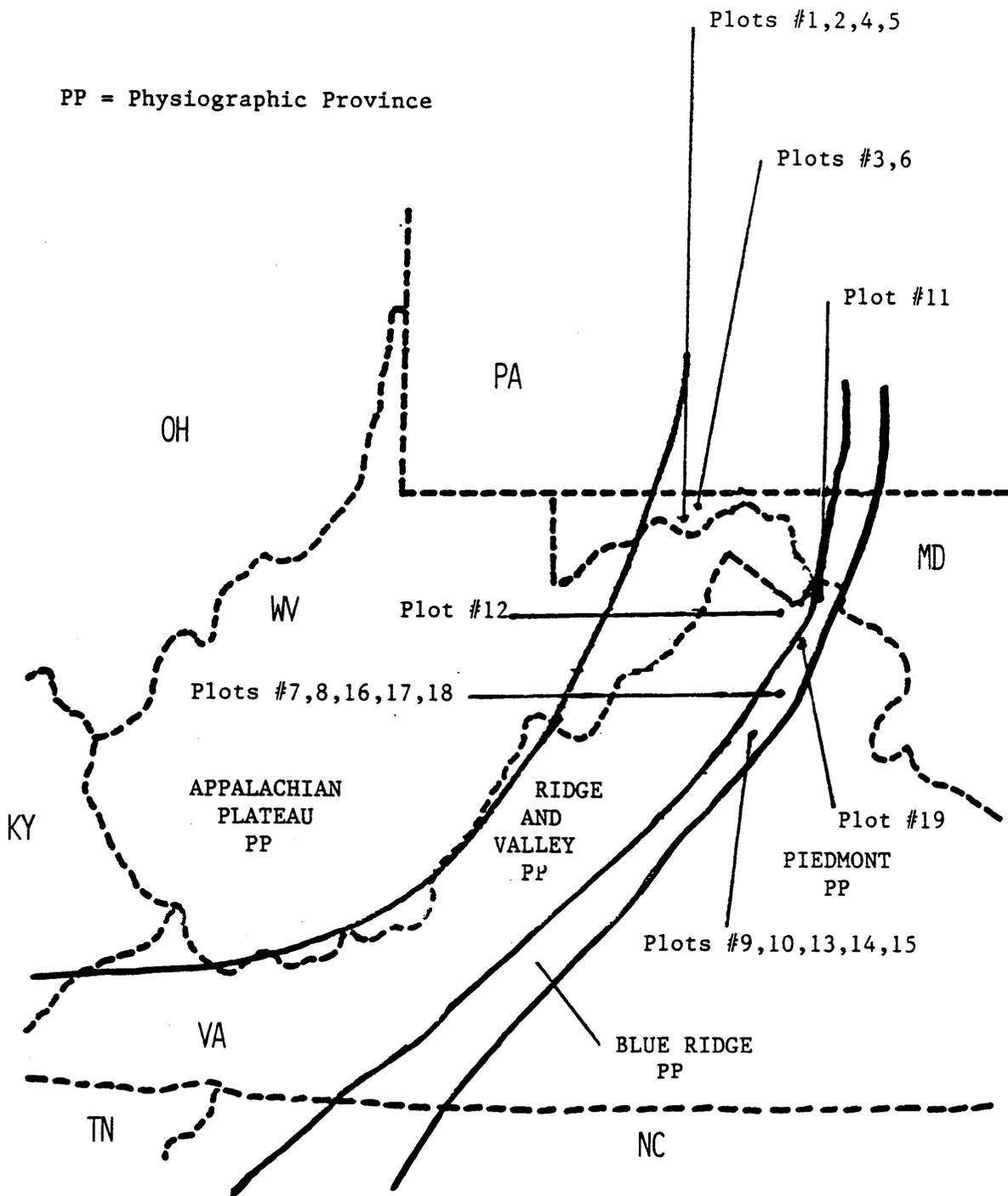


Figure 1. Study plot locations in the Green Ridge state Forest in Maryland, the Billmeyer Wildlife Management Area in Maryland, privately owned land in Northern Virginia, and in the Shenandoah National Park.

study criteria were easily determined.

In 1985, areas that were not going to be treated with insecticides or otherwise disturbed by human activity, and which met the desired criteria of stand characteristics and defoliation level were very limited in both Virginia and Maryland. With the limited selection of study areas available, it was not possible to maintain uniformity of many plot parameters such as slope, aspect, elevation, species composition, basal area, age, size, and site quality (estimated by site index). Plot descriptions including these characteristics were collected in the summer of 1986 (Table 1).

C. Study Design

Study plots were established in areas where trees were heavily defoliated, moderately defoliated, and not defoliated by gypsy moth larvae. Trees on heavily defoliated areas suffered greater than 60% defoliation and refoliated the same growing season. Trees in areas of moderate defoliation were obviously defoliated but did not refoliate in the same growing season. Ocular estimates of the percentage of defoliation of trees suffering moderate defoliation ranged from 20% to 60%. The nondefoliated plots had no ocularly discernible defoliation and only minimal evidence of gypsy moth activity (at least one egg mass was found at each plot). No control treatment was undertaken to prevent defoliation on these plots, however, so normal background levels of defoliation by endemic insects and very minimal levels of gypsy moth defoliation occurred. Typical annual defoliation on "nondefoliated" plots is usually between 5% and 10% (Bray and Gorham 1964, Crawley 1985). This defoliation percent is probably

Table 1 - Study Plot Characteristics. Plots are grouped where similarities exist between stands. Characteristics by which plots are grouped include location, defoliation history, basal area of the overstory, and species composition of the overstory.

Plot #	Basal area (m ² /ha)			Defoliation History		Age (Years)	Height (m)	Site Index ₅₀ (m)	Slope %	Aspect ° Azimuth	Elevation (m)				
	1/ BO	1/ CO	1/ RO	1/ SO	1/ WO							1/ Other	1985	1986	
1	27.5	2.8	-	4.6	5.0	9.6	5.5	Moderate	None	64	17.4	15.8	24	79°	259
2	26.6	-	-	-	9.6	16.1	0.9	Moderate	None	52	14.3	14.0	8	103°	311
4	22.9	-	-	-	4.6	16.1	2.3	Moderate	None	67	18.9	16.5	12	252°	274
5	25.7	-	-	-	12.9	10.5	2.3	Moderate	None	50	16.8	15.2	11	240°	311
Low Elevation Maryland Plots Established in 1985															
3	28.5	-	17.0	10.6	-	-	0.9	None	None	92	22.6	17.1	30	323°	506
6	27.1	-	13.8	7.8	-	-	5.5	None	None	76	22.3	18.6	33	135°	506
High Elevation Maryland Plots Established in 1985															
Shenandoah National Park Plots Established in 1985															
7	31.2	-	16.1	12.4	-	-	2.8	None	Heavy	62	23.8	20.7	43	4°	518
8	40.8	13.8	14.2	2.3	-	1.4	9.2	None	Heavy	75	30.5	25.0	21	164°	549
Shenandoah National Park Plots Established in 1985															
9	34.4	-	13.8	16.5	-	-	4.1	None	None	89	24.4	19.2	12	104°	701
10	34.4	0.5	17.4	11.9	-	-	5.0	None	None	91	27.4	21.0	34	270°	732
Northern Virginia Plots Established in 1985															
11	20.2	-	17.0	-	-	-	3.2	Heavy	N/A	61	23.8	21.3	20	130°	265
12	19.3	1.8	-	3.7	-	8.3	5.5	Heavy	None	102	24.1	18.3	22	212°	390

Table 1 - Study Plot Characteristics (Cont.).

Plot #	Basal area (m ² /ha)				Defoliation History		Age (Years)	Height (m)	Site Index ₅₀ (m)	Slope %	Aspect ° Azimuth	Elevation (m)	
	1/BO	1/CO	1/SO	1/RO	1985	1986							
3/													
Shenandoah National Park Plots Established in July, 1986													
13	23.9	17.9	2.3	-	-	3.7	N/A	Heavy	63	17.4	25	315°	701
15	36.3	17.9	11.5	-	0.9	6.0	N/A	Heavy	70	24.7	35	64°	762
16	30.7	20.7	8.3	-	-	1.8	N/A	Heavy	58	18.3	10	40°	747
17	33.5	1.8	12.9	-	12.4	6.4	N/A	Heavy	71	25.0	12	102°	701
Shenandoah National Park Plots Established in July, 1986													
14	29.4	12.4	4.1	-	-	12.9	N/A	Moderate	64	22.9	23	82°	762
18	31.2	15.1	12.4	-	1.8	1.8	N/A	Moderate	71	21.3	22	54°	701
Plot in Northern Virginia Established in May, 1986													
19	29.3	0.6	5.2	-	4.0	6.9	N/A	Heavy	67	23.2	22	0°	488

1/ BO = black oak (*Quercus velutina* Lam.), CO = chestnut oak (*Quercus prinus* L.), RO = northern red oak (*Quercus rubra* L.), SO = scarlet oak (*Quercus coccinea* Muenchh.), WO = white oak (*Quercus alba* L.).

2/ "Other" species include: American chestnut (*Castanea dentata* (Marsh.) Borkh.), ash (*Fraxinus* sp.), basswood (*Tilia americana* L.), black birch (*Betula lenta* L.), black cherry (*Prunus serotina* Ehrh.), black gum (*Nyssa sylvatica* Marsh.), black locust (*Robinia pseudoacacia* L.), butternut (*Juglans cinerea* L., flowering dogwood (*Cornus florida* L.), eastern white pine (*Pinus strobus* L.) hackberry (*Celtis laevigata* Willd.), pignut hickory (*Carya glabra* (Mill.) Sweet)), pitch pine (*Pinus rigida* Mill.), redbud (*Cercis canadensis* L.), red maple (*Acer rubrum* L.) downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern.), striped maple (*Acer pennsylvanicum* L.), tulip poplar (*Liriodendron tulipifera* L.).

3/ None = no discernible defoliation in current year.
Moderate = visible defoliation ranging from 20 to 60%, trees did not refoliate.
Heavy = defoliation above 60%, trees refoliated in the same year.
N/A indicates that the plot was not in place for the given sample year.

4/ Site Index is for upland oaks, calculated from Schnur (1937).

representative for the nondefoliated plots in this study.

On the study plots selected, sampling equipment (acorn and litter traps) were set out to collect foliar and woody biomass, and acorns. Locations were also established within these plots for collection of forest floor biomass samples and depth measurements on a systematic basis. Plot configuration is discussed in detail in the next section (III-D).

Limited availability of areas with moderate and heavy defoliation in 1985 precluded an even distribution of plots among defoliation levels. Two plots were established in areas where trees were heavily defoliated, four were established in areas where trees were moderately defoliated, and six were established in areas where there was no apparent defoliation in September, 1985. Six more plots were established in SNP in July of 1986. The trees on two of the plots established in 1986 were moderately defoliated and trees were heavily defoliated on the other four plots. One of the plots established in 1985 in Northern Virginia, Plot 11, was dismantled and the equipment moved to a new location, Plot 19, in May of 1986 after it was determined that Plot 11 was within a Dimilin^R treatment area. Because of equipment limitations, manpower constraints, and defoliation levels that were different than anticipated, data collection from Plots 1,2,4,5,12 and 19 was reduced to include only collection from the acorn traps for sampling trips occurring from the early summer of 1986 to March, 1987. Plot characteristics are presented in Table 1. Plot defoliation level groupings are presented in Table 2. Plot locations are shown in Figure 1 and in Appendix A.

Table 2 - Sample plot groupings by defoliation level and year.

	1986 no defoliation	1986 moderate defoliation	1986 heavy defoliation
1985 no defoliation	1 1 3,6,9,10 1	1 1 14*,18* 1	1 7, 8, 13*, 1 1 15*, 16*, 1 1 17*, 19** 1
1985 moderate defoliation	1 1 1,2,4,5 1	1 1 1	
1985 heavy defoliation	1 1 11***,12 1	1 1 1	

* indicates plots established mid-July 1986.

** indicates plot established mid-May 1986.

*** indicates plot removed mid-May 1986.

Stands with similar characteristics but differing levels of defoliation were compared rather than obtaining base-line information for a given set of stands, and comparing pre- and post-defoliation conditions. Schnur (1937) used this method (temporary-plot method) to develop site index equations for upland oaks, and Grace (1986) used similar methodology to determine differences in the nutrient status of the forest floor following gypsy moth defoliation in Pennsylvania. The uncertainty involved in predicting gypsy moth movement and the time constraints on the project precluded the alternate approach.

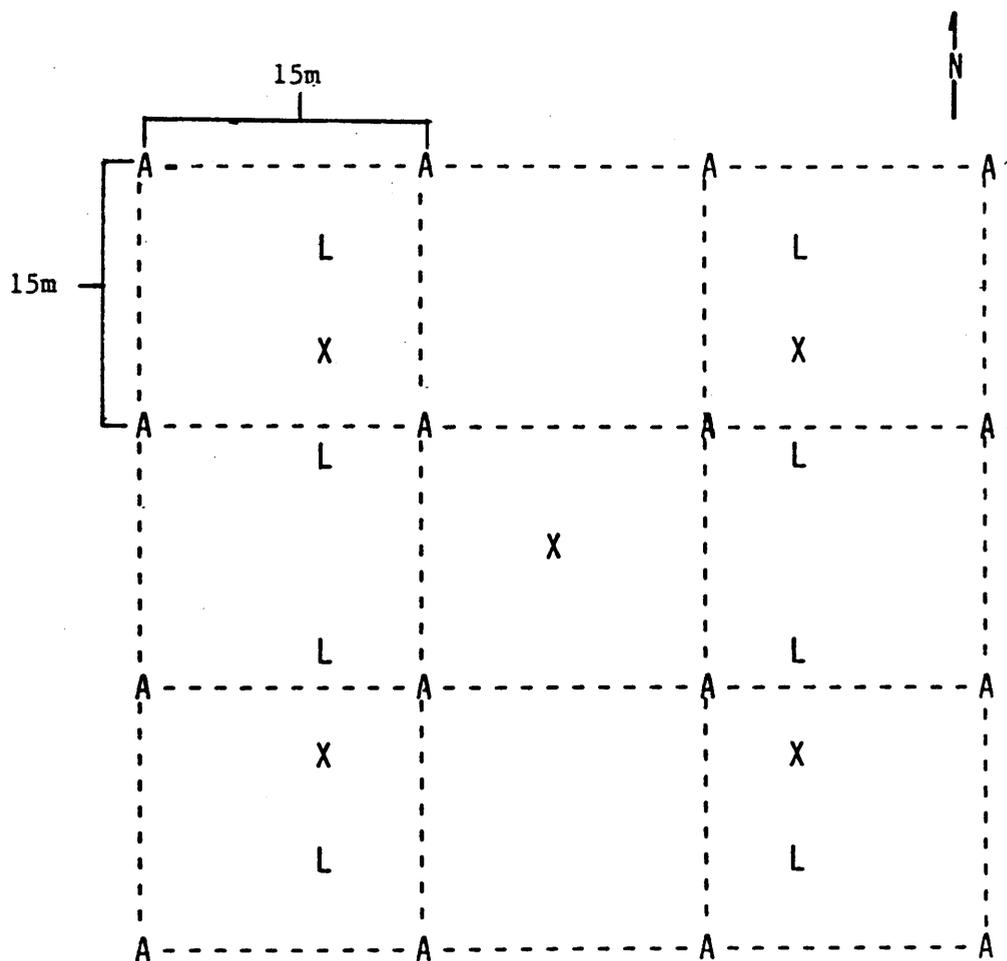
D. Plot Design

1. Plot configuration

One 75m x 75m (0.6 ha) study plot was established in each sample stand (Figure 2). On each study plot, 16 0.5 m^2 area acorn traps and 8 0.25 m^2 area litter traps were set out on a systematic basis. The first trap at each plot was located randomly.

Acorn traps were located using a 4 trap by 4 trap grid pattern following cardinal magnetic directions. Traps were placed 15 m apart providing for an even distribution of acorn traps over the plot (Figure 2). In the closed forest canopies common to all of the study plots, setting traps out on a grid pattern allowed for sampling on an area basis, and potential bias from selecting sample trees was avoided.

The litter traps were set out, one 6.5 m north and one 6.5 m south of four "subplot center stakes". The four subplot center stakes were located on a grid pattern so that they were equidistant from each other and from the plot boundaries nearest to each (Figure 2).



A = Acorn Trap

L = Litter Trap

X = Subplot Center Stake

Figure 2. Sample plot configuration.

The acorn traps were set out in late March and removed in late November (except for the initial establishment of the plots in September of 1985). Acorn traps were removed during the winter because their design makes them susceptible to snow damage, and there is minimal acorn and litterfall during this period.

2. Acorn trap design

The acorn trap frames were made from 32 mm diameter steel pencil rod bent in a circle with two parallel end pieces, twelve cm in length, turned out at a 90° angle from the closure of the circle (Figure 3). The diameter of the frame was 79.8 cm forming a trap surface area of 0.5 m^2 . Four-mil clear plastic was cut in a semicircle and duct tape applied along the edges of the cut plastic sheeting, both the curved and straight edges, to provide material for staples to join and add strength. Duct tape was also added to the bottom ten cm of the cone, inside and out. The seam was stapled to form a cone, and the circular top edge folded over the frame and stapled to attach the collection bag to the frame. Holes (0.6 cm diameter) were punched in the bottom through the duct tape and plastic, using a paper punch, to allow for water drainage (Figure 3).

The traps were mounted on two 1.5 m long treated 5 cm x 5 cm wooden poles. Two parallel holes were drilled 10 cm from the top of one pole and the end pieces from the frame fitted through these holes. A nail was pounded into the other pole creating a lip for the frame, on the side opposite the the end pieces, to rest upon. Twenty gauge wire was wrapped around the frame, the pole, and the nail. Placement in the ground was accomplished by sliding each of the poles over 95 mm

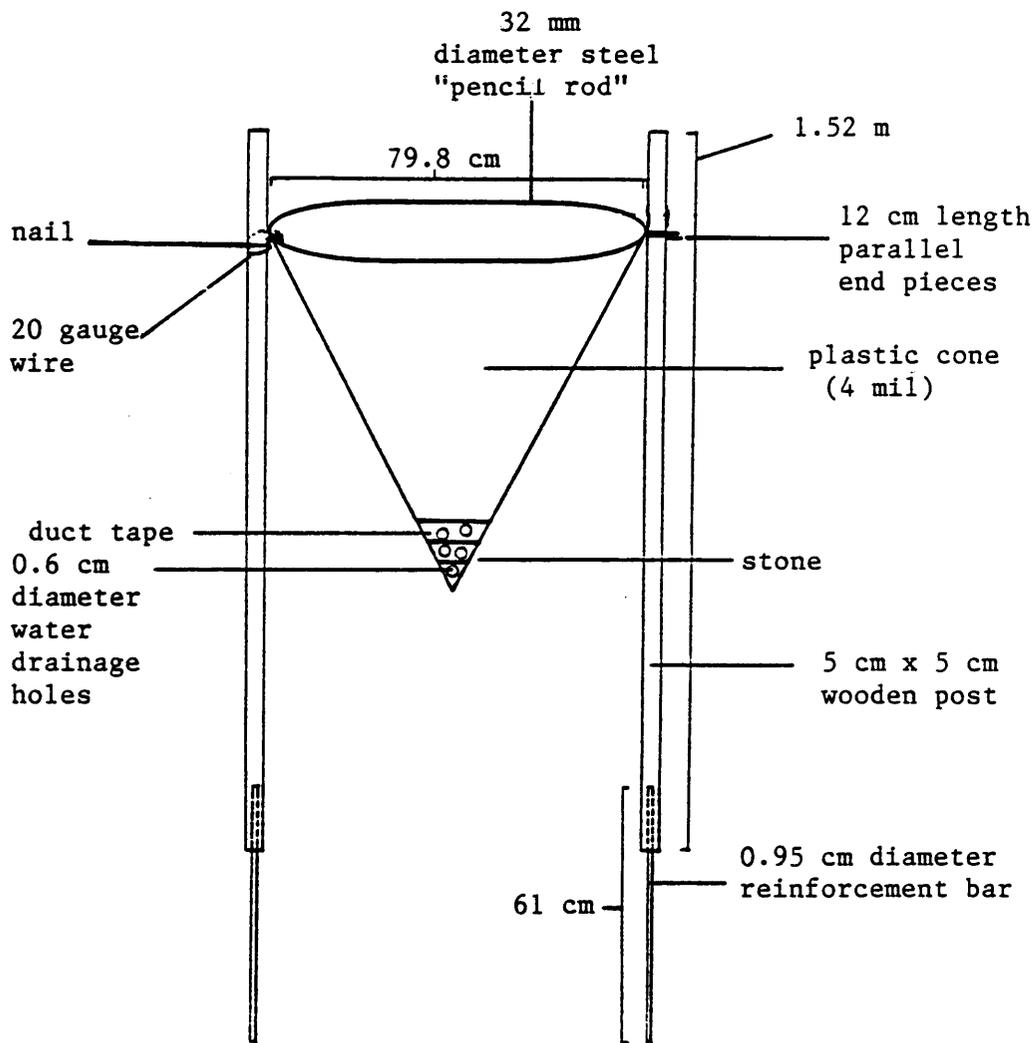


Figure 3. Acorn trap specifications and design.

diameter reinforcing rod pounded into the ground (holes were drilled into the bottom of each pole). The reinforcing rod allowed for placement of this trap design in the rocky sites characteristic of the study area. Stones were placed into the traps to provide stability and to prevent wind from inverting the traps (Figure 3).

This trap design is similar to that used by Myers (1978). The conical design, elevated off the ground, formed from plastic, and put together on the plot is desirable in that predation by animals has been found to be minimal, losses from acorns bouncing off of or out of the traps are minimal when compared to other trap designs that have been used, and this model is less expensive to construct and more portable than other types of traps commonly used (Christisen and Kearby 1984).

3. Litter trap design

The litter traps were made from 2.5 cm (width) x 10 cm (height) treated pine cut and nailed together in the shape of a square with a sample area of 0.25 m^2 . Aluminum screen was attached to the bottom, and the corners were reinforced by nailing hanger iron around each end piece. Litter traps were placed on the ground and leveled to horizontal by placing wooden blocks under traps as needed.

E. Sampling Times

Full sample collection for each sampling time consisted of biomass (foliar, woody, and acorn) collection from litter and acorn traps, collection of "duff" samples, and recording of litter depths (Section F-1). The sample dates selected were based on expected biological occurrences:

- 1) Late March - before gypsy moth larval emergence and early leaf production. Litter layer may have matted down and little decomposition of the previous autumn's leaf fall was expected.
- 2) Late June - the end of maximum gypsy moth defoliation activity, and immediately following the period of peak litterfall for the season on heavily defoliated plots. Light penetration into defoliated stands is at a maximum, biological activity is near the annual maximum rate, and rapid litter decomposition is occurring.
- 3) Mid-September - just prior to leaf fall, and during early acorn drop. Litter depths and forest floor biomass are at an annual minimum on nondefoliated plots.
- 4) Late November - leaf fall and acorn drop are complete. Litter depths and biomass are at an annual maximum on nondefoliated plots. The amount of biomass produced and dropped for the season is largely complete.

Complete data collections were conducted a total of seven times during the study (Table 3). The first sampling time was mid-October of 1985 and the last sampling time was late-March of 1987. Two partial sample collection trips were also made on which only material from acorn and litter traps was collected; one of these was in mid-July, 1986, the other was in mid-October 1986.

F. Data Collection for Individual Objectives

1. Field methods

a) Acorn, foliar, and woody biomass collection

Except in March, the acorn, foliar, and woody biomass accumulated in

Table 3 - Sample collection dates, and sampling intensity.

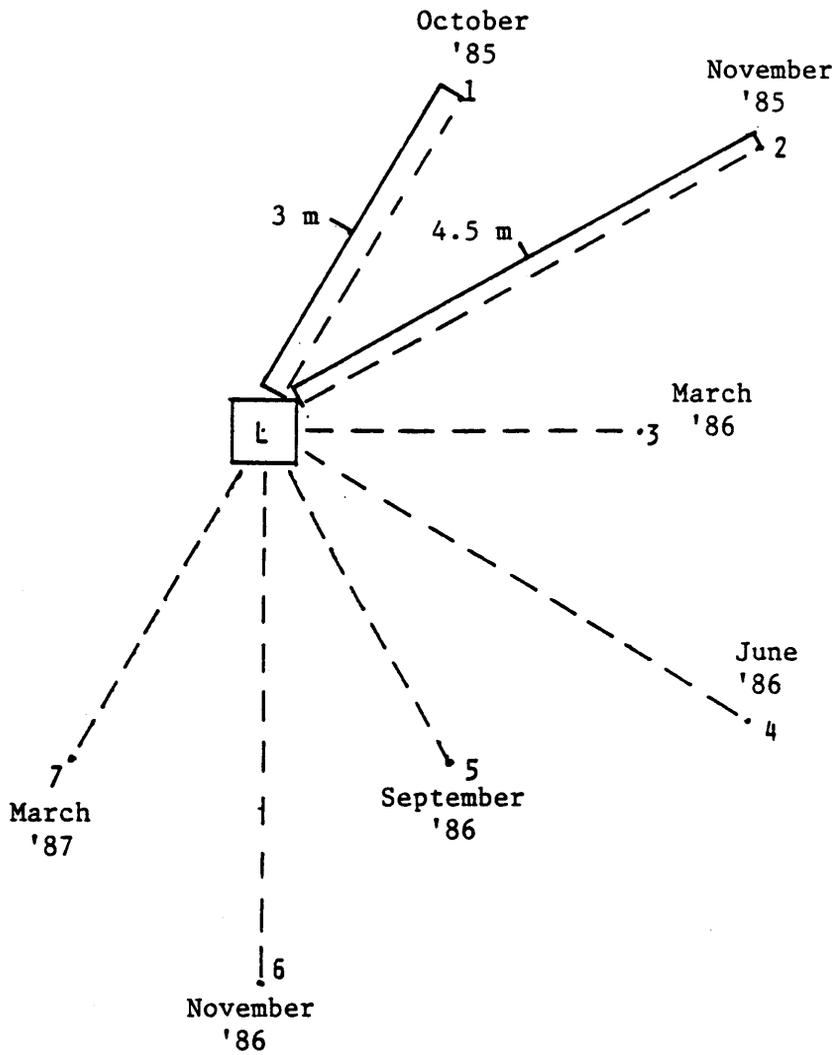
Date	Trap types from which acorns, and foliar and woody biomass were collected	Forest floor biomass collected & depth recorded?
plots established mid-Sept. 1985	Not collected	No
Trip 1 Mid-Oct. 1985	Acorn & Litter	Yes
Trip 2 Mid-Nov. 1985	Acorn & Litter	Yes
Trip 3 Mid-March 1986	Litter	Yes
Trip 4 Late-June 1986	Acorn & Litter	Yes
Trip 4a) Mid-July 1986	Acorn & Litter	No
Trip 5 Mid-Sept. 1986	Acorn & Litter	Yes
Trip 5a) Mid-Oct. 1986	Acorn & Litter	No
Trip 6 Mid-Nov. 1986	Acorn & Litter	Yes
Trip 7 Mid-March 1986	Litter	Yes

the litter and acorn traps were collected at each sampling date and taken to the laboratory (no samples were collected from the acorn traps during the late-March sample times because the acorn traps were taken down for the winter).

b) Forest floor biomass accumulation - "duff samples"

At each sample date duff samples consisting of the organic horizons from the L, F, and H layers and excluding the A1 layer (Hoover and Lunt 1952) were collected and taken to the lab. The collection points for duff samples were located systematically (Figure 4). At each sample time (1 through 7), a bearing from the litter traps, used as plot center stake, 30° greater than that used during the preceding sampling time was used. On sample collection times 1,3,5, and 7, duff samples were collected 3 m from the litter traps, samples collected on sample times 2,4, and 6 were collected 4.5 m from litter traps.

Duff samples were collected by placing a 0.25 m^2 template over a sample point and cutting the border of the area using a sharp knife with serrated edges. All of the biomass within the template was collected with the exception of live material such as grass, moss, seedlings etc., and woody material exceeding 2.5 cm in diameter. Woody material greater than 2.5 cm diameter was excluded because of the high variability associated with its occurrence on the forest floor (Bray and Gorham 1964, Harmon et al. 1986). If more than 25% of the duff sample sample location were rock, bare ground, or woody material exceeding 2.5 cm diameter the sample location was not used. A new location was found by extending the distance from the litter trap in one meter increments until a suitable location was found.



L = Litter Trap

Figure 4. Forest floor biomass collection location for each sample collection date.

Acorns which were germinating and beginning to develop were included in the duff sample for all sample times except in late-June. Acorns belonging to the the white oak group begin to germinate in the fall immediately after falling. With the limited number of sample collection times for this project, white oak group acorns were usually not collected before germination. Acorns that had developed into seedlings were excluded based on the criterion of being living material, beginning with the late-June sample time. Plant roots were also excluded by the same criterion.

c) Forest floor biomass accumulation - depth measurements

Two litter depth measurements were taken to the nearest 0.1 cm, each taken at a distance of 1 m from opposing sides of each duff sample (16 total depth measurements/plot), following cardinal directions. The direction ($^{\circ}$ azimuth) from each duff sample at which depth measurements were taken was consistent throughout each plot.

2. Laboratory Methods

a) Acorn, foliar, and woody biomass collection

All materials collected were dried at 60 C° for at least 5 days or until constant weight was achieved. For the acorn and litter traps each sample was then separated into foliar material, woody material, acorns, and acorn caps, and weighed to the nearest 0.01 g on a Mettler PC 4400, DeltaRange^R scale. Foliar biomass includes materials produced and aborted on an annual basis (excluding fruits) such as flower parts, leaves, leaf petioles, and insect frass. Woody biomass typically stays on the tree more than one growing season (excluding fruits) and includes bark, and twigs less than 2.5 cm diameter.

Weight was the only parameter recorded for foliar and woody material, while acorns and acorn caps were categorized, counted, and weighed as described in Section 2-c.

b) Forest floor biomass accumulation - "duff samples"

Duff samples from the first three sample trips were separated into groupings of "woody" material consisting of material that typically stays on trees for more than one growing season such as bark and twigs (excluding fruits); "acorn", consisting of acorns in all categories and acorn caps; and "foliar" material which included all annual material collected (except fruits) and may have included some humus from material broken down beyond recognition from the woody or acorn groups described above. Acorns and acorn caps were combined and weighed as a group and not categorized as for the acorn and litter traps because it was not possible to discern which year acorns on the forest floor fell. Acorns on the forest floor are also subject to predation by wildlife and therefore have limited use for monitoring mast production. For Trips 4 through 7 duff samples were not separated into foliar, woody, and acorn groups and only total biomass was recorded. Duff samples for trips 4 through 7 were not sorted because no trends that differed from total biomass were identified for either foliar or woody biomass' separated out, and the separation procedure was extremely time consuming (30 minutes to 1 hour per sample).

c) Acorn quantity, weight, viability, and development

Acorns and acorn caps collected in the litter and acorn traps, were dried, weighed, and separated as described previously. Acorns were

classified according to their stage of development by the following classification: 1) undeveloped, 2) partially developed, and 3) fully developed. Undeveloped acorns have the cap completely enclosing the acorn nut. Partially developed acorns range from having the tip of the nut visible but still largely enclosed by the acorn cap, to having the broad bottom surface of the nut visible but the cap still surrounding the sides of the nut halfway down its length. Fully developed acorns have the cap only covering the top of the nut. Size is not always related to the stage of development and the acorn may be green or have darkened. This classification procedure is similar to that used by Myers (1978). Myers (1978) separated acorns into five development categories, but for analysis recombined them to only a developed and an immature category. The undeveloped and partially developed categories in the present study correspond to Meyers immature category. The developed category is the same in Meyers' study and the present study.

The partially developed and fully developed acorns were further classified into viability categories: 1) sound, 2) unsound insect-infested, 3) unsound-rotten, 4) unsound-animal damaged. Soundness of the acorns in which the viability was questionable was determined by cutting tests; acorn viability was determined by cutting the acorn open and confirming the presence or absence of cotyledonary reserves, and an intact embryo. This technique has been used by other researchers, notably Gottschalk and Gibson (1981), Goodrum et al. (1971), and Beck (1977).

The classification system for acorn viability used is similar to

classification systems used by Gottschalk and Gibson (1981), Meyers (1978), and Burns et al. (1954). Each of these researchers had acorn viability categories of sound, unsound-insect damaged, and unsound-animal damaged. Each of their classification systems differed from the present study in some ways, however. Myers (1978) and Burns (1954) did not have a category for rotten acorns. Gottschalk and Gibson (1981), had a category for damaged or diseased acorns which probably accounted for most rotten acorns, but had an additional category of "damaged, cause unknown". Acorns from Gottschalk and Gibson's "damaged, cause unknown" category would probably be included in the "rotten" category of the present study. Meyers (1978) had acorn viability categories for "malformed or aborted" and "other"; these categories probably would both be classified with the "rotten" viability category of the present study. Burns et al. (1954) looked only at fully developed acorns; his system did not include a category for fully developed rotten acorns, and did not differentiate undeveloped and partially developed acorns. Meyers (1978) had five insect-damaged categories according to the species of insect attacking the acorn. This detail was outside the interest of the present study; insect infested acorns were placed in a single category. Other researchers have come up with still more classification categories different from these (Nicholas and White 1984). There is a need for standardization of nomenclature and categorization of acorn groupings.

The number of acorns in each of the groupings of species, development stage, and viability category was recorded. The group dry weight of the acorns in each of these groupings from each trap at each

sampling date was also recorded. Undeveloped acorns were an exception. Undeveloped acorns were not weighed as a group because they have little usefulness to wildlife and are not capable of germinating. Undeveloped acorns were instead grouped with the acorn caps and a weight of these two categories together was recorded. Acorn caps were identified by species and tallied. Positive identification of undeveloped acorns by species or species group was not possible so only a total number was tallied for undeveloped acorns.

G. Analysis

1. General

Prior to analysis of foliar and woody biomass collection, and acorn collection, a comparison of the collection ability of acorn vs. litter traps was conducted (Appendix B). This comparison used the trap as the sample unit. Based on the results of these analyses, only acorn traps were used to determine collection of foliar and woody biomass, and partially and fully developed acorns. Undeveloped acorns were collected more efficiently by litter traps so litter traps were used for analysis of undeveloped acorns.

Foliar and woody biomass collection, and acorn collection were compared over both the sample year (March through November) and by separating data into two collection periods. In Year 2, data were collected on some plots from March to November and annual data was divided into two collection periods. The first period was from mid-March to mid-July, the second period was from mid-July to late November. In Year 1, data collection did not begin until

mid-September and only one data collection period, mid-September to late November, was used. The effects of defoliation for both litterfall and acorn drop are observed most strongly by separating annual data into these two time periods.

2. Foliar and woody biomass collection

All plots were included in this analysis. Plots defoliated in Year 1 and not defoliated in Year 2 were observed to have similar litterfall to plots which had never been defoliated and were included with nondefoliated plots in year 2.

Using all plots, sample sizes were sufficiently large to test for significant differences. Analyses were conducted using either paired t-tests or Tukey-Kramer's multiple range test. The plot was the sampling unit for all comparisons. Where differences between two levels of defoliation were tested, paired t-tests were used. The t-test used was determined by first testing for equality of variance ($\alpha=.05$) and using the t-test appropriate to the equality of variance test. Where differences between three levels of defoliation were tested, Tukey-Kramer's multiple range test was used because of unequal sample sizes (SAS Manual 1986). Significant differences were determined using $\alpha=.05$.

3. Forest floor depth and biomass accumulation

Forest floor depth and biomass were analyzed by looking at data in graphical displays and observing trends. Means tests and t-tests showed significant differences by defoliation levels, but interpretation of the data indicated that differences observed were more likely attributable to site quality differences between study

plots than to defoliation.

Forest floor depth is reported in Appendix C because depth is considered a less reliable measure of forest floor characteristics than is biomass and never decreased below levels thought to be important to the forest floor regeneration environment. A side study was conducted to test the hypothesis that forest floor depth could be used to estimate forest floor biomass and is reported in Appendix D.

4. Acorn collection

Analyses were conducted to determine differences in: 1) the total quantity of acorns produced, and 2) the quantity of acorns produced in each of the three development categories (undeveloped, partially developed, and fully developed). For the partially developed and fully developed acorns analyses were further broken down by viability category (sound, unsound-insect-damaged, unsound-rotten, and unsound-animal-damaged).

Acorn production was extremely low from plots that were defoliated the previous year and not defoliated in the current year (discussed in Results section IV-3). Because of this, analysis for year 2 acorn production included only the ten plots in SNP and two plots in Maryland with no previous defoliation (only the effects of defoliation in the year of defoliation were of interest in this comparison). Plot 19 in Northern Virginia, which was not defoliated the previous year, was also excluded from the analysis of Year 2 acorn production because of its' low basal area in oak (Table 1).

Analyses consisted simply of presenting and interpreting mean acorn counts by development stage and/or viability category for each

defoliation level, by sample period. Means were obtained using the plot as the sample unit. The small sample size precluded use of statistical tests. Problems with interpretation of the data such as the unequal sample collection periods in Years 1 and 2, differing acorn crop size in Years 1 and 2, the poor acorn crop in the white oak group in Year 2, lack of data collection for a full year from moderately defoliated plots, and differing species compositions on plots also make these data less suitable for interpretation using standard statistical tests.

IV. RESULTS and DISCUSSION

A. Effects of Defoliation on Foliar and Woody Biomass Collection

There are no differences in foliar or woody annual biomass production as a result of gypsy moth defoliation for plots suffering their first year of heavy defoliation (Tables 4 and 5, Sample Period D). The timing of leaf fall was substantially changed by heavy defoliation (Table 4), however. The peak period of leaf fall occurred in the early summer, when heavy gypsy moth defoliation of the forest canopy occurred, rather than in the fall (Table 4, Sample Period B). The timing of woody biomass drop may also be altered by heavy gypsy moth defoliation in a pattern similar to that of leaf fall (Table 5).

Data was not collected for moderately defoliated plots for the early part of the summer in either Year 1 or Year 2. Moderately defoliated plots were observed to have foliar biomass collections intermediate to those of nondefoliated and heavily defoliated plots in the fall of each year (Table 4, Sample Period A, C, and E). Because the trees on these plots did not re-leaf it is probable that the reason for the difference in foliar biomass between nondefoliated plots and moderately defoliated plots for the fall months was that a portion of the canopy was removed by gypsy moth larvae in the early summer before data collection began. The annual differences observed in Sample Periods A and E (Table 4) between nondefoliated, moderately defoliated, and heavily defoliated plots can also be accounted for by foliar biomass that was removed by defoliation before data collection began.

Woody biomass collection was greater from heavily defoliated plots

Table 4 - Mean foliar biomass collection by defoliation level and year. Includes all materials produced and aborted on an annual basis (excluding fruits) such as flower parts, leaves, frass, and leaf petioles.

Sample Period	1/ Defoliation Level	# of Plots	Mean Foliar Biomass (kg/ha)	standard deviation
YEAR 1 (1985); Fall			2/	
A) mid-Sept. '85 to late Nov. '85	none	6	3065 a	408.7
	moderate	4	2157 b	246.7
	heavy	2	1380 b	570.2
YEAR 2 (1986); Spring, Fall, and Full Year			4/ p-value	
3/				
B) mid-March '86 to mid-July '86	none	9	342	63.3
	heavy	3	1523	.1445 876.1
C) mid-July '86 to late Nov. '86	none	9	3390	641.4
	heavy	3	2078	.0605 701.9
D) mid-March '86 to late Nov. '86	none	9	3732	617.9
	heavy	3	3601	.7565 607.8
YEAR 2 (1986); Fall			2/	
E) mid-July '86 to late Nov. '86	none	9	3390 a	641.4
	moderate	2	3056 a	86.2
	heavy	5	1795 b	674.8

1/ Plots sampled in each period:

A) Plots 1,2,3,4,5,6,7,8,9,10,11,12

B, C, and D) Plots 3,6,7,8,9,10

E) Plots 1,2,3,4,5,6,7,8,9,10,12,13,14,17,18,19

2/ Differences were determined using Tukey-Kramer's Multiple Range Test ($\alpha=.05$). Means followed by different letters within a sample period indicate means are significantly different.

3/ Sample periods B,C, and D had no moderately defoliated plots.

4/ P-values were determined using paired t-tests; equality of variance was tested for ($\alpha=.05$) and the t-test appropriate to the equality of variance test used.

Table 5 - Mean woody biomass collection by defoliation level and year. Includes all materials produced over more than one growing season (excluding fruits).

Sample Period	1/ Defoliation Level	# of Plots	Mean Woody Biomass (kg/ha)	standard deviation
YEAR 1 (1985); Fall			2/	
A) mid-Sept. '85 to late Nov. '85	none	6	299 a	133.1
	moderate	4	247 a	134.3
	heavy	2	228 a	30.8
YEAR 2 (1986); Spring, Fall, and Full Year			4/ 3/ p-value	
B) mid-March '86 to mid-July '86	none	9	150	93.0
	heavy	3	348	.4365 205.2
C) mid-July '86 to late Nov. '86	none	9	465	248.9
	heavy	3	279	.2411 46.6
D) mid-March '86 to late Nov. '86	none	9	615	290.0
	heavy	3	627	.9487 309.5
YEAR 2 (1986); Fall			2/	
E) mid-July '86 to late Nov. '86	none	9	465 a	248.9
	moderate	2	300 a	121.6
	heavy	5	275 a	35.6

1/ Plots sampled in each period:

A) Plots 1,2,3,4,5,6,7,8,9,10,11,12

B, C, and D) Plots 3,6,7,8,9,10

E) Plots 1,2,3,4,5,6,7,8,9,10,12,13,14,17,18,19

2/ Differences were determined using Tukey-Kramer's Multiple Range Test ($\alpha=.05$). Means followed by different letters within a sample period indicate means are significantly different.

3/ Sample periods B,C, and D had no moderately defoliated plots.

4/ P-values were determined using paired t-tests; equality of variance was tested for ($\alpha=.05$) and the t-test appropriate to the equality of variance test used.

than from nondefoliated plots in the collection periods immediately following defoliation. During the fall collection periods in Year 1 and Year 2, collection of woody biomass was greater from nondefoliated plots than from heavily defoliated plots (Table 5). Table 5 shows a trend for a difference in timing of woody input in both Year 1 and Year 2. In each year woody biomass was presumably higher from nondefoliated plots for the fall sample period because woody biomass input over the year was approximately the same, but input immediately following defoliation, which tended to be greater on defoliated plots, was missed (Table 5). This trend was stronger in Year 1 than Year 2 possibly because Year 1 data collection occurred only in the fall (beginning mid-September), while in Year 2 data was collected over much of the summer as well (beginning mid-July).

An increase in woody biomass collection from heavily defoliated plots compared to nondefoliated plots may occur because newly formed twigs may be abscised as trees respond to the stress of defoliation. Increased woody production in the year of defoliation is an unlikely explanation. Reduced growth of forest trees has been shown to occur following defoliation (Baker 1941, and Brown et al. 1979). Trees reallocate resources to higher priority functions such as producing a photosynthetic source and to defense mechanisms rather than increased production of woody material (Parker 1981).

An increase in foliar production (and collection), rather than a decrease, would appear to be the more likely hypothesis in the first year of defoliation because trees lose their initial set of leaves and then refoliate if defoliation levels exceed 60% (Campbell and Sloan

1977c). Previous studies have shown no significant change in foliar production in the first year of gypsy moth defoliation, however (Carlisle et al. 1966, Grace 1986, Rafes 1971). One possible explanation may be that trees respond to the stress of gypsy moth defoliation by curtailing allocation of resources to leaf expansion (gypsy moth defoliation begins before leaves are fully expanded). The resources may then be put into a second flush and the total biomass is approximately the same over the year. A second possible explanation may be that secondary wall thickening never occurs to a substantial degree in either the initial or secondary leaves on defoliated trees. Foliar biomass is less because of this. Calcium, the major nutrient associated with secondary wall thickening, is found in reduced quantities on defoliated sites as compared to nondefoliated sites (Grace 1986).

A third possible explanation may be that the second flush of leaves contributes to biomass production in approximately equal amounts to the biomass that is utilized in metabolic reactions and lost by respiration from the gypsy moth. Grace (1986) reported that refoliated leaves weighed 28% that of normal leaves. He also cited an unpublished study by Ahmad and Forgash where the average frass production over a season for gypsy moths was 71% of leaf the weight ingested, indicating that 29% was retained or metabolized. Differences in biomass production possibly are not detected without incorporating a conversion factor for gypsy moth utilization into the equation. There may also be interactions between these factors.

Gypsy moth defoliation affected the timing of litterfall by

consuming and cutting tree foliage during defoliation. Some abortion of partially consumed leaves and petioles also occurred. Continued foliar input to the forest floor that was apparently a response to defoliation was observed through mid-July, several weeks after the cessation of defoliation. Grace (1986) observed a similar result.

B. Effects of Defoliation on Forest Floor Biomass

Total forest floor biomass was not shown to be either reduced or increased following gypsy moth defoliation. On Plots 7, 8, 9, and 10 forest floor biomass data was collected in both Year 1 and Year 2. These plots are in close proximity to each other in the SNP and represent the best data set available in terms of length of data collection and similarity of study areas. Mean forest floor biomass' from these plots are presented in Table 6 and Figure 5, by season. No trends indicating either a reduction or increase in forest floor biomass are evident from these data. Table 7 gives mean biomass' by season for all plots. These data show high variability for most plots. This is a reflection of the high variability associated with measuring forest floor biomass. Plots with generally low or high biomass' reflect the site quality of the plot. Plots with low biomass are typically higher in site quality.

Forest floor biomass was relatively unaffected by the defoliation level experienced by the trees on the plot. The anticipated result of decreased forest floor biomass resulting from increased rates of decomposition following defoliation by the gypsy moth was not disproved. It is probable that the impact of gypsy moth defoliation on forest floor biomass is small, however, when making comparisons for only a one year period, especially compared to the effect gypsy moth defoliation has on litterfall (discussed previously) and acorn production (discussed in the next section).

Table 6 - Mean forest floor biomass (1000 kg/ha) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.

1/ Plot #	2/ September		November		March	
	1985	1986	1985	1986	1986	1987
7	16.3	14.6	17.7	16.4	14.6	10.2
8	10.3	9.3	14.7	14.4	14.2	15.3
9	17.5	11.5	19.1	16.4	15.1	18.5
10	22.1	12.7	22.7	34.1	20.4	23.6

1/ Plots 7 and 8 were not defoliated in 1985 and heavily defoliated in 1986; Plots 9 and 10 were not defoliated in 1985 or 1986.

2/ In 1985, data was collected in early October, in 1986 data was collected in late September. The collection time was before substantial leaf fall occurred on nondefoliated plots (normal seasonal leaf fall) each year.

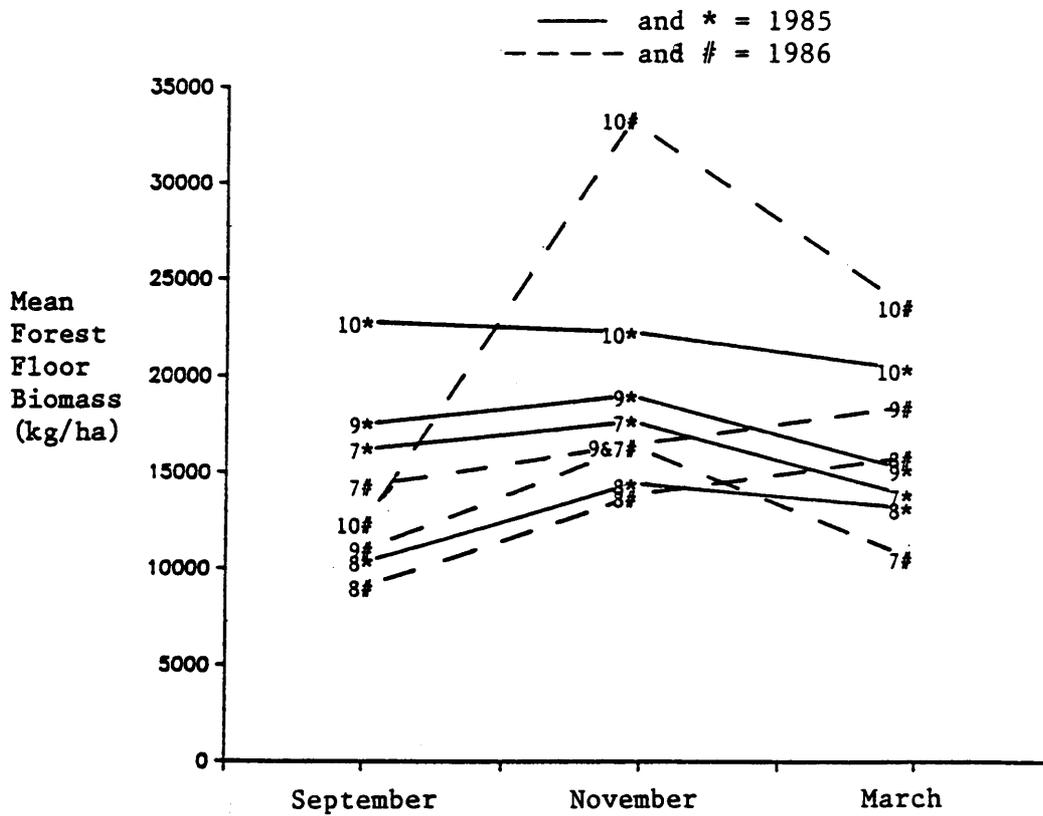


Figure 5. Mean forest floor biomass (kg/ha) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.

Table 7 - Mean forest floor biomass (1000 kg/ha) by sample collection trip # (season), and plot. An "*" is used where forest floor biomass was not sampled.

Plot #	-- 1985 --		-- 1986 --				-1987-
	Trip 1 Oct.	Trip 2 Nov.	Trip 3 March	Trip 4 June	Trip 5 Sept.	Trip 6 Nov.	Trip 7 March
1	14.0	14.1	15.1	15.2	*	*	*
2	17.7	14.6	14.6	12.9	*	*	*
3	18.8	17.7	20.1	21.1	18.1	22.5	18.1
4	16.5	12.4	15.1	10.2	*	*	*
5	14.8	12.7	12.6	11.5	*	*	*
6	17.3	20.2	17.8	18.8	18.7	27.6	25.3
7	16.3	17.7	14.6	16.6	14.6	16.4	10.2
8	10.3	14.7	14.2	11.2	9.3	14.4	15.3
9	17.5	19.1	15.1	17.7	11.5	16.4	18.5
10	22.1	22.7	20.4	15.8	12.7	34.1	23.6
11	18.3	18.0	15.5	*	*	*	*
12	16.4	15.8	16.9	12.7	*	*	*
13	*	*	*	*	17.8	21.1	13.3
14	*	*	*	*	13.0	23.0	19.9
15	*	*	*	*	19.5	27.0	18.2
16	*	*	*	*	13.4	21.3	13.3
17	*	*	*	*	8.2	11.9	10.3
18	*	*	*	*	13.2	15.9	14.3
19	*	*	*	15.4	*	*	*

C. Effects of Defoliation on Acorn Quantity, Weight, Viability, and Development

1. Quantity, weight (stand basis), and development of acorns

The quantity of acorns produced in each development category was substantially changed over each sample collection period and year by heavy gypsy moth defoliation (Table 8). On heavily defoliated plots most of the acorn crop did not develop and dropped in the early part of the growing season; very few of the acorns became fully or partially developed. When data were analyzed by sampling trip rather than combining sample trips into "spring" and "fall", practically all of the acorn crop on plots on which trees were heavily defoliated plots dropped by early September in Year 2, mostly while acorns were still undeveloped. In Year 1 data collection did not begin until early September and the total number of acorns collected from plots with trees that were heavily defoliated was substantially less than from plots where trees were moderately defoliated or were not defoliated. No undeveloped or partially developed acorns were collected on plots with trees that were heavily defoliated in Year 1. For plots with moderately defoliated or nondefoliated trees, the peak period of acorn drop was in the fall and a larger proportion of the acorn crop was collected on these plots in Year 1. Had data been collected over the entire growing season, the total number of acorns collected may have been more equal between plots in the differing defoliation levels in both Years 1 and 2.

While there were substantially more acorns collected from plots on which trees were heavily defoliated in Year 2 it is more likely that

Table 8 - Mean number of acorns collected by sample period, year, and defoliation level; separated by stage of development.

Sample Period	1/ Defoliation level	2/ # of Plots	Un- developed [. . . .]	Partially developed 1000 acorns/ha	Fully developed	Total
YEAR 1 (1985); Fall						
A) mid-Sept. '85 to late Nov. '85	none moderate heavy	6 4 2	23.3 42.5 0.0	5.3 7.2 0.0	210.3 213.8 3.1	238.9 263.5 3.1
YEAR 2 (1986); Spring, Fall, and Full Year 3/						
B) mid-March to mid-July '86	none heavy	4 2	118.8 295.0	7.3 0.0	2.2 0.0	128.3 295.0
C) mid-July to late Nov. '86	none heavy	4 2	55.8 207.5	17.7 5.3	194.4 11.4	268.0 224.2
D) mid-March to late Nov. '86	none heavy	4 2	174.6 502.5	25.0 5.3	196.7 11.4	396.2 519.3
YEAR 2 (1986); Fall						
E) mid-July '86 to late Nov. '86	none moderate heavy	4 2 4	55.8 15.0 170.7	17.7 25.0 3.0	194.4 132.6 6.3	268.0 172.7 180.0

1/ none = no discernible defoliation in the current year.
 moderate = visible defoliation ranging from 20 to 60%, trees did not re-foliate.
 heavy = defoliation greater than 60%, trees re-foliated in the same year.

2/ Plots sampled in each period:
 A) Plots 1,2,3,4,5,6,7,8,9,10,11,12
 B,C, and D) Plots 3,6,7,8,9,10
 E) Plots 3,6,7,8,9,10,13,14,15,18

3/ There were no moderately defoliated plots for sampling periods B,C, and D.

this difference is attributable to species differences rather than to defoliation. Plot 8 has a high percentage of black oak trees which appeared to have higher production of acorns than other trees in 1986. Trees in the red oak group that are heavily defoliated may also bias total acorn counts high because these trees carry both the current seasons acorns and the following seasons acorns at the same time.

In Year 2 data collection from moderately defoliated plots began in mid-July (Table 8, Sample Period E). Plots on which trees were moderately defoliated produced more partially developed acorns than plots on which trees were either nondefoliated or heavily defoliated. Intermediate amounts of fully developed acorns were produced and undeveloped acorn production was lower than for plots on which trees were either nondefoliated or heavily defoliated. More partially developed acorns may be produced by trees suffering moderate defoliation than nondefoliated trees because the stress of moderate defoliation induces trees to abort acorns prior to full development. Trees suffering heavy defoliation are stressed severely enough that acorns are induced to abort while undeveloped and few acorns remain to develop to partial or fully developed categories.

Fewer fully developed acorns were produced from trees that were moderately defoliated than from nondefoliated trees, presumably because the stress of moderate defoliation caused more acorns to abort while undeveloped or partially developed. Substantially more fully developed acorns were produced by trees that were moderately defoliated than by trees that were heavily defoliated, however. The difference between heavy and moderate defoliation in terms of the

stress level to the tree, and to the quantity of fully developed acorns produced is great.

The number of undeveloped acorns produced on plots on which trees were moderately defoliated was not an expected result and may reflect variability affected by the small sample size. Undeveloped acorns were collected from litter traps; the total area sampled is only 25% that of the area sampled by acorn traps. The anticipated result was for a stepwise increase in the number of undeveloped acorns collected from plots with increasing severity of defoliation. This trend may not have been reflected in the data because only two moderately defoliated plots were sampled. Heavy defoliation has a very obvious affect on increasing the number of undeveloped acorns.

In Year 1 approximately equal numbers of fully and partially developed acorns fell on plots that were either heavily or moderately defoliated for the September to November sample period. This seems to contradict the results in Year 2 which show fewer developed acorns produced on plots on which trees were moderately defoliated. The difference between the years can be accounted for by the species differences on the moderately defoliated plots each year and the average weight of acorns from the species involved. Elevation differences also affected the total number of acorns collected in Year 1 since plots were not established until early September and a portion of the acorn crop was missed, especially on the higher elevation plots.

The species on the plots which were modertely defoliated produced smaller acorns and may have produced more of them. Because of

elevation differences (204 m for moderately defoliated plots vs. 506 to 732 m for nondefoliated plots), the fully developed acorns dropped earlier on the nondefoliated plots, many before study plots were established. The apparent difference in Year 1 is possibly a result of a higher proportion of the total acorn crop being collected, and more acorns being produced overall on the plots with moderately defoliated trees. Comparing biomass (Table 9) shows that by weight the trend for greater acorn production on nondefoliated plots is consistent with the results of Year 2. The species composition of the plots used in Year 2 are much more similar between defoliation level groups than in Year 1, and trends in weight more closely parallel number of acorns (Tables 8 and 9) in Year 2.

A probable reason that most acorns dropped prior to full development following heavy defoliation is that trees abort them as they adjust to the stress of defoliation. Fruit crops are extremely expensive for trees to produce in terms of expenditure of photosynthates (Kozlowski 1971), and trees may abort acorns in favor of allocating resources to refoliation. In the case of trees suffering moderate defoliation (less than 60% defoliated) that are not induced to refoliate, photosynthates may be allocated to defense mechanisms and to maintaining carbohydrate reserves.

Aborted acorns on plots with trees suffering heavy defoliation began to fall sometime after peak defoliation in mid-June and the bulk of abortion was complete by mid-September. During this time trees may have adjusted to defoliation by abscising materials that did not help them photosynthesize, especially materials that are a drain to

Table 9 - Mean biomass of sound acorns, and of all developed acorns, by year and defoliation level; separated by stage of development.

Sample Period	1/ Defoliation level	2/ # of Plots	Partially Developed & Sound [- - - - -]	Fully Developed & Sound (kg/ha)	3/ Fully & Partially Developed
YEAR 1 (1985); Fall					
A) mid-Sept. to late Nov. '85	none	4	1.53	410.62	464.96
	moderate	2	1.67	177.90	242.29
	heavy	6	0.00	0.93	2.44
YEAR 2 (1986); Full Year					
4/					
B) mid-March to late Nov. '86	none	4	5.84	311.65	429.79
	heavy	2	0.15	5.75	9.95
YEAR 2 (1986); Fall					
C) mid-July to late Nov. '86	none	4	4.58	311.65	427.23
	moderate	2	0.88	178.49	271.34
	heavy	4	0.08	2.87	5.24

1/ none = no discernible defoliation in the current year.
 moderate = visible defoliation ranging from 20 to 60%, trees did not re-leaf.
 heavy = defoliation greater than 60%, trees re-leafed in the same year.

2/ Plots sampled in each period:

A) Plots 1,2,3,4,5,6,7,8,9,10,11,12

B) Plots 3,6,7,8,9,10

C) Plots 3,6,7,8,9,10,13,14,15,18

3/ Includes acorns in all viability categories: Sound, Unsound -insect damaged, Unsound-rotten, and Unsound-animal-damaged.

4/ There were no moderately defoliated plots for sampling period B.

photosynthates such as seed crops. It was noted earlier that collection of foliar material remained high for several weeks after peak defoliation on plots on which trees were heavily defoliated. This was attributed mostly to trees abscising leaf petioles from which the leaves had been consumed or cut off by gypsy moth larvae.

It is probable that the same levels of defoliation that trigger refoliation, (typically 60% and above, Wargo 1981), also trigger abortion of the acorn crop. This defoliation level may be a threshold above which a tree may abort almost its entire acorn crop, and below which a tree may carry a high proportion of its normal acorn crop. Attempts to try to relate the level of defoliation to acorn production beyond this would probably be of very limited use because abortion of undeveloped acorns is apparently related to stress. The stress level of a tree varies widely year to year, dependent on other conditions, especially microclimate.

There was no evidence that oak trees defoliated by the gypsy moth produced a "stress" crop of seed, and in fact an almost complete abortion of the seed crop was observed (Tables 8 and 9) in the year of defoliation. Limited data from nondefoliated plots that were defoliated the previous year (discussed later) show evidence that acorn production may remain low the year after defoliation. Stress seed crops have been shown to occur in some species prior to their death (Kozlowski 1971). Although many of the trees in the present study were weakened to the point that secondary organisms were able to invade and cause mortality in the year following defoliation, there was no increase in acorn production associated with an increased level

of stress on the tree. The prolonged drain of carbohydrate reserves associated with defoliation and subsequent refoliation may prevent trees from successfully forming acorns. Drain of reserves is one of the factors to which the failure of bumper acorn crops to occur in consecutive years is attributed (Kozlowski 1971). Drainage of reserves following defoliation may preclude development of acorn crops.

Hannah (1987) suggested that gypsy moth defoliation may affect mast production based on the observation that poor mast crop years occurred in years of gypsy moth defoliation. He speculated that it may be reduced because gypsy moths either ate the flowers or caused abortion of the seed crop. In the present study the most probable cause is stress to trees, resulting in abortion of acorns while they are still undeveloped, reducing the crop of developed acorns. Consumption of flowers by the gypsy moth is not apparently a factor in trees' failure to form a stress acorn crop following defoliation.

2. Acorn viability

In addition to moderate defoliation reducing the number of fully developed acorns, the number and percentage of unsound-rotten (non-viable with no obvious defect) acorns was higher than on nondefoliated plots. This trend was consistent in both years of the study for both partially developed and fully developed acorns (Tables 10 and 11). On heavily defoliated plots a high percentage of the few developed acorns produced were also rotten.

Some rotten acorns were holdovers from the previous year that were not abscised with the rest of the crop. Most, however, were acorns

Table 10 - Mean number of fully-developed acorns by sample period, year, and defoliation level; separated by viability category.

YEAR 1 (1985); Fall

Sample Period	1/		Sound	Insect Damage	Rotten	Animal Damage	Total
	Defoliation Level	# of Plots					
A) mid-Sept. to late Nov. '85	none	6	181.3	25.0	3.2	0.8	210.3
	moderate	4	140.0	54.7	17.5	1.6	213.8
	heavy	2	1.3	1.3	0.6	0.0	3.1

YEAR 2 (1986); Spring, Fall, and Full Year

3/

B) mid-March to mid-July '86	none	4	0.3	0.3	0.6	1.9	3.1
	heavy	2	0.0	0.0	0.0	0.0	1.3
C) mid-July to late Nov. '86	none	4	127.3	44.4	14.1	8.7	194.5
	heavy	2	4.0	2.5	4.2	0.7	11.4
D) mid-March to late Nov. '86	none	4	127.6	44.7	14.7	10.6	197.6
	heavy	2	4.0	2.5	4.2	0.7	6.4

YEAR 2 (1986); Fall

E) mid-July to late Nov.	none	4	127.3	44.4	14.1	8.7	194.5
	moderate	2	74.3	23.5	29.7	5.2	132.7
	heavy	4	2.0	1.3	2.7	0.4	6.4

1/ none = no discernible defoliation in the current year.
 moderate = visible defoliation ranging from 20 to 60%, trees did not re-foliate.
 heavy = defoliation greater than 60%, trees re-foliated in the same year.

2/ Plots sampled in each period:
 A) Plots 1,2,3,4,5,6,7,8,9,10,11,12
 B,C, and D) Plots 3,6,7,8,9,10
 E) Plots 3,6,7,8,9,10,13,14,15,18

3/ There were no moderately defoliated plots for sampling periods B,C, and D.

Table 11 - Mean number of partially-developed acorns by sample period, year, and defoliation level; separated by viability category.

Sample Period	YEAR 1 (1985); Fall						
	1/ Defoliation Level	2/ # of Plots	Sound	Insect Damage	Rotten	Animal Damage	Total
A) mid-Sept. to late Nov. '85	none	6	4.0	0.2	0.6	0.4	5.2
	moderate	4	4.7	0.0	1.9	0.6	7.2
	heavy	2	0.0	0.0	0.0	0.0	0.0

YEAR 2 (1986); Spring, Fall, and Full Year
3/

B) mid-March to mid-July '86	none	4	5.7	0.3	1.6	0.6	8.2
	heavy	2	0.0	0.0	0.0	0.0	0.0
C) mid-July to late Nov. '86	none	4	11.1	1.0	4.7	0.9	17.7
	heavy	2	0.8	1.7	2.0	0.8	5.3
D) mid-March to late Nov. '86	none	4	16.8	1.3	6.3	1.6	26.0
	heavy	2	0.8	1.7	2.0	0.8	5.3

YEAR 2 (1986); Fall

E) mid-July to late Nov.	none	4	11.1	1.0	4.7	0.9	17.6
	moderate	2	2.7	0.7	21.7	0.0	24.8
	heavy	4	0.4	0.8	1.3	0.4	2.9

- 1/ none = no discernible defoliation in the current year.
 moderate = visible defoliation ranging from 20 to 60%, trees did not re-foliate.
 heavy = defoliation greater than 60%, trees re-foliated in the same year.

- 2/ Plots sampled in each period:
 A) Plots 1,2,3,4,5,6,7,8,9,10,11,12
 B,C, and D) Plots 3,6,7,8,9,10
 E) Plots 3,6,7,8,9,10,13,14,15,18

- 3/ There were no moderately defoliated plots for sampling periods B,C, and D.

that developed in the season in which they fell. Acorns from the different years were not separated, but recorded in the year they dropped. On plots on which trees were heavily defoliated, collection of only a few residual acorns from the previous season's acorn crop could substantially bias the data on a proportional basis because so few developed acorns of any type were collected from heavily defoliated plots, making conclusions from these plots suspicious. On the plots suffering moderate defoliation more acorns are produced and holdover rotten acorns are a low percentage of the total and can not substantially bias results.

More rotten acorns may be produced by trees which were moderately or heavily defoliated because acorns may receive lower carbohydrate inputs as trees allocate reserves and adjust to the stress of defoliation. Cotyledonary materials may not build normally with reduced carbohydrate input. Acorns may also desiccate more readily following defoliation because of increased temperatures that result from greater solar insolation into the forest canopy. By either scenario, or in combination, the result is acorns that are unsound and have had most of the fruit desiccated or rotted away. Acorns that were non-viable because they were rotten dropped earlier in the season than sound acorns on average.

3. Acorn production the year after defoliation

There is a trend for nondefoliated plots with no previous defoliation history to have a higher total acorn crop than for plots not defoliated during the subject year that were heavily or moderately defoliated the previous year (Table 12). This could be a result of

Table 12 - Mean number of acorns from plots not defoliated in the sample year but with differing defoliation histories; separated by stage of development. Includes acorns in all viability categories (sound, unsound insect-damaged, unsound rotten, unsound animal-damaged).

YEAR 2 (1986); Spring, Fall, and Full Year

Sample Period	1/	2/	Partially Developed [- 1000 acorns/ha -]	Fully Developed
	Defoliation History Group	# of Plots		
A) mid-March to mid-July '86	1)none	4	7.3	2.2
	2)moderate	4	0.0	0.6
	3)heavy	1	0.0	0.0
B) mid-July to late Nov. '86	1)none	4	17.7	194.4
	2)moderate	4	17.5	14.8
	3)heavy	1	6.3	11.3
C) mid-March to late Nov. '86	1)none	4	25.0	196.7
	2)moderate	4	17.5	15.4
	3)heavy	1	6.3	11.3

1/ Defoliation history groups:

Group 1 has no previous defoliation (Plots 3,6,9,10)
 Group 2 had trees moderately defoliated in each of the 2 previous years (Plots 1,2,4,5).
 Group 3 had trees heavily defoliated the previous year (Plot 12).

2/ Undeveloped acorns are not reported because litter traps were removed from plots 1,2,4,5, and 12 in Year 2. Acorn traps were shown to be unreliable collectors of undeveloped acorns (Appendix B).

residual stress inducing trees to produce fewer flowers and abort developing acorns. Moderate defoliation has been shown to reduce tree diameter growth (Brown et al. 1979) because carbohydrate resources available to the tree are reduced by defoliation (Parker 1981), and because the tree is allocating resources to higher priority functions (Kramer and Kozlowski 1979). The present study indicates that in the year of defoliation, early abortion of a large portion of the acorn crop occurs, presumably a result of trees responding to physiological stress. This stress level may carry over to the next year and affect both flower production and acorn production in each of the development categories in the year following defoliation.

Comparisons between the groups of plots shown in Table 12 must be made cautiously, however, because they differ in a number of regards other than defoliation history. Many of the differences may affect acorn production including species, elevation, location, and weather.

The high acorn production in Year 1 on moderately defoliated plots appears to disagree with this trend for lower acorn production following defoliation. In fact it may not disagree. By weight, acorn production was lower on plots with trees that were moderately defoliated than would have been the case with no defoliation. It is possible that the acorn crop on moderately defoliated plots was reduced in Year 1 and that the lack of comparable plots with no defoliation precluded observation of this. It is also possible that two years of defoliation was enough to cause stress sufficient to severely affect the acorn crop while one was not. The substantial reduction in Year 2 may have been a response to two years of moderate

defoliation. The reduced acorn crop in Year 2 may also may be a reflection of a poor acorn crop year in the white oak group, and in scarlet oak. A combination of residual defoliation related effects decreasing acorn production, and a naturally poor acorn crop year may also have occurred.

V. SUMMARY AND CONCLUSIONS

There were no differences in the amount of foliar or woody annual biomass production following either heavy or moderate gypsy moth defoliation. Timing of foliar biomass input to the forest floor, however, was greatly affected by gypsy moth defoliation. Foliar biomass drop was very high on heavily defoliated plots immediately following gypsy moth defoliation, and was much lower than that of the nondefoliated plots in the fall. Plots with trees that were moderately defoliated were not monitored in the early summer of either year but had foliar drop that was intermediate to plots that had trees that were not defoliated and plots with trees that were heavily defoliated. Presumably moderately defoliated trees lost intermediate levels of foliar biomass to defoliation early in the season accounting for the difference. Woody biomass collection followed this pattern as well, but the differences were not as pronounced, probably because of the greater variability associated with drop of woody biomass and the lower overall biomass involved.

Forest floor depth did not decrease below those cited as minimum for successful germination of acorns following defoliation. Forest floor biomass also did not show defoliation related changes. To determine the overall effect of gypsy moth defoliation to the forest floor regeneration environment, however, other gypsy moth caused changes in forest floor conditions should be considered. Factors such as higher temperatures on the forest floor, the addition of nitrogen-rich frass, and probable increased moisture content of the soil caused by decreased transpiration may affect forest floor conditions. Effects

to forest floor biomass resulting from increased temperatures, nutrients and soil water contents resulting from defoliation probably take several years to fully manifest themselves, however. Because the net effect of defoliation related changes from these factors is unknown, the effect to the germination environment in gypsy moth defoliated stands could not be determined.

Gypsy moth defoliation did not affect the total number of acorns produced on an annual basis. However, the timing of acorn drop and the apportionment between development categories was substantially changed. Defoliation caused many acorns to abort before developing, decreasing the number of fully and partially developed acorns. The undeveloped acorns dropped shortly after defoliation, presumably as trees responded to physiological stress. Trees that were heavily defoliated and refoliated in July following defoliation aborted almost their entire acorn crop. Trees that were moderately defoliated produced more partially developed acorns than trees that were not defoliated or were heavily defoliated.

Defoliation also affected acorn viability. Significantly more rotten acorns were collected from trees on plots that were moderately defoliated than plots on which trees were not defoliated. Plots on which trees were heavily defoliated had a higher proportion of rotten acorns than plots with either moderately defoliated or nondefoliated trees.

There is no evidence that trees respond to defoliation by producing a bumper "stress" acorn crop. There is more evidence for the reverse situation, since total production of developed and undeveloped acorns

was lower on stands in which trees were previously defoliated by the gypsy moth than stands on which trees were never defoliated. Moderate and heavy gypsy moth defoliation, then, reduced the number of viable seeds available for either forest regeneration or wildlife use, in at least the year of defoliation and possibly for at least one year afterwards.

Future studies to better quantify the effect of gypsy moth defoliation on acorn crops in the year following defoliation could confirm some possible trends noted in this study. Because wildlife are so dependent on acorn crops, information on the length of time that defoliation may have an effect on acorn production would be useful to wildlife managers. Forest managers attempting to establish oak seedlings and develop advance regeneration to perpetuate the oak component of forest stands are also interested in knowing how long natural seed crops may be affected by gypsy moth defoliation.

VI - LITERATURE CITED

- Anderson, J. F., and S. W. Gould. 1974. Defoliation in Connecticut 1969-74. The Conn. Agr. Exp. Sta. Bull. 794.
- Arend, J. L., and L. W. Geysel. 1952. Less oak reproduction on better sites. Lake States For. Exp. Sta. Tech. Note 378, 1 p.
- Baker, W. L. 1941. Effects of gypsy moth defoliation on certain forest trees. J. For. 39:1017-1022.
- Barrett, L. I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, Quercus montana. Willd. Ecology 12:476-484.
- Beck, D. E. 1977. Twelve-year acorn yield in southern Appalachian oaks. USDA-FS Res. Note. SE-244, 8 p.
- Beck, D. E., and R. M. Hooper. 1986. Development of a Southern Appalachian hardwood stand after clearcutting. S. J. Appl. For. 10:168-172.
- Bess, H.A., S. H. Spurr, and E. W. Littlefield. 1947. Forest site conditions and the gypsy moth. Harvard Forest Bull. 22, 56 p.
- Braun, E. L. 1950. Deciduous forests of eastern North America. Country Life Press, Garden City, N.Y., 596 p.
- Bray, J. R. and E. Gorham. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2:101-158.
- Brown, J. H. Jr., D. B. Halliwell, and W. P. Gould. 1979. Gypsy moth defoliation: impact on Rhode Island forests. J. For. 77:30-32.
- Burns, P. Y., D. M. Christisen, and J. M. Nichols. 1954. Acorn production in the Missouri Ozarks. Missouri Agr. Expt. Sta. Bull. 611, 8 p.
- Campbell, R. W., and R. J. Sloan. 1977a. Natural regulation of innocuous gypsy moth populations. Env. Entomol. 6:315-322.
- Campbell, R. W., and R. J. Sloan. 1977b. Release of gypsy moth populations from innocuous levels. Env. Entomol. 6:323-330.
- Campbell, R. W., and R. J. Sloan. 1977c. Forest stand responses to defoliation by the gypsy moth. For. Sci. Monogr. 19, 34 p.
- Campbell, R. W. 1979. Gypsy moth: forest influence. USDA-FS Dep. Agric. Bull. 381, 27 p.

- Carlisle, A., A. H. F. Brown, and E. J. White. 1966. Litter fall, leaf production and the effects of defoliation by Tortrix viridana in a sessile oak (Quercus petraea) woodland. *J. Ecol.* 54:65-85.
- Carvell, K. L., and E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. *For. Sci.* 7:98-105.
- Cassman, K. G., and D. N. Munns. 1980. Nitrogen mineralization as affected by soil moisture, temperature, and depth. *Soil Sci. Soc. Am. J.* 44:1233-1237.
- Christisen, D. M., and W. H. Kearby. 1984. Mast measurement and production in Missouri (with special reference to acorns). Missouri Dept. of Cons. Terrestrial Series 13, 34 p.
- Clark, F. B., and R. F. Watt. 1971. Silvicultural methods for regenerating oaks. IN: Proc. oak symposium. USDA-FS, NE For. Exper. Sta., Morgantown, West Virginia, 16-20 August, p. 37-43.
- Collins, C. W. 1915. Dispersion of gipsy moth larvae by the wind. *USDA Bull.* 273, 23 p.
- Collins, S. 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. *Ecology* 42:836-838.
- Cote, W. A. III. 1976. The biology of the two-lined chestnut borer and its impact on defoliated oaks. Ph.D. Dissertation, State Univ. N.Y. Coll. Environ. Sci. For., Syracuse. (Abstract only).
- Cottam, C. A., L. Nelson, and T. E. Clarke. 1939. Notes on early winter food habits of the black bear in George Washington National Forest. *J. Mammal.* 20:310-314.
- Cowan, I. R. 1965. Transport of water in the soil-plant-atmosphere system. *J. Appl. Ecol.* 2:221-239.
- Crawley, M. J. 1985. Reduction of oak fecundity by small herbivore damage. *Nature* 314:163-164.
- Downs, A. A., and W. E. McQuilkin. 1944. Seed production of southern Appalachian oaks. *J. For.* 42: 913-920.
- Dunbar, D. M., and G. R. Stephens. 1975. Association of two-lined chestnut borer and shoe string fungus with mortality of defoliated oak in Connecticut. *For. Sci.* 21:169-174.
- Ehrenfield, J. G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. *Bull. Torrey Bot. Club.* 107:29-41.

- Federer, C. A. 1982. Subjectivity in the separation of organic horizons of the forest floor. *Soil Sci. Soc. of Am. J.* 46:1090-1093.
- Fedde, G. E. 1962. Elm spanworm, a pest of hardwood forests in the Southern Appalachians. *J. For.* 62:102-107.
- Fenneman, N. M. 1938. *Physiography of the eastern United States.* McGraw-Hill Book Co., New York, 714 p.
- Forbush, E. H. and C. H. Fernald. 1896. *The gypsy moth.* Wright and Potter, Boston, 495 p.
- Frank, L. O. 1982. Natural and artificial regeneration. IN: Proc. coping with the gypsy moth. Penn. State For. Issues Conf., Feb. 17-18, University Park, PA; p. 51-59.
- Gansner, D. A. 1985. Ten years after the gypsy moth and still no regeneration. *Penn. For.* 75:6,12.
- Gansner D .A., O. W. Herrick, M. S. DeBald, and R. E. Acciavatti. 1983. Changes in forest condition associated with gypsy moth. *J. For.* 81:155-157.
- Goodrum, P. D., V. H. Reid, and C. E. Boyd. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. *J. Wildl. Mgmt.* 35:520-532.
- Gosz, J. R. 1984. Biological factors influencing nutrient supply in forest soils. IN: *Nutrition of plantation forests.* Academic Press, London, p. 119-146.
- Gottschalk, K. W. 1982. Silvicultural alternatives for coping with the gypsy moth. IN: Proc. coping with the gypsy moth. Penn. State For. Issues Conf., Feb. 17-18, University Park, PA; p. 137-156.
- Gottschalk, K. W. 1983. Management strategies for successful regeneration: oak-hickory. IN: Proc. 1983 Penn. State For. Issues Conf., March 15-16, University Park, PA; p. 190-213.
- Gottschalk, K. W. 1984. Research on silvicultural options for the gypsy moth. IN: Proc. of the 1984 National Gypsy Moth Review. Charleston, West Virginia, Nov. 26-29, 1984, p. 96-98.
- Gottschalk, K. W. In press. Silvicultural guidelines for forest stands threatened by the gypsy moth. USDA-FS Gen. Tech. Rep. NE.
- Gottschalk, K. W., and L. P. Gibson. 1981. Study plan: Acorn production, predation, and infestation with insects as affected by overstory density and understory control. Study number: 4110-FS-NE-1152-114, 4110-FS-NE-2213-40. *NE For. Expt. Sta.*, Warren PA., 11 p.

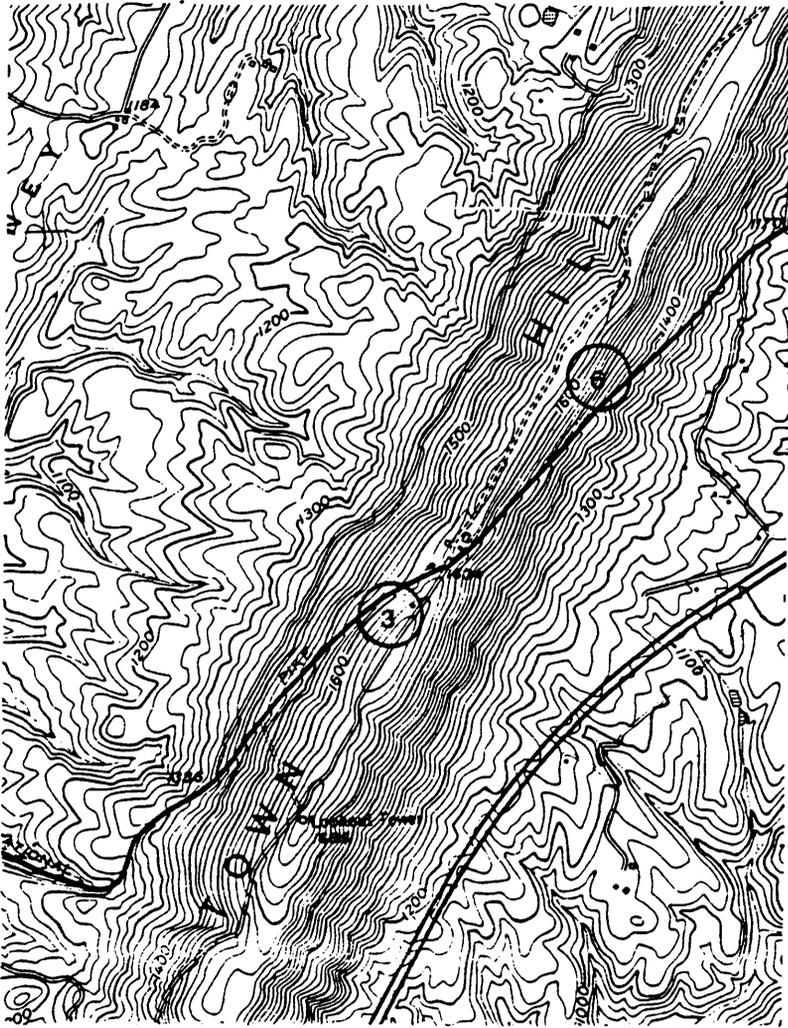
- Grace, J. R. 1986. The influence of gypsy moth on the composition and nutrient content of litter fall in a Pennsylvania oak forest. *For. Sci.* 32:855-870.
- Gysel, L. W. 1956. Measurement of acorn crops. *For. Sci.* 2:305-312.
- Gysel, L. W. 1958. Prediction of acorn crops. *For. Sci.* 4:239-245.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkamper, K. Cromack, Jr., and K. W. Cumins. 1986. The ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133-302.
- Hannah, P. R. 1987. Regeneration methods for oaks. *N. J. of Appl. For.* 4:97-101.
- Heichel, G. H., and N. C. Turner. 1976. Phenology and leaf growth of defoliated hardwood trees. IN: *Perspectives in forest entomology.* Academic Press, New York. p. 31-40
- Henry, V. G., and R. H. Conley. 1972. Fall foods of European wild hogs in the southern Appalachians. *J. Wildl. Mgmt.* 36:854-860.
- Hicks, R. R., Jr., and D. E. Fosbroke. 1987. Mortality following gypsy moth defoliation in the Central Appalachians. IN: *Proc. Sixth central hardwood forest conf., Knoxville, Tennessee,* p. 423-426.
- Hoover, M. D., and H. A. Lunt. 1952. A key for the classification of forest humus types. *Soil Sci. Soc. Am. Proc.* 16:368-370.
- Houston, D. R. 1979. Classifying forest susceptibility to gypsy moth defoliation. *USDA Ag. Hdbk.* 542, 24 p.
- Houston, D.R., and H. T. Valentine. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. *Can. J. For. Res.* 7:447-461.
- Kegg, J. D. 1971. The impact of gypsy moth: repeated defoliation of oak in New Jersey. *J. For.* 69:852-854.
- Kegg, J. D. 1973. Oak mortality caused by repeated gypsy moth defoliation of oak in New Jersey. *J. Econ. Entomol.* 66:629-641.
- Koroleff, A. 1954. Leaf litter as a killer. *J. For.* 52:178-182.
- Korschgen, L. J. 1962. Foods of Missouri deer, with some management implications. *J. Wildl. Mgmt.* 26:164-172.
- Korstian, C. F. 1927. Factors controlling the germination and early survival in oaks. *Yale Univ. School of For. Bull.* 19, 115 p.

- Kozlowski, T. T. 1971. Growth and Development of trees. Vol. 2. Academic Press, New York, 514 p.
- Kramer, P. J, and T. T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, Inc., New York, 811 p.
- Lay, D. W. 1965. Fruit utilization by deer in southern forests. J. Wildl. Mgmt. 29:370-375.
- Leonard, D. E. 1968. Effects of density of larvae on the biology of the gypsy moth Porthetria dispar. Ent. Exp. and Appl. 11:291-304.
- Leonard, D. E. 1971. Air-borne dispersal of larvae of the gypsy moth and its influence on concepts of control. J. Econ. Entomol. 64:638-641.
- Leonard, D. E. 1981. Bioecology of the gypsy moth. IN: The gypsy moth: Research towards integrated pest management. USDA-FS Tech. Bull. 1584. p. 9-23.
- Liming, F. G., and J. P. Johnston. 1944. Reproduction in oak-hickory forest stands of the Missouri Ozarks. J. For. 42:175-180.
- Liscinsky, S. 1985. Tree seed production. Pennsylvania Game News. 55:23-25.
- Marquis, D. A., P. L. Eckert, and B. A. Roach. 1976. Acorn weevils, rodents, and deer all contribute to oak-regeneration difficulties in Pennsylvania. USDA-FS Res. Paper NE-356, 5 p.
- Mason, C. J. and M. L. McManus. 1981. Larval dispersal of the gypsy moth. IN: The gypsy moth: Research towards integrated pest management. USDA-FS Tech. Bull. 1584. p. 161-202.
- Matschke, G. H. 1964. The influence of oak mast on European wild hog reproduction. IN: Proc. SE Assoc. Game and Fish Comm. Conf. 18:35-39.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. Science 190:515-522.
- McManus, M. L. and T. McIntyre. 1981. Introduction. IN: The gypsy moth: Research towards integrated pest management. USDA-FS Tech. Bull. 1584. p. 1-7.
- McQuilkin, R. A. 1975. Growth of four types of white oak reproduction after clearcutting in the Missouri Ozarks. USDA-FS Res. Paper NC-116, 5 p.
- Merrill, W. and E. B. Cowling. 1966. Role of nitrogen in wood deterioration: amounts and distribution in tree stems. Can. J. Bot. 44:1555-1580.

- Merz, R. W., and S. G. Boyce. 1956. Age of oak seedlings. *J. For.* 54:774-775.
- Minckler L. S. and C. E. Jensen. 1959. Reproduction of upland central hardwoods as affected by cutting, topography and litter depth. *J. For.* 57:424-428.
- Minott, C. W. and I. T. Guild. 1925. Some results of the defoliation of trees. *J. Econ. Entomol.* 18:345-348.
- Myers, S. A. 1978. Insect impact on acorn production in Missouri. Unpubl. Ph.D thesis, Univ. of Missouri-Columbia. 246 p.
- Nicholas, N. S. and P. S. White. 1984. Great Smoky Mountains National Park hard mast survey: an evaluation of the current survey, analysis of past data, and discussion of alternatives for future surveys. U. S. Department of the Interior, National Park Service, Research/Resources Management Report SER-68, 66 p.
- Nichols, J. O. 1961. The gypsy moth in Pennsylvania. PA Dept. Agric. Misc. Bull. 4404, 82 p.
- Nichols, J. O. 1968. Oak mortality in Pennsylvania; a ten year study. *J. For.* 66:681-694.
- Olson, D. F. and S. G. Boyce. 1971. Factors affecting acorn production and germination and early growth of seedlings and seedling sprouts. IN: Proc. oak symposium. USDA-FS, NE For. Exper. Sta., Morgantown, West Virginia, 16-20 August, p. 44-48.
- Parker, J. 1981. Individual tree relationships; Effects of defoliation on oak chemistry. IN: The Gypsy Moth: Research Towards Integrated Pest Management. USDA-FS Tech. Bull. 1584. p. 219-225.
- Pekins, P. J. and W. W. Mautz. 1987. Acorn usage by deer: significance of oak mnagement. *N. J. of Appl. For.* 4:124-128.
- Rafes, P. M. 1971. Pests and the damage which they cause to forests. IN: Productivity of forest ecosystems. Proc. Brussels Symp. UNESCO, Paris, p. 357-367.
- Rockwood, L. L. 1973. The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54:1363-1369.
- Ross, M. S., T. L. Sharik, and D. Wm. Smith. 1986. Oak regeneration after clear falling in Southwest Virginia. *For. Sci.* 32:157-169.
- SAS Institute Inc. 1985. SAS^R Users Guide: Statistics, Version 5 Edition. Gary, NC: SAS Institute Inc. 956 p.

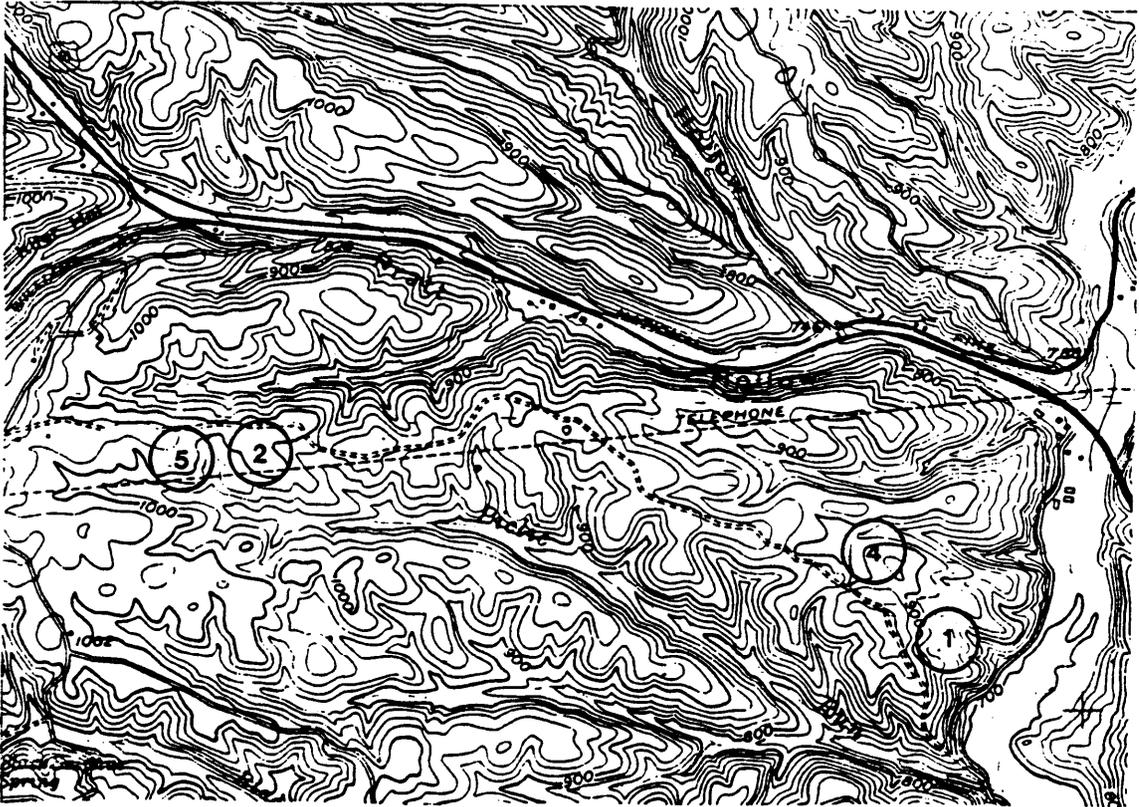
- Sander, I. L. 1979. Regenerating oaks with the shelterwood System. IN: Proc. 1979 John S. Wright For. Conf., Regenerating oaks in upland hardwood forests. Feb. 22-23, West Lafayette, Indiana, p. 54-60.
- Schnur, L. G. 1937. Yield, stand and volume tables for even-aged upland oak forests. USDA Tech. Bull. 560, 88 p.
- Sharp, W. M. and V.G. Sprague. 1967. Flowering and fruiting in the white oaks II. Pistillate flowering, acorn development, weather and yields. Ecology 48:243-251.
- Shaw, M. W. 1968. Factors affecting the natural regeneration of sessile oak (Quercus petraea) in North Wales: 1. A preliminary study of acorn production, viability and losses. J. Ecol. 56:565-583.
- Schowalter, T. D., W. W. Hargrove, and D. A. Crossley. 1986. Herbivory in forested ecosystems. Ann. Rev. Entomol. 31:177-196.
- Smith, H.R. 1985. Wildlife and the gypsy moth. Wildl. Soc. Bull. 13:166-174.
- Smith, D. Wm., and N. E. Linnartz. 1980. The southern hardwood region. IN: Regional Silviculture of the United States. John Wiley and Sons Inc., New York, p. 145-230.
- Stanford, G., M. H. Frere, and D. H. Schwaninger. 1973. Temperature coefficient of soil N mineralization. Soil Sci. 115:321-323.
- Stalter, R., and J. Serrao. 1983. The impact of defoliation by gypsy moth on the oak forest at Greenbrook Sanctuary, New Jersey. Bull. Torrey Bot. Club 110:526-529.
- Stephens, G. R. 1971. The relation of insect defoliation to mortality in Connecticut forests. Conn. Agric. Exp. Sta. Bull. 723, 16 p.
- Stephens, G. R. and D. E. Hill. 1971. Drainage, drought, defoliation, and death in unmanaged Connecticut forests. Conn. Agric. Exp. Sta. Bull. 718, 43 p.
- Stephens, G. R. 1981. Defoliation and mortality in Connecticut forests. Conn. Agric. Exp. Sta. Bull. 796, 13 p.
- Taylor, R. A. J. and D. Reling. 1986. Density/height profile and long-range dispersal of first-instar gypsy moth (Lepidoptera: Lymantriidae. Env. Entomol. 15:431-435.
- Torrent, J. A. 1956. Oak tortrix and its control in Spain. FAO Pl. Prot. Bull. 3:117-121.

- Tryon, E. H. and K. L. Carvell. 1958. Regeneration under oak stands. W. Va. Agric. Exp. Sta. Bull. 424T, 22 p.
- Turner, N. 1963. Effects of defoliation by the gypsy moth. Conn. Agric. Exp. Sta. Bull. 658, 30 p.
- US Dept. of Agriculture. 1974. Seeds of woody plants in the United States. Agric. Hndk. 450 USDA-FS, Washington D.C., p. 699-700.
- US Dept. of Commerce - National Oceanic and Atmospheric Administration. 1985. Climatological Summaries. IN: Climatology of the US no. 20. National Climatic Data Center, Asheville, North Carolina.
- Wargo, P. M. 1977. Armillaria mellea and Agrilus bilineatus and mortality of defoliated oak trees. For. Sci. 23:485-492.
- Wargo, P. M. 1981. Defoliation and tree growth. IN: The Gypsy Moth: Research Towards Integrated Pest Management. USDA-FS Tech. Bull. 1584, p. 225-240.
- Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press Inc., Orlando, Florida, 340 p.
- Watt, A. S. 1919. On the causes of failure of natural regeneration in British oak woods. J. Ecol. 7:173-203.
- Watt, R. F. 1979. The need for adequate advance regeneration in oak stands. IN: Proc. 1979 John S. Wright For. Conf., Regenerating oaks in upland hardwood forests. Feb. 22-23, West Lafayette, Indiana, p. 11-17.
- Weitzman, S., and G. R. Trimble Jr. 1957. Some natural factors that govern the management of oaks. USFS NE For. Expt. Sta. Paper. 88, 40 p.



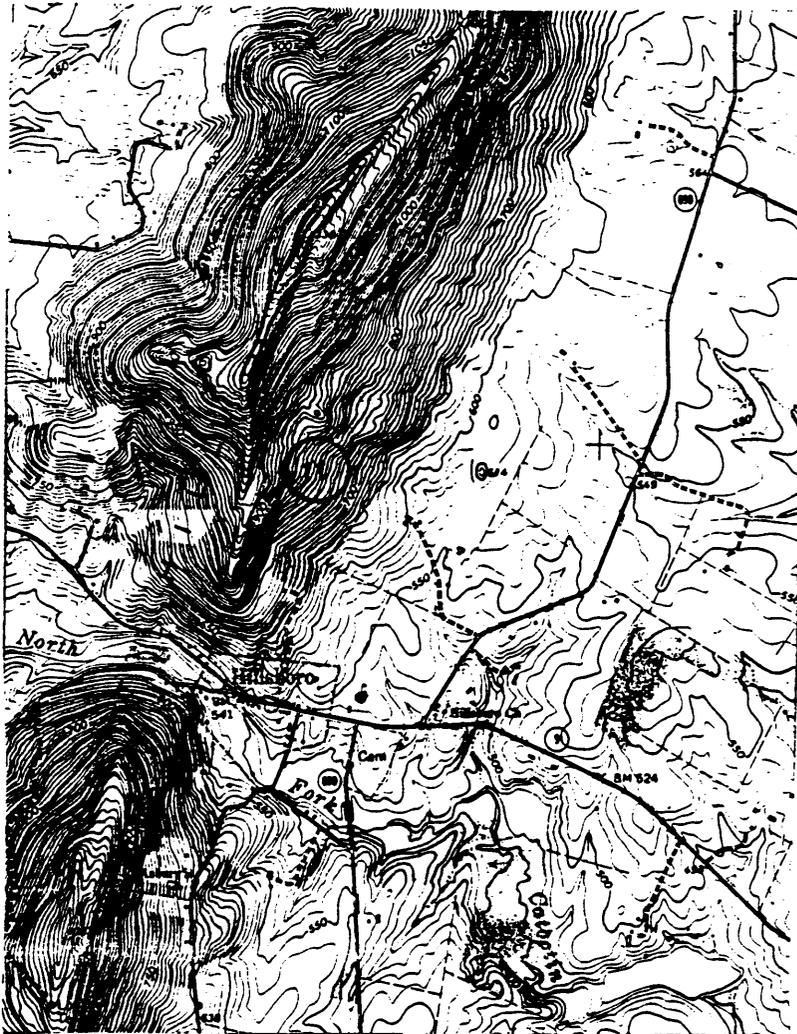
Appendix A.

Figure A1. Plots 3 and 6, high elevation Maryland plots, not defoliated in either 1985 or 1986, located in the Billmeyer Wildlife Management area, near Flintstone, Maryland.



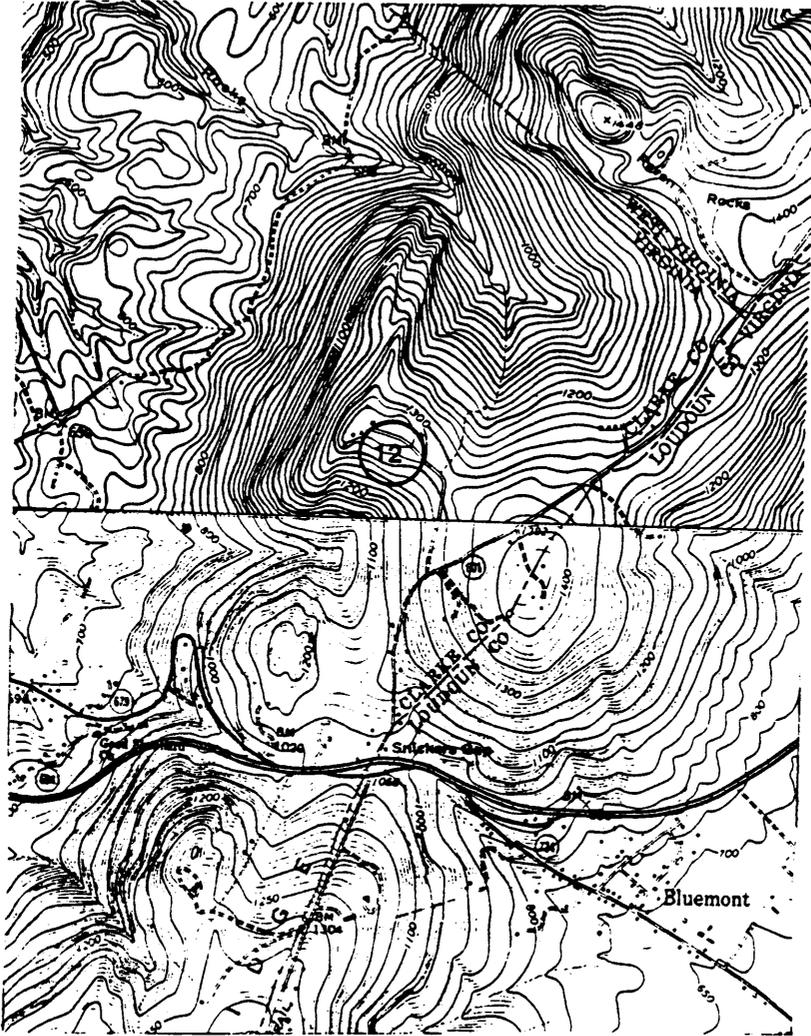
Appendix A.

Figure A2. Plots 1,2,4, and 5, low elvation Maryland plots, moderately defoliated in 1985 and not defoliated in 1986, located in the Green Ridge State Forest, near Flintstone, Maryland.



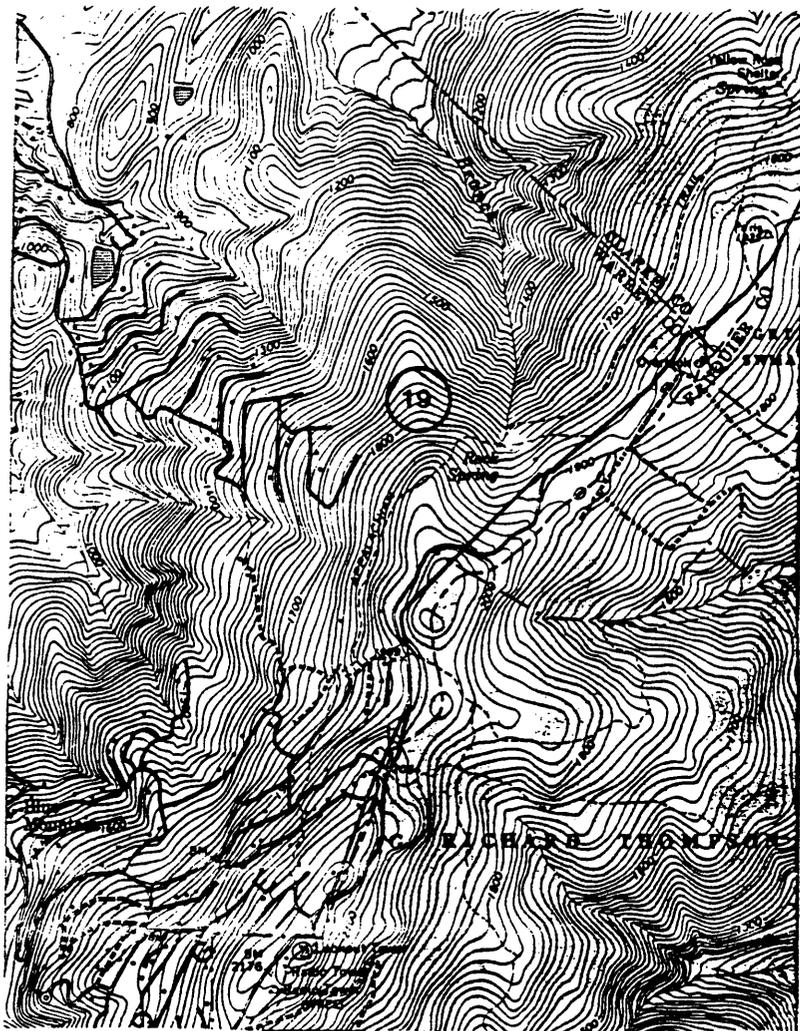
Appendix A.

Figure A3. Plot 11, heavily defoliated in 1985, equipment removed from plot in May of 1986, located on privately owned land north of Hillsboro, Virginia.



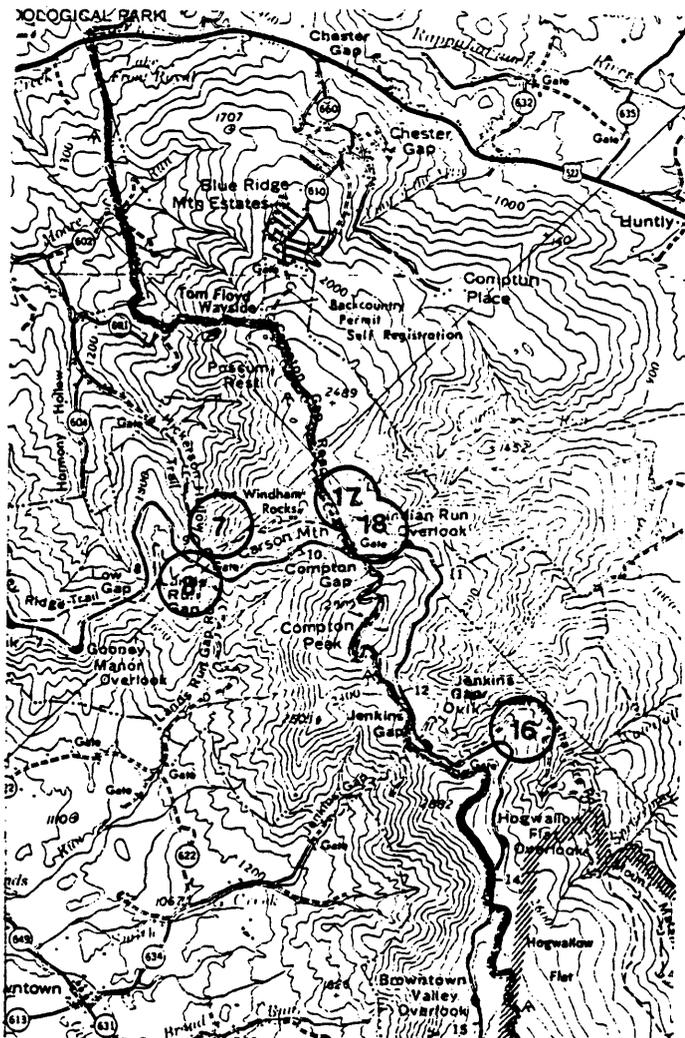
Appendix A.

Figure A4. Plot 12, heavily defoliated in 1985, not defoliated in 1986 (treated with Dimilin), located on privately owned land near Bluemont, Virginia.

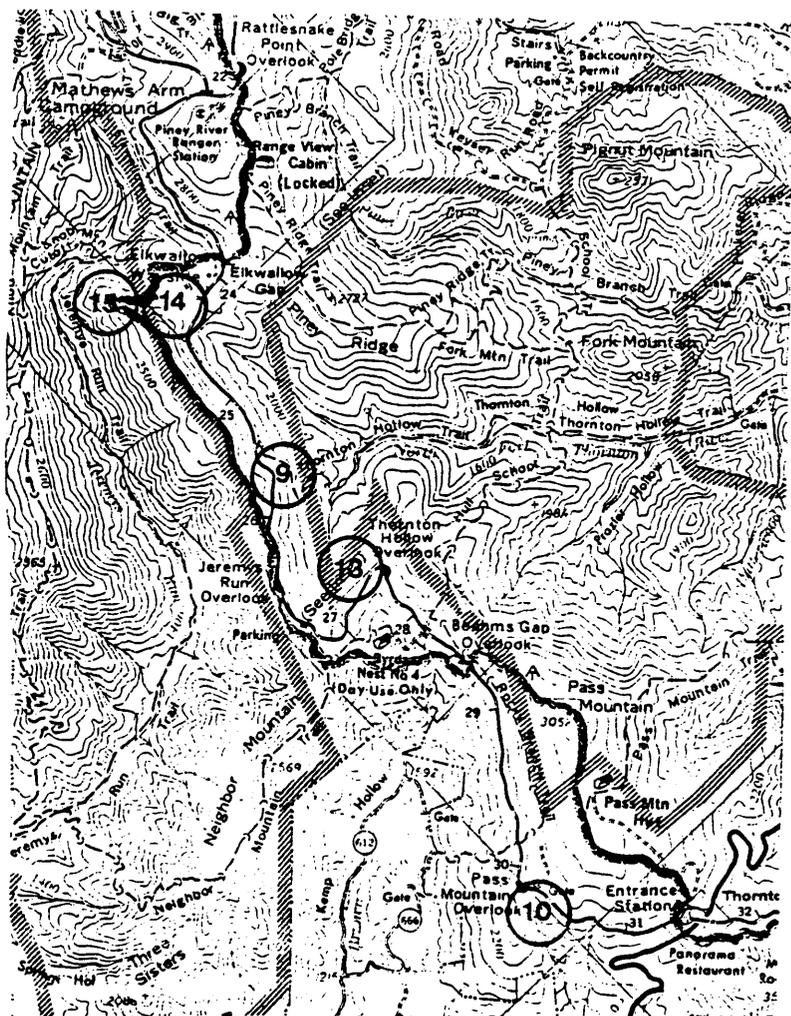


Appendix A.

Figure A5. Plot 19, established in May of 1986, heavily defoliated in 1986, located on privately owned land near Paris, Virginia.



Appendix A.
 Figure A6. Plots 7, 8, 16, 17, and 18, in the Shenandoah National Park. Plots 7 and 8 were not defoliated in 1985 and heavily defoliated in 1986. Plots 16, 17, and 18 were established in 1986; Plots 16 and 17 were heavily defoliated but had all acorn traps destroyed by bears for one collection period, Plot 18 was moderately defoliated.



Appendix A.
 Figure A7. Plots 9,10,13,14, and 15 in the Shenandoah National Park. Plots 9 and 10 were not defoliated in 1985 or 1986. Plots 13,14, and 15 were established in 1986; Plots 13 and 15 were heavily defoliated, Plot 14 was moderately defoliated.

Appendix B. Trap Comparison Study

1. Introduction and Justification

Litterfall is a commonly collected parameter of many ecological studies. Litter collection devices, however, are usually placed on the ground where they are subject to disturbance by animals and may be affected by wind blowing material from the forest floor into or out of them. The traps used to monitor acorn collection (Figure 3, and section III-D-2) are elevated above the ground and presumably are above the region which may be affected by wind shifting and depositing leaves from the forest floor. Because of this it was reasoned that acorn traps may more accurately measure litterfall than the more traditional ground-level litter traps.

The purpose of this side study was to determine the difference between the two trap types in terms of their rate of collection of acorns in all of the development and viability categories, foliar biomass, and woody biomass. The results were important to analysis of the data for this thesis and suggest trap designs most appropriate for future studies.

2. Analysis

a) acorn collection

The analysis of the effectiveness of each trap type for acorn collection was conducted using only Plots 3,6,7,8,9, and 10. These are the only plots that had both trap types on them for the duration of the study. Plots 3,6,9, and 10 received no defoliation; Plots 7 and 8 were not defoliated in 1985 and heavily defoliated in 1986. These six plots are similar in terms of stand composition with the

exception of Plot 8 which has a high proportion of black oak, while the other plots have mostly northern red oak and chestnut oak (Table 1). Other plots were excluded from the trap comparison analysis for one or more of the following reasons: 1) little or no acorn production occurred in many of the categories (development and viability) of interest and inclusion of these plots would add little to the analysis, 2) phenological differences (induced by differences in elevation), and late plot establishment resulted in different proportions of the 1985 acorn crop being missed between plots, 3) species composition differed substantially, 4) bears damaged all traps on some plots.

b) foliar and woody biomass collection

To analyze foliar and woody biomass collection between trap types, all plots which had both litter traps and acorn traps on them, and had at least four traps not damaged by bears or wind, were included to make trap comparisons on a sampling period basis. Comparisons on a yearly basis were made with plots that had both types of traps on them for the entire year and had a minimum of four undamaged traps at each sample collection time. The six plots established in 1986 were also analyzed on a yearly basis but separately from the plots established in 1985 because of the unequal sample collection period.

Selection of plots to incorporate into the analysis for foliar and woody biomass collection differed for the following reasons: 1) Only three plots (3,6, and 7) have two full years of foliar and woody biomass data because foliar and woody biomass were not recorded separately from litter traps for half of the plots following the first

sample collection. Some plots were also excluded because of damage to traps by bears and wind, and differing plot establishment dates, 2) foliar and woody biomass are collected with much greater consistency than are acorns which may range from no production to bumper crops for plots only miles or less apart, or on the same plot but in different years, as acorn crops sometimes will (Sharp and Sprague 1967). Leaves and twigs by contrast, are produced every year in relatively predictable amounts. Because of this it is less critical to have long-term data from the same plots to determine differing trap collection characteristics for foliar and woody biomass than for acorn collection, 3) leaves and twigs falling to the forest floor are also not as highly desirable to wildlife as are acorns (Pekins and Mautz 1987). Wildlife predation of foliar and woody biomass is not considered to be an important source of loss from either litter or acorn traps, and the rate of loss probably varies little year to year. By contrast, collection rates of acorns may be affected differently year to year depending on the size of the acorn crop and the intensity with which wildlife seek acorns. Little predation from traps may occur in years of bumper acorn crops while all acorns may be consumed in years of acorn crop failure.

Paired t-tests were used to determine the significance of differences between trap types for collection of foliar biomass, woody biomass, and acorns in each of the development and viability categories. The t-test used was determined by first testing for equality of variance ($\alpha=0.05$), then using a t-test appropriate to results of the equality of variance test. The individual trap was the

sampling unit for this analysis. P-values are reported for each comparison. Significant differences discussed in the Results section have a P-value less than 0.05 unless otherwise stated.

3. Results and Discussion

a) Acorn collection

Acorn traps contained fully-developed-and-sound acorns in significantly higher numbers per m^2 than did litter traps on a yearly basis (Table B1-a). Partially-developed-and-sound acorns were collected at nearly equal rates between trap types (Table B1-b) but there are far fewer acorns in this category and their smaller size may affect their desirability to animal predators and the likelihood that they may bounce out of traps (discussed later). Acorn traps collected acorns of all viability and development categories (sound, unsound insect-damaged, unsound rotten, unsound animal-damaged; fully and partially developed) at a significantly higher rate than litter traps (Table B1-e).

It is doubtful that the design of the acorn traps caused them to overestimate actual acorn drop; instead the litter traps probably underestimate drop. Possible explanations include: 1) acorns bounce out of litter traps, and 2) more acorns are removed by animal predation from litter traps.

The conclusion that the litter traps underestimate acorn collection is substantiated by observing the relationship between acorns and acorn caps (Table B2). Acorn caps, compared with the total number of developed acorns, showed that significantly more acorn caps than acorns were collected from litter traps for Year 1. The trend is

Appendix B.

Table B1 - Collection rates of different categories of acorns (number/m²) from acorn and litter traps, by year.

<u>1/ Year</u>	<u>acorn trap mean</u>	<u>litter trap mean</u>	<u># of acorn traps</u>	<u># of litter traps</u>	<u>standard deviation acorn traps</u>	<u>standard deviation litter traps</u>	<u>2/ P- value</u>
a) Sound-and-fully-developed acorns							
1	17.80	9.74	88	46	25.56	15.59	.03
2	9.65	2.17	69	46	18.21	8.93	.003
b) Sound-and-partially-developed acorns							
1	0.39	0.43	88	46	1.45	1.93	>.5
2	1.19	0.78	69	46	5.96	3.31	.33
c) Animal-damaged acorns							
1	0.14	1.57	88	46	0.51	3.15	.004
2	0.75	2.52	69	46	2.28	6.14	.08
d) Acorn caps							
1	22.33	26.43	88	46	30.50	32.66	>.5
2	16.64	19.48	69	46	31.49	36.94	>.5
e) All acorns (sound, unsound-insect-damaged, unsound-rotten, and unsound-animal-damaged; fully and partially developed).							
1	21.30	13.30	88	46	29.43	19.20	.03
2	16.58	8.70	69	46	28.46	16.15	.03
f) Insect-damaged acorns							
1	2.59	1.13	88	46	4.50	2.36	.002
2	3.44	0.96	69	46	6.41	2.11	.003
g) Rotten acorns							
1	0.39	0.43	88	46	1.00	1.52	>.5
2	1.54	2.26	69	46	2.95	4.54	.35
h) Partially-developed acorns							
1	0.52	0.52	88	46	1.54	2.47	>.5
2	1.86	1.48	69	46	3.34	3.23	>.5
i) Undeveloped acorns							
1	2.75	2.43	88	46	4.66	4.41	>.5
2	11.45	26.26	69	46	18.90	49.41	.06

1/ Year 1 = mid-September to late November, 1985.

Year 2 = mid-March to late November, 1986.

2/ P-values were determined using paired t-tests; equality of variance was tested for (alpha=.05) and the t-test appropriate to the equality of variance test used.

Appendix B.

Table B2 - Acorn and acorn cap collections (number/m²) from acorn and litter traps, by year. "Acorn" includes all developed acorns, sound and unsound.

1) Acorn traps						
Sample Period	acorn mean	cap mean	# of traps	standard deviation acorn counts	standard deviation cap counts	1/p-value
mid-Sept. to late Nov. '85	21.30	22.33	88	29.43	30.50	>0.5
mid-March to late Nov. '86	16.58	16.64	69	28.46	31.49	>0.5
2) Litter traps						
Sample Period	acorn mean	cap mean	# of traps	standard deviation acorn counts	standard deviation cap counts	1/p-value
mid-Sept. to late Nov. '85	13.30	26.43	46	19.20	32.66	.03
mid-March to late Nov. '86	8.70	19.48	46	16.15	36.94	.07

1/ P-values were determined using paired t-tests; equality of variance was tested for ($\alpha=.05$) and the t-test appropriate to the equality of variance test used.

similar in year 2 as well, though statistical significance was not attained. Although the number of acorn caps collected is similar (there are slightly more in the acorn traps) for the two trap types, the acorn traps accumulated almost twice as many acorns as the litter traps (Table B2). The ratio of acorns to acorn caps is almost 1.0 for the acorn traps, but is only 0.5 for the litter traps. The low ratio of acorns to acorn caps suggests that, while similar numbers of acorns fell in each trap, many of the acorns in the litter traps bounced out or were removed by predators. The higher rates of animal-damaged acorns in litter traps (Table B1-c) further substantiate this conclusion.

Acorn caps have no nutritive value for wildlife and thus are not likely to be removed by animals. Acorn caps are also light and not likely to bounce out of traps of either type. One of the suspected sources of loss, animal predation, is shown to occur at significantly higher rates from litter traps than from acorn traps (Table B1-c) for each collection period. It is likely that complete removal of acorns from litter traps by animals also occurs. Much of the animal damage found occurring in acorn traps probably occurred as a result of animals cutting acorns while still in the tree which then drop into the traps, rather than damage occurring to acorns in the acorn traps.

More acorn caps were collected from litter traps than from acorn traps for each time period of comparison (Table B1-d). This may be because acorn caps blow into litter traps along with leaf litter. Input of loose acorn caps to litter traps without corresponding input of acorns would cause the collection efficiency of litter traps for

acorns to appear worse than the actual case. The higher input of acorn caps accounts for only a small portion of the difference between acorn numbers and acorn cap numbers (Table B2). Greater input of acorn caps can account for only a small portion of the difference in the ratio of caps to acorns observed between acorn and litter traps. Addition of acorn caps to litter traps only shows that the ratio of acorns to acorn cap collection from litter traps may be reduced by cap blow-in, but it does not explain any of the difference in number of acorns collected. It does not explain enough of the difference between acorns and acorn caps to make litter traps appear to be a useful tool for acorn collection.

Another factor likely to result in fewer acorns collected from litter traps is acorns bouncing out of traps. This appears to occur at disproportionately higher rates from litter traps than from acorn traps. Neither type is likely to over-collect acorns by having acorns bounce into them. Acorns may bounce out of traps of either type, however. No tests were conducted to compare the rates at which acorns bounce out of each trap type. Because litter traps are shallow and have a taut aluminum bottom, while acorn traps have a deep collection volume and a bottom that will "give" somewhat on impact, it is likely that acorns bounce out of litter traps at much greater rates than from acorn traps.

Insect-damaged acorns (Table B1-f) follow the same trend as the sound, and sound-and-fully-developed acorns; significantly greater numbers were collected from acorn traps for each sample period. Insect-damaged acorns are very similar to sound acorns in two

important regards: 1) they are firm and have a high mass and are thus likely to bounce as easily as a sound acorn, 2) insect-damaged acorns have value to wildlife. Except in extreme cases insect-damaged acorns have cotyledonary material not damaged by an insect predator that is of use to wildlife. Insect-damaged acorns will frequently sprout (Korstian, 1927), as evidence of the presence of a food source for wildlife in acorns.

Rotten acorns (Table B1-g) have characteristics that contrast with sound acorns. Rotten acorns have no value to wildlife as a food source, so removal by wildlife should be low. They also have a comparatively low mass and are sometimes "spongy" so they are unlikely to bounce out of traps. No differences between trap types in the numbers of rotten acorns collected on a yearly or combined basis was observed.

There is no difference in the number of partially developed acorns collected for any time period (Table B1-h). Partially developed acorns are typically smaller than fully developed acorns and therefore bounce less readily. They are large enough, however, that it is very unlikely that they may be lost out of the water drainage holes in the bottom of acorn traps. Because of their lower biomass they probably have less value to wildlife as a food source than fully developed acorns and may be overlooked by animal predators.

Undeveloped acorns (Table B1-i) were collected at similar rates for the two trap types in 1985. In 1986, however, the litter traps collected undeveloped acorns at a much greater rate. This may have been partially caused by the missed data collection period early in

the growing season in 1985. A large proportion of the undeveloped acorns that fall each year fall early in the season. In 1986, undeveloped acorns began falling as early as mid-June. In 1985 many may have fallen before the study plots were established.

The difference in collection rates of undeveloped acorns between the two trap types in 1985 and 1986 may be a result of two factors: 1) undeveloped acorns falling early in the year may be smaller than those falling later in the season. Some undeveloped acorns may have slipped through the water drainage holes in the bottom of acorn traps before leaves or other material blocked the holes, 2) Many of the acorns classified as undeveloped in 1985 were attached to acorn caps: Table B1-d shows that caps are collected at approximately equal rates between the two trap types. Undeveloped acorns attached to caps are not susceptible to loss through drainage holes in the bottom of traps. The mesh on the aluminum screens in litter traps is too small for undeveloped acorns to pass through. Loss of undeveloped acorns to wildlife probably does not occur because they have little food value. Undeveloped acorns probably do not bounce out of either type of trap because of their light weight.

The undeveloped acorns dropping in 1986 were mostly separate entities (not attached to caps) and much smaller than caps. Most of the undeveloped acorns in 1986 fell early in the summer, while the equivalent collection period was missed in 1985 due to the late plot establishment date. The undeveloped acorns in 1986 may have slipped through the drainage holes in acorn traps resulting in a lower collection rate from acorn traps over a full season. The different

characteristics of undeveloped acorns in each year of the study and the differing time periods of collection probably explain the differing collection rates of undeveloped acorns from each trap type in each year. Over a full year litter traps are presumed to be better collectors of undeveloped acorns. Only litter traps were used to analyze the effects of gypsy moth defoliation on production of undeveloped acorns.

b) Foliar and woody biomass collection

Foliar biomass collected from litter traps was greater than from acorn traps for every time period of comparison used, either by sample collection date or sample year, but not all differences were significant (Table B3). Greater foliar biomass collection from litter traps was probably caused by more leaves blowing in from the surrounding forest floor than blowing out. Litter traps were placed on the ground and have walls only 10 cm high. With this placement and design, leaves from the forest floor around the traps, as well as falling leaves from above the traps, are able to blow in. Acorn traps, because of their height of placement off the ground, do not receive input of leaves blown from the forest floor. Acorn traps, then, are a better tool to measure leaf fall but are not appropriate for measuring accumulation in areas such as clearcuts or openings. Litter traps are a poor tool to measure leaf fall and leaf accumulation because of their tendency to over-estimate each of these.

Woody biomass did not differ significantly between trap types on any of the sample collection dates or on a yearly basis (Table B4), and there is no consistent trend reflecting a greater woody biomass

Appendix B.

Table B3 - Mean foliar biomass collection (kg/ha) from litter and acorn traps, by sample period. Includes all materials produced and aborted on an annual basis (excluding fruits) such as flower parts, leaves, frass, and leaf petioles.

Sample Period	trap type	mean biomass	# of traps	standard deviation	coefficient of variation	1/ p-value
mid-Sept. to mid-Oct. '85	acorn litter	376.24 470.39	112 44	196.93 193.57	52 41	.008
mid-Oct. to late-Nov. '85	acorn litter	2121.84 2556.39	183 93	878.75 1059.91	41 42	.0008
mid-March to mid-June '86	acorn litter	482.33 1079.13	142 85	575.33 1658.20	119 154	.0018
mid-June to mid-July '86	acorn litter	48.85 68.27	88 48	52.65 111.10	108 163	.2576
mid-July to mid-Sept. '86	acorn litter	157.55 164.59	174 96	93.57 81.43	59 49	.543
mid-Sept. to mid-Oct. '86	acorn litter	545.49 625.19	161 85	362.85 441.67	67 71	.1553
mid-Oct. to late-Nov. '86	acorn litter	1829.94 2226.41	125 74	814.42 912.70	45 41	.0018

Sample Period	trap type	mean biomass	# of traps	standard deviation	coefficient of variation	1/ p-value
mid-Sept. to late-Nov. '85	acorn litter	2325.35 2522.84	95 33	599.09 775.01	24 31	.1848
mid-March to late-Nov. '86	acorn litter	3564.77 5177.34	57 46	829.47 1762.57	23 34	.0001
mid-July to late-Nov. '86	acorn litter	2049.76 2379.89	40 38	960.58 1030.58	47 41	.1472

1/ P-values were determined using paired t-tests; equality of variance was tested for ($\alpha=0.05$) and the t-test appropriate to the equality of variance test used.

Appendix B.

Table B4 - Mean woody biomass collection (kg/ha) from litter and acorn traps, by sample period. Includes all materials produced over more than one growing season (excluding fruits).

Sample Period	trap type	mean biomass	# of traps	standard deviation	coefficient of variation	1/ p-value
mid-Sept. to mid-Oct. '85	acorn litter	45.23 75.56	112 45	58.78 140.14	130 185	.1668
mid-Oct. to late-Nov. '85	acorn litter	221.76 181.20	184 94	452.24 227.14	204 125	.3204
mid-March to mid-June '86	acorn litter	124.07 270.43	143 85	272.26 270.41	219 200	.7604
mid-June to mid-July '86	acorn litter	57.39 88.37	88 48	129.29 210.91	225 239	.4139
mid-July to mid-Sept. '86	acorn litter	89.50 120.59	174 96	156.69 415.99	175 345	.4827
mid-Sept. to mid-Oct. '86	acorn litter	102.89 128.55	161 85	174.72 305.13	170 237	.4756
mid-Oct. to late-Nov. '86	acorn litter	86.76 148.46	125 74	210.83 488.81	243 329	.3056
mid-Sept. to late-Nov. '85	acorn litter	252.49 335.14	95 35	495.17 332.24	196 96	.2700
mid-March to late-Nov. '86	acorn litter	423.85 686.79	57 46	485.49 1041.88	196 152	.1196
mid-July to late-Nov. '86	acorn litter	300.25 239.57	40 38	344.81 184.21	115 77	.3330

1/ P-values were determined using paired t-tests; equality of variance was tested for ($\alpha=0.05$) and the t-test appropriate to the equality of variance test used.

collection rate from one trap type over the other. Twigs (which form the majority of woody biomass) have a much greater mass than do leaves and are not easily blown into or out of traps. The elongated configuration of twigs, and somewhat lower mass as compared to acorns, makes twigs less likely to bounce out of traps than acorns.

The variation of foliar and woody biomass measurements is high. There is no obvious trend for greater variability from either trap type for leaf or twig weights when trap size is accounted for. The coefficient of variation for foliar and woody biomass differs little between trap types and has no obvious trend (Tables B3 and B4). Variation in the amount of woody biomass collected was great for both trap types, even though woody material exceeding 2.5 cm diameter was excluded.

4. Conclusions and Summary

Acorn traps were determined to be a better tool for collecting fully and partially developed acorns, and foliar biomass than litter traps. No differences were found between trap types in the collection of woody biomass. Litter traps were determined to be better collectors of undeveloped acorns.

Evidence suggested that litter traps underestimated acorn production due to animal predation and acorns bouncing out. Few animal damaged acorns were found in acorn traps and there were nearly as many acorns as acorn caps collected. Undeveloped acorns, however, may have been lost through the water drainage holes in the bottom of acorn traps.

Foliar biomass collected in acorn traps was consistently less than that in litter traps. Since acorn traps were up off the ground, they

were presumably less affected by wind blowing materials in, and it was presumed that acorn traps more accurately reflect litterfall. Litter traps were not used in analysis of foliar or woody biomass, or the number of partially or fully developed acorns, because of the evidence that they are substantially biased by wind, animal predation, and subject to having acorns bounce out.

Appendix C. Effects of Defoliation on Forest Floor Depth

1. Introduction and Justification

Forest floor depth is a commonly measured stand attribute in many research projects, and has been identified as a factor of critical importance to the successful germination of acorns (Korstian 1927). Forest litter protects acorns from desiccation, and provides a surface to facilitate root penetration as acorns develop into seedlings. Depth is often an unreliable measure to obtain, however, because it is subject to a great deal of observer bias (Federer 1982), and is a highly variable measure. Where the interest of research is to relate the forest floor characteristics to processes such as nutrient transfer or other measure more closely related to forest floor biomass, depth measurements are likely to have little meaning because consistent relationships between depth and biomass have never been established (James E. Johnson, Assistant Professor-Silviculture, University of Wisconsin - Stevens Point, Personal Communication 1985, and Appendix D).

Forest floor biomass is a better measure of forest floor conditions because it is less affected by observer bias and does not rely on unknown relationships between depth and biomass to have meaning. Because forest floor depths never went below those identified as critical for the germination environment, both biomass and depth were collected, and depth measurements have the problems cited above, only forest floor biomass was reported in the main text.

2. Analysis

Forest floor depth was analyzed by looking at data graphically and

observing trends. Multiple Range tests (Tukey-Kramer), and t-tests showed significant differences in forest floor depth by defoliation level, but interpretation of data revealed that the differences observed were more likely attributable to site quality differences between stands than to defoliation.

3. Results and Discussion

Forest floor depth was not shown to be either reduced or increased following gypsy moth defoliation. On Plots 7, 8, 9, and 10 forest floor depth was collected in both Year 1 and Year 2. These plots are in close proximity to each other in the SNP and represent the best data set available in terms of length of data collection and similarity of study areas. Mean forest floor depths from these plots are presented in Table C1 and Figure C1, by season.

All plots showed a reduction in forest floor depth in the second year of the study. There was no greater decrease in depth on the defoliated plots than on plots which were not defoliated. Table C2 gives mean depth by season for all plots. These data show high variability for most plots. It is possible that the consistently lower depths in the second year of the study are related to problems with observer bias. Numerous individuals were involved in collection of this measure and may have recorded it differently. It is also possible that the drought, which was more severe in the second year of the study than the first, may have had some affect on decreasing leaf fall. Depth would be more affected by drought than a measure of total biomass which may explain why a similar trend was not observed for biomass.

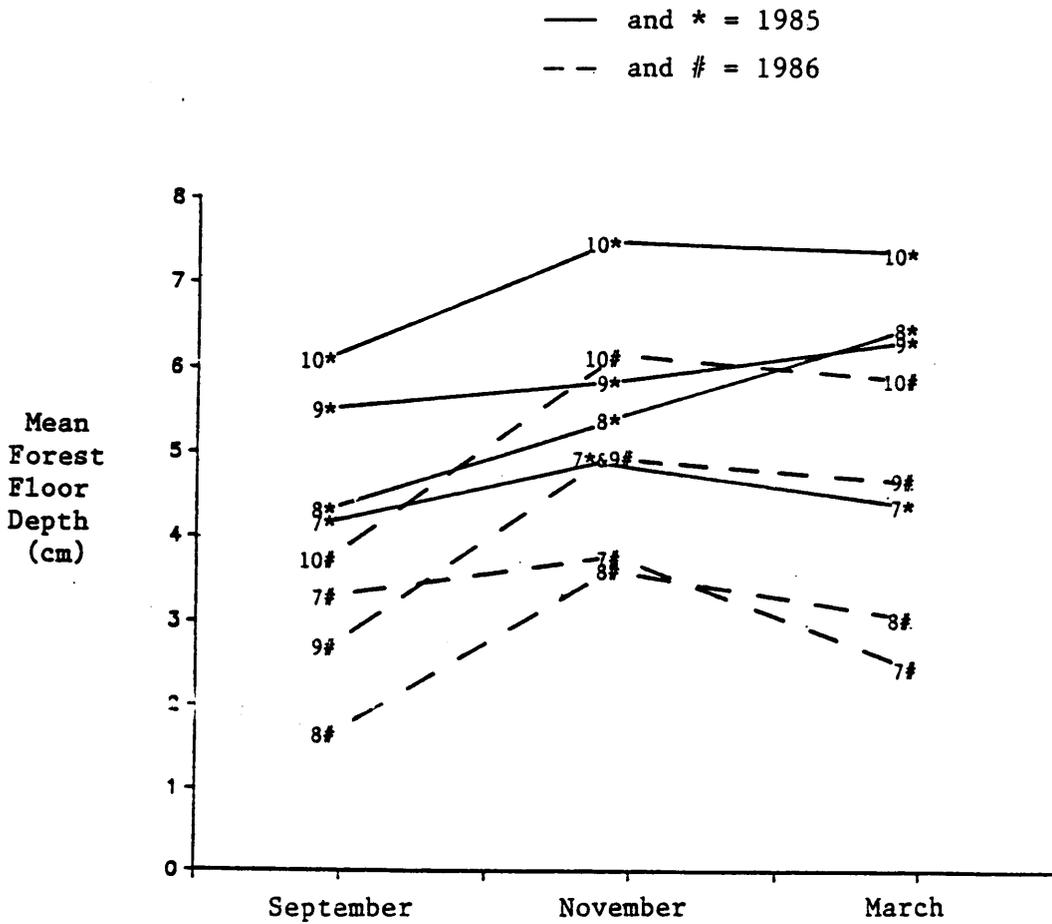
APPENDIX C.

Table C1 - Mean forest floor depth (cm) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.

1/ Plot #	2/ September		November		March	
	1985	1986	1985	1986	1986	1987
7	4.1	3.2	5.0	3.9	4.4	2.5
8	4.3	1.6	5.4	3.6	6.4	3.0
9	5.4	2.7	5.8	5.0	6.1	4.8
10	6.1	3.7	7.6	6.1	7.3	5.7

1/ Plots 7 and 8 were not defoliated in 1985 and heavily defoliated in 1986; Plots 9 and 10 were not defoliated in 1985 or 1986.

2/ In 1985, data was collected in early October, in 1986 data was collected in late September. The collection time was before substantial leaf fall occurred on nondefoliated plots (normal seasonal leaf fall) each year.



Appendix C.
 Figure C1. Mean forest floor depth (cm) of plots in the Shenandoah National Park from which data was collected in both 1985 and 1986.

APPENDIX C.

Table C2 - Mean forest floor depth (cm) by sample collection trip # (season), and plot. An "*" is used where depth was not measured on the plot for the given sample trip.

Plot #	-- 1985 --		-- 1986 --				-1987-
	Trip 1 Oct.	Trip 2 Nov.	Trip 3 March	Trip 4 June	Trip 5 Sept.	Trip 6 Nov.	Trip 7 March
1	6.1	4.0	4.8	2.7	*	*	*
2	6.4	4.3	4.8	4.0	*	*	*
3	6.5	5.7	7.5	6.2	4.5	4.7	4.0
4	5.2	3.2	4.5	4.1	*	*	*
5	5.4	3.7	3.8	3.6	*	*	*
6	6.2	5.7	4.9	4.4	2.5	4.2	5.4
7	4.1	5.0	4.4	4.3	3.2	3.9	2.5
8	4.3	5.4	6.4	3.7	1.6	3.6	3.0
9	5.4	5.8	6.1	5.1	2.7	5.0	4.8
10	6.1	7.6	7.3	5.3	3.7	6.1	5.7
11	4.9	4.4	5.3	*	*	*	*
12	3.4	4.5	4.9	3.2	*	*	*
13	*	*	*	*	4.9	5.1	4.8
14	*	*	*	*	3.4	5.7	3.4
15	*	*	*	*	3.4	5.7	3.5
16	*	*	*	*	4.0	4.3	3.5
17	*	*	*	*	1.9	2.1	2.6
18	*	*	*	*	3.3	4.5	3.2
19	*	*	*	3.6	*	*	*

In Table C2, plots with generally lesser or greater depths reflect the site quality of the plot. Shallow forest floor organic layers are typically found on higher quality sites. The trends for forest floor depths for each plot were similar to those observed for forest floor biomass (Table 7).

Forest floor depth was not shown to be affected by the defoliation level experienced by the trees on the plot. The problems cited in consistent measurement of depth, and the uncertainty of the affect of weather year to year may have precluded showing an affect that in fact exists, however.

4. Summary and Conclusions

Forest floor depth did not decrease below those cited as minimum for successful germination of acorns. This may be beacuse of problems in measurement, however, forest floor biomass, which is probably a more reliable measure of forest floor characteristics also did not show defoliation related changes.

While forest floor depth is an important factor in the forest floor regeneration environment other gypsy moth caused changes in which affect forest floor conditions should be considered. Factors such as higher temperatures on the forest floor, and the changing physical characteristics of leaves may be indirect affects of defoliation. Because the affect of these factors is unknown, the affect to the germination environment in gypsy moth defoliated stands can not be determined from the present data.

Appendix D. Forest Floor Depth vs. Biomass Correlation

1. Introduction and Justification

Forest floor biomass is a commonly reported parameter in many studies. It is used to characterize study site attributes and is often a principal focus of research. To measure biomass directly is time consuming and requires allocation of resources to collection, transport, storage, drying, and weighing of samples. Measuring forest floor depth, conversely, is a quick and easy measure which may be recorded on the site. If forest floor depth could be used to reliably estimate forest floor biomass, time and resources could be conserved or reallocated in many studies. This purpose of this study was to determine the relationship between forest floor depth and biomass. The principal goal was to determine whether forest floor depth may be used to reliably estimate forest floor biomass. Factors that affect the relationship between forest floor depth and biomass were also determined.

2. Analysis

Forest floor depth and biomass measurements were obtained as discussed in the Methods and Materials section of the main text of this thesis. To determine the relationship between forest floor biomass and forest floor depth the natural logarithm (\ln) of forest floor biomass was regressed against the \ln of forest floor depth. Total forest floor biomass was used for this analysis (sum of the "foliar", "woody", and "acorn" components). The \ln was used because there was heteroscedasticity of variance. The model fit was:

$$\ln(\text{biomass}) = A + B_1 * \ln(\text{depth}).$$

Residual values from this equation were fitted against dummy variables for plot, season, and defoliation level to determine the effect of these variables on the relationship between litter depth and biomass. The model used was:

$$\begin{aligned} \text{Residual} &= \ln(\text{biomass}) - [(A + B_1 * \ln(\text{depth})] \\ &= A + B_1' * \text{Dummy Season}(1) + \dots + B_6' * \text{Dummy Season}(6) \\ &\quad + B_7' * \text{Dummy Defoliation Level}(1) + \dots + B_8' * \\ &\quad \text{Dummy Defoliation Level}(2) + B_9' * \text{Dummy Plot}(1) + \dots \\ &\quad \dots + B_{26}' * \text{Dummy Plot}(18). \end{aligned}$$

3. Results and Discussion

The relationship between depth and biomass of the forest floor was significant, but the correlation was low ($R^2=0.149$). Season, defoliation level, and plot were all significant factors in the model fit on the residuals of the biomass/depth model. Incorporating these factors explained only a little more variability than when only depth and biomass were used, though ($R^2 = .272$).

Regression of the dummy variables on the residuals yielded coefficients which may be useful for describing variable effects. Where estimators are negative it indicates that the ratio of depth per unit of biomass is greater for that value (either plot, season, or defoliation level) than for other values in the same category. The

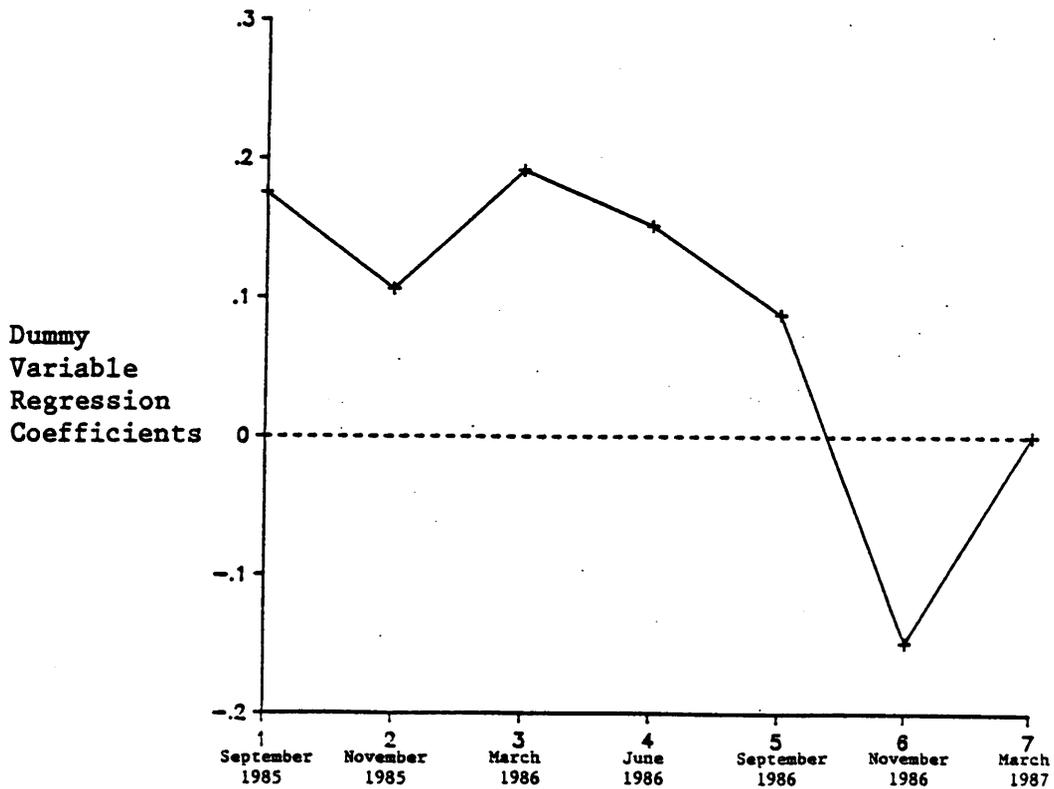
effect that each of these factors had can be seen by looking at the coefficients produced when each of these were added into the model.

Season has a significant effect because of the change in the characteristics of the forest floor by season (Figure D1). Loose leaves in the fall increase depth changing the relationship between biomass and depth. Compressed and decomposing leaves in mid-summer have lower depth and a higher depth to biomass ratio.

Figure D2 shows both the effects of defoliation level and the variability of plot. A stepwise increase in the magnitude of the coefficient occurs from nondefoliated plots to heavily defoliated plots as the proportional biomass to unit depth increases. Defoliation may be a factor because defoliation breaks leaves down and may reduce forest floor depth, increasing the biomass to depth relationship. When the models were fit on data from plots that were never defoliated, however, the relationship between depth and biomass was still poor. The correlation obtained using only ln depth on plots never defoliated was slightly higher ($R^2=0.168$) than for all plots ($R^2=0.149$) but with all variables in the residual model the correlation was identical ($R^2=0.272$).

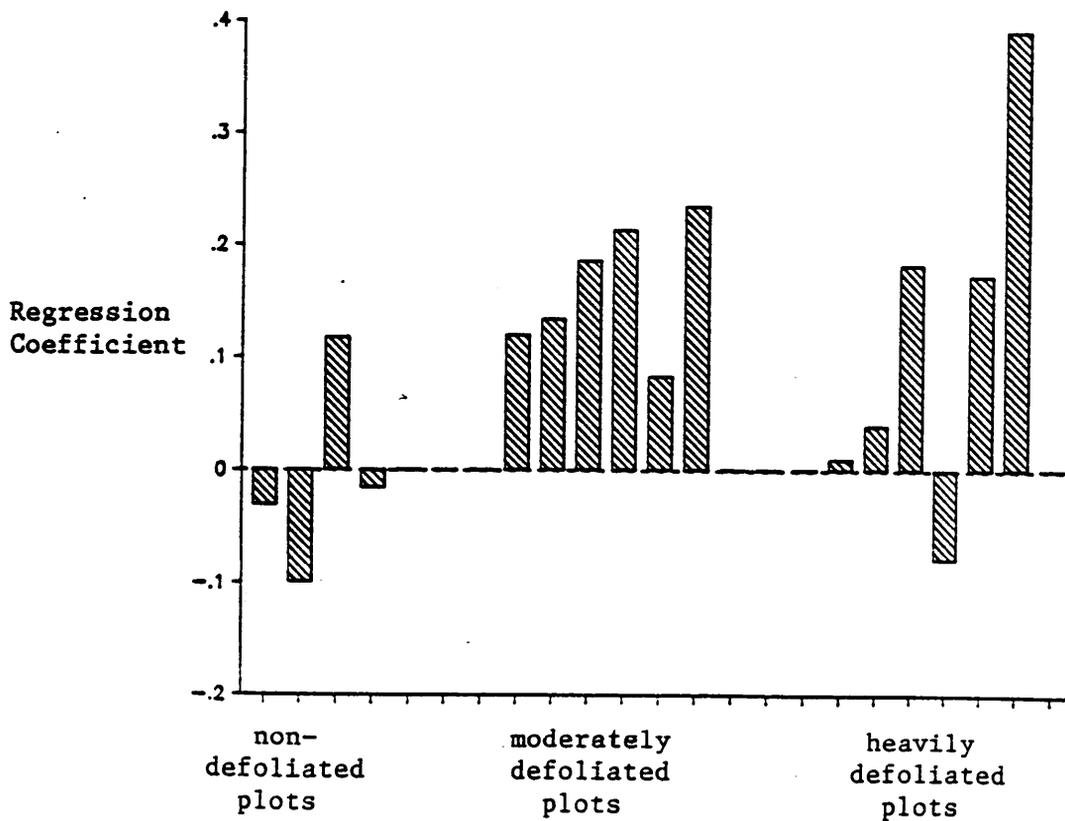
Differences in site characteristics among plots are perhaps the most important factor affecting the relationship between forest floor depth and forest floor biomass because they are so variable. Forest floor biomass varies with site quality, and species composition of the overstory (Harmon et al. 1986). The depth to biomass relationship could vary with these factors as well.

4. Summary and Conclusions



Appendix D.

Figure D1. Dummy variable regression coefficients, by sample collection date (season).



Appendix D.

Figure D2. Coefficients of dummy variable regression incorporating plot, and defoliation level.

The relationship between forest floor depth and forest floor biomass was extremely poor, though statistically significant. Plot characteristics, season, and defoliation level affect the relationship between depth and biomass. Inclusion of these factors in regression analysis explained some of the variation between depth and biomass, but 73% of the variation was left unexplained by even the best model. Forest floor depth cannot be used as a reliable estimator of forest floor biomass.

**The vita has been removed from
the scanned document**