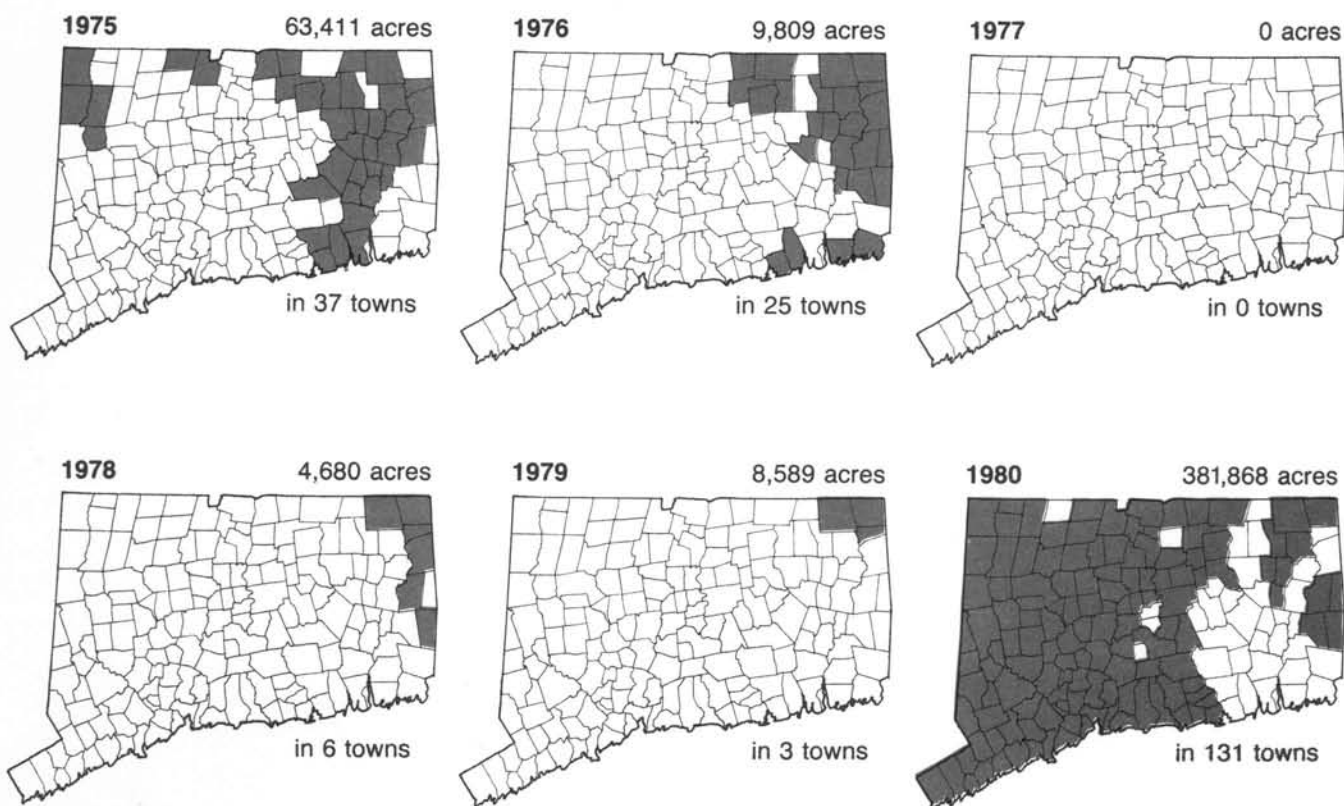


The Gypsy Moth in Connecticut

1. Defoliation 1975-1980
2. Review of Biological Control Studies

By John F. Anderson and Ronald M. Weseloh



TOWNS IN WHICH NOTICEABLE DEFOLIATION OCCURRED IN CONNECTICUT DURING 1975-1980.

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Although the first gypsy moth, *Lymantria dispar* (L.)¹, was collected in Connecticut in 1905 (Britton 1906), extensive defoliation (> 1000 acres) did not occur until 1938 (Friend 1945). Outbreaks covering thousands of acres began in the 1950s (Turner 1963a), with the most extensive ones developing in the early 1970s (Anderson and Gould 1974). Gypsy moth populations declined in the late 1970s, but increased substantially in 1980.

Early methods of controlling gypsy moths relied upon ground spraying of infested trees with chemical pesticides and procedures such as egg mass destruction (Hitchcock 1974). Aerial spraying of some infested forest land with chemical pesticides began in the 1950s and continued through 1971. State regulations now prohibit the aerial application of chemical pesticides to forests and require written release statements from all land owners subject to aerially

applied chemical sprays for agricultural purposes or biological sprays aerially applied to woodlands. Citizens still rely upon methods used decades ago to cope with gypsy moth infestations, although insecticide formulations have changed.

This publication documents defoliation from 1975 through 1980 and reviews the Station's biological control investigations. An earlier publication described Connecticut outbreaks from 1969 through 1974 (Anderson and Gould 1974) and another recent publication reported the history, life cycle, and methods of control of the gypsy moth in Connecticut (Anderson 1980). Effects of defoliation on tree mortality and forest succession in Connecticut were examined in a series of papers (Turner 1963b, Stephens 1963, 1971, Stephens and Hill 1971, Stephens and Waggoner 1970, 1980).

¹ Lepidoptera: Lymantriidae

Defoliation, 1975-1980

Annual defoliation data document duration of outbreaks and caterpillar dispersal, and may assist in relating gypsy moth feeding to tree mortality and forest succession. These data may also assist in predicting caterpillar dispersal and the length of future outbreaks. The location, intensity, spread, and duration of gypsy moth outbreaks during 1975-1980 are reported.

Methods used were essentially those reported by Anderson and Gould (1974). Aerial defoliation surveys were made in early July of each year. Intensity of defoliation and its magnitude were recorded on a topographic survey map with a scale of 1:125,000. Acreage defoliated within each town was calculated by using a modified acreage grid.² Defoliation categories used were: 10-25%, 26-50%, 51-75%, and 76-100%.

Table 1 shows the intensity of defoliation recorded by county and the total for the state for each year. Total defoliation for each town is shown in Tables 3-10. Figures 1-5 illustrate the location and intensity of defoliation for 1975, 1976, 1978, 1979 and 1980 (no defoliation occurred in 1977).

1975 Gypsy moth defoliation totalled 63,411 acres, 57,569 acres less than in 1974 (Fig. 1). Outbreaks were recorded in 37 towns in five counties. Windham County recorded the largest acreage of defoliation (43,374 acres) and was the only county to experience an increase from 1974. The Town of Canterbury had 11,397 acres affected. Brooklyn and Pomfret had 5,000 to 6,000 acres defoliated. The intensity of defoliation was 75% or less in all areas.

1976 Defoliation totalled 9,809 acres, 53,602 acres less than in 1975 (Fig. 2). Caterpillars were abundant in 25 towns within the three eastern counties of Tolland, Windham and New London. Population densities had declined to nondefoliation levels in Litchfield and Hartford Counties. Defoliation was less than 2,000 acres in each town. Defoliation was most extensive again in Windham County, although it totalled slightly less than 6,000 acres. The intensity of defoliation was 75% or less in all areas. This was the fifth year in succession that total defoliation had declined significantly from the year before.

1977 For the first time since 1949, gypsy moths caused no defoliation.

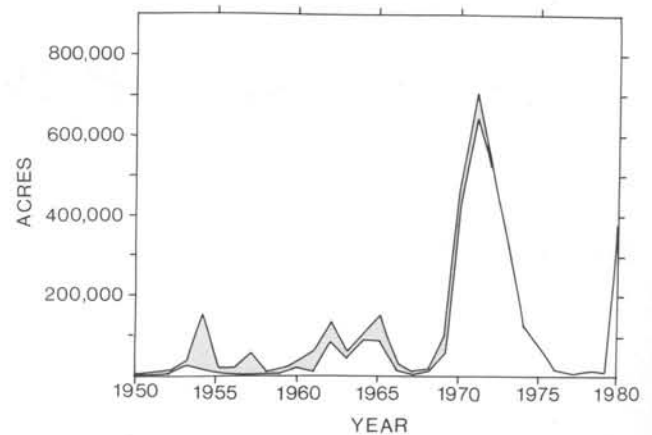
1978 Outbreaks in six towns in Tolland and Windham Counties resulted in 4,680 acres being defoliated (Fig. 3). Defoliation in each town was less than 2,000 acres, and 390 acres were completely defoliated.

1979 Defoliation totalled 8,589 acres, an increase of 3,909 from the year before (Fig. 4). It occurred in three towns in Windham County. In Thomp-

son, 7,292 acres were affected. Most of the acreage was defoliated 26-50%, although 700 acres were nearly completely defoliated.

1980 Gypsy moth defoliation totalled 381,868 acres in 131 towns, 373,279 acres more than the year before (Fig. 5). It was recorded in all eight counties, but was most extensive in the western counties of Fairfield, Litchfield, Hartford, and New Haven. Five towns (Thompson, Burlington, Stamford, Oxford, and Voluntown) had 10,000-15,000 acres defoliated. Another 22 towns had 5,000-10,000 acres defoliated. A total of 110,877 acres was 75-100% defoliated, the largest amount ever recorded in that category. An additional 120,802 acres were 51-75% defoliated. Fall cankerworms, *Alsophila pometeria* (Harris), were abundant in some areas of New Haven, Fairfield and Hartford counties.

Origin, geographical spread and duration of outbreaks The cyclic nature of gypsy moth outbreaks in Connecticut is evident in the figure. When the state



Total forest acreages defoliated and aerially sprayed (shaded area) in Connecticut since 1950. Acreage defoliated from 1970-1972 includes defoliation by the elm spanworm. (Data to 1962 from Turner (1963a); data from 1969 to 1974 from Anderson and Gould (1974)).

as a whole is considered, dense caterpillar populations feeding over large acreages of woodland recurred at eight- to ten-year intervals and persisted for five or six years. If this trend continues, large acreages will be defoliated in the early 1980s. The significant increase in defoliation in the 1970s was due not only to the presence of the elm spanworm, but also to the fact that for the first time, outbreaks originated in southwestern Connecticut and subsequently spread through central portions of the state. The 1980 outbreak in large part had similar origins, and, although

² Forestry Suppliers, Inc., Jackson, Miss.

Table 1. Intensity of defoliation by county in Connecticut, 1975-1980.

County	Year	Acres/Percent Defoliation				Total Defoliation	County Acreage
		10-25	26-50	51-75	76-100		
Litchfield	1975	1,673	507			2,180	607,168
	1976						
	1977						
	1978						
	1979						
	1980	5,772	18,369	25,057	25,974	75,172	
Hartford	1975	1,595	312			1,907	480,128
	1976						
	1977						
	1978						
	1979						
	1980	6,162	14,644	17,160	28,197	66,183	
Tolland	1975	1,867	973	1,673		4,513	268,848
	1976		3,075			3,075	
	1977						
	1978						
	1979						
	1980	2,340	1,443			3,783	
Windham	1975	13,926	12,448	17,000		43,374	332,740
	1976		5,954	39		5,993	
	1977						
	1978		1,248	1,365	390	3,003	
	1979		7,683	234	672	8,589	
	1980	19,539	507	8,190	897	29,133	
Fairfield	1975						422,031
	1976						
	1977						
	1978						
	1979						
	1980	9,633	22,269	35,412	29,952	97,266	
New Haven	1975						399,016
	1976						
	1977						
	1978						
	1979						
	1980	4,758	19,617	31,239	25,545	81,159	
Middlesex	1975						248,028
	1976						
	1977						
	1978						
	1979						
	1980	3,861	10,725	3,744	312	18,642	
New London	1975	8,714	2,489	234		11,437	448,576
	1976	312	234	195		741	
	1977						
	1978	1,677				1,677	
	1979						
	1980	10,530				10,530	
State Totals	1975	27,775	16,729	18,907		63,411	
	1976	312	9,263	234		9,809	
	1977					0	
	1978	1,677	1,248	1,365	390	4,680	
	1979		7,683	234	672	8,589	
	1980	62,595	87,594	120,802	110,877	381,868	

the defoliation was caused almost entirely by gypsy moths, fall cankerworms were abundant locally.

Gypsy moth outbreaks crash naturally from epizootics of the nuclear polyhedrosis virus and insufficient quantities of food for the caterpillars (Campbell 1963, Doane 1970). Although causes of outbreaks are less understood, the immigration of large numbers of wind blown caterpillars into an area may be a source of inoculum. In Connecticut, outbreaks tend to move in a northeasterly direction (Anderson and Gould 1974). The 1975 and 1976 outbreaks appear to have been extensions of those in previous years. The 1978 and 1979 outbreaks in northeastern Connecticut may have originated *de novo*, or they could have arisen from outbreaks occurring in 1978 in nearby Massachusetts towns (USDA, APHIS defoliation map). The 1980 outbreak in western Connecticut may have had its origin in Dutchess, Putnam and Westchester Counties, New York where defoliation occurred in 1978-1980 (USDA, APHIS defoliation map). Caterpillars probably blew into Connecticut from New York in the spring of 1978 and 1979 to contribute to the outbreak in 1980. However, part of the 1980 outbreak may have been due to increases in indigenous populations. Infestations along the Connecticut River in Middlesex and Hartford Counties are substantially removed from inoculum sources in New York and some may have originated *de novo*. The sudden appearance of the 1980 outbreak in western Connecticut was similar to that of the elm spanworm-gypsy moth outbreaks of a decade before (Anderson and Gould 1974). It is likely that areas to the east of presently infested locations (Fig. 5) will be defoliated in 1981 and the following years, as in the early 1970s.

The colonization by the gypsy moth of vast acreages of woodland to the west and southwest of Connecticut during the past three decades (Campbell 1979) has influenced, and will probably continue to influence, gypsy moth populations in the state. All towns in Connecticut and towns in eastern New York were known to be infested in 1952. By 1974, the gypsy moth had spread throughout most of New York, much of Pennsylvania, and all of New Jersey. With prevailing winds coming from the southwest, caterpillars developing in outbreaks in these areas to the west (particularly in southeastern New York and in northern New Jersey) may spread into Connecticut as they apparently did in 1978 and 1979. We therefore believe that outbreaks will continue to occur at frequent intervals and, at times, will encompass vast areas of the state's woodland.

The duration of outbreaks was determined by calculating the number of consecutive years of defoliation within town boundaries for the period 1969-1977. Data were compiled from Tables 3-10 and from Anderson and Gould (1974). The mean number of consecutive years of defoliation was 2.9 ± 1.6 SD years per town, with a range of 1 to 8 years. Analysis of

towns within specific counties revealed that outbreaks persisted longer in the eastern counties. In the four western counties (Litchfield, Hartford, Fairfield and New Haven), outbreaks averaged 1.8 to 2.8 years. In contrast, outbreaks in the eastern counties (Tolland, Windham, New London and Middlesex) averaged 3 to 4.4 years (Table 2).

Table 2. Duration of town outbreaks arranged by County, 1969-1977.

County	\bar{X} duration (consecutive years) of defoliation per town
Litchfield	2.6 \pm 1.2
Hartford	2.2 \pm 0.9
Tolland	4.0 \pm 1.4
Windham	4.4 \pm 2.4
Fairfield	1.8 \pm 0.5
New Haven	2.8 \pm 1.0
Middlesex	3.0 \pm 0.8
New London	3.5 \pm 2.0

The less persistent outbreaks in western Connecticut reflect the inclusion of elm spanworm defoliation data. Outbreaks of this insect in western Connecticut lasted only 1 or 2 years (Kaya and Anderson 1974). The data from the eastern counties are more representative of gypsy moth infestations. Thus, gypsy moth outbreaks usually last 3-4 years within a town and may persist as long as 8 years, but some also collapse after only 1 year. (Since outbreaks from one year to the next within a town will vary in size and location, the number of successive years of defoliation within a given locale of a particular town will often be smaller than that reported here for town outbreaks.)

Table 3. Noticeable defoliation by town in Middlesex County, 1975-1980. No defoliation was experienced during 1975-1979.

Town Name	Acres/year	
	1980	Town Acreage
Chester	117	10,176
Clinton	1,365	11,008
Cromwell		8,640
Deep River	468	9,088
Durham	702	14,912
East Haddam		36,864
East Hampton	429	23,552
Essex	624	7,808
Haddam	1,755	29,888
Killingworth	7,293	23,040
Middletown	1,053	27,392
Middlefield		8,412
Old Saybrook	1,365	11,712
Portland	1,677	15,168
Westbrook	1,794	10,368

Table 4. Noticeable defoliation by town in Litchfield County, 1975-1980. No defoliation was experienced during 1976-1979.

Town Name	Acres/year		Town Acreage
	1975	1980	
Barkhamsted		3,744	24,960
Bethlehem		1,170	12,608
Bridgewater		1,677	10,432
Canaan		2,340	21,376
Colebrook			21,120
Cornwall	350	1,950	29,952
Goshen		195	29,184
Harwinton		8,736	20,096
Kent		234	31,680
Litchfield		7,683	36,672
Morris		3,783	12,032
New Hartford		9,535	24,512
New Milford		2,613	41,126
Norfolk		1,131	29,888
North Canaan		1,248	12,544
Plymouth		7,800	14,336
Roxbury		3,276	16,896
Salisbury	78	1,092	38,720
Sharon	1,090	355	38,592
Thomaston		1,716	7,680
Torrington		3,705	25,600
Warren	662	819	17,920
Washington		3,744	24,768
Watertown		2,028	19,072
Winchester		195	21,760
Woodbury		4,407	23,552

Table 5. Noticeable defoliation by town in Fairfield County, 1975-1980. No defoliation was experienced during 1975-1979.

Town Name	Acres/year		Town Acreage
	1980		
Bethel	1,794	10,880	
Bridgeport	39	11,200	
Brookfield	1,248	12,672	
Danbury	3,393	28,160	
Darien	897	9,536	
Easton	5,616	18,432	
Fairfield	3,900	19,584	
Greenwich	6,123	32,384	
Monroe	3,276	16,896	
New Canaan	5,226	14,812	
New Fairfield	2,613	16,512	
Newtown	9,399	38,643	
Norwalk	1,014	17,728	
Redding	7,059	20,608	
Ridgefield	6,240	22,400	
Shelton	2,847	20,096	
Sherman	5,031	15,040	
Stamford	10,842	24,640	
Stratford	741	11,968	
Trumbull	1,989	15,040	
Weston	8,853	13,312	
Westport	1,092	14,336	
Wilton	8,034	17,152	

Table 6. Noticeable defoliation by town in New London County, 1975-1980. No defoliation was experienced during 1977 and 1979.

Town Name	Acres/year				Town Acreage
	1975	1976	1978	1980	
Bozrah	467				12,800
Colchester	156				31,100
East Lyme	1,245	78			22,272
Franklin	1,985				12,800
Griswold		78		78	24,064
Groton		78			24,512
Lebanon	117				35,904
Ledyard					25,920
Lisbon	1,011	78			10,560
Lyme	117				21,120
Montville	311				28,096
New London					4,672
North Stonington					36,032
Norwich	661				17,344
Old Lyme	2,528	156			17,344
Preston					20,032
Salem					19,136
Sprague	2,217				8,576
Stonington		78			27,238
Voluntown		195	1,677	10,452	25,408
Waterford	622				23,488

Table 7. Noticeable defoliation by town in Hartford County, 1975-1980. No defoliation was experienced during 1976-1979.

Town Name	Acres/year		Town Acreage
	1975	1980	
Avon		6,201	15,040
Berlin		2,184	17,280
Bloomfield		1,482	16,896
Bristol		2,925	17,024
Burlington		14,976	19,584
Canton		6,981	16,000
East Granby		117	11,136
East Hartford		1,053	11,584
East Windsor			17,152
Enfield	428	2,769	21,632
Farmington		4,680	18,368
Glastonbury		2,808	33,600
Granby	1,206	4,875	26,432
Hartford		117	11,776
Hartland	273	780	22,080
Manchester		39	17,408
Marlborough			15,040
New Britain		312	8,512
Newington		312	8,448
Plainville		1,404	6,336
Rocky Hill			8,896
Simsbury		6,201	22,080
Southington		3,081	23,616
South Windsor		312	18,240
Suffield		663	27,584
West Hartford		1,014	14,208
Wethersfield		234	8,320
Windsor		351	19,968
Windsor Locks		312	5,888

Table 8. Noticeable defoliation by town in Tolland County, 1975-1980. No defoliation was experienced during 1977-1979.

Town Name	Acres/year			Town Acreage
	1975	1976	1980	
Andover				9,984
Bolton			1,092	9,920
Columbia				13,952
Coventry			897	23,872
Ellington	1,362	272	351	22,144
Hebron				24,000
Mansfield	895			28,928
Somers	1,633	117	195	18,368
Stafford		389	624	38,512
Tolland	234	1,713	507	25,856
Union	311			19,136
Vernon			117	11,904
Willington	78	584		22,272

Table 9. Noticeable defoliation by town in Windham County, 1975-1980. No defoliation was experienced during 1977.

Town Name	Acres/year					Town Acreage
	1975	1976	1978	1979	1980	
Ashford	39					25,792
Brooklyn	5,563	545				18,368
Canterbury	11,397	506				25,600
Chaplin	895	39			741	12,672
Eastford		428			6,825	18,304
Hampton	4,317	233			1,716	16,192
Killingly	1,129	1,168	195			32,000
Plainfield	856	272	507		2,379	27,328
Pomfret	5,990	1,401			507	25,984
Putnam	2,178	233	546	273		12,864
Scotland	2,568				156	11,716
Sterling		39			1,716	17,408
Thompson		117	1,482	7,292	14,274	31,168
Windham	4,435	389				17,920
Woodstock	4,007	623	273	624	819	39,424

Table 10. Noticeable defoliation by town in New Haven County, 1975-1980. No defoliation was experienced during 1975-1979.

Town Name	Acres/year	
	1980	Town Acreage
Ansonia	1,872	3,968
Beacon Falls	1,326	6,472
Bethany	3,861	13,440
Branford	156	17,856
Cheshire	7,254	21,120
Derby	1,053	3,392
East Haven	351	8,064
Guilford	819	30,464
Hamden	7,176	21,120
Madison	2,730	23,232
Meriden	858	15,360
Middlebury	3,315	11,520
Milford	351	15,240
Naugatuck	2,730	10,368
New Haven	1,170	13,504
North Branford	390	17,112
North Haven	702	13,440
Orange	1,911	11,264
Oxford	10,608	21,120
Prospect	6,123	9,152
Seymour	2,340	9,408
Southbury	6,162	26,176
Wallingford	624	25,472
Waterbury	3,315	18,432
West Haven	468	6,784
Wolcott	8,034	13,184
Woodbridge	5,460	12,352

Biological Control Investigations

In Connecticut, the importance of attempting to control the gypsy moth through biological means was recognized by Britton as early as 1906. Significant early work included experiments with a *Calosoma* (Carabidae) beetle and the discovery of diseased caterpillars (Britton 1907). The Station and the USDA collaborated in attempts to establish parasites, and by 1931, Britton (1931) reported that nine parasites were established in Connecticut. Beginning in the 1950s, microorganisms, such as the nuclear polyhedrosis virus (NPV) that causes wilt disease, and

insect parasites or predators were investigated in great detail. The parasites are various species of Hymenoptera in the superfamilies of Ichneumonoidea or Chalcidoidea, or flies from the family Tachinidae. Their immatures develop within gypsy moths of various stages and the adults are free-living. The only predators studied were the large ground beetles belonging to the genus *Calosoma*. Additional control studies were carried out with the gypsy moth sex attractant (pheromone).

Nuclear polyhedrosis virus The nuclear poly-

hedrosis virus (NPV) is the dominant natural enemy during gypsy moth outbreaks. It appears to have been accidentally introduced into North America from Europe. Britton (1907) reported finding diseased caterpillars in Connecticut in 1906. No experimental studies were carried out until the 1950s. Wallis (1957, 1962) began studying the relationship between epizootics and environmental stresses and found that most egg masses in the field were contaminated with the virus. Doane began his extensive studies in the 1960s. His significant findings were: (1) determination of the relative susceptibility of larvae to a Connecticut strain of NPV (Doane 1967a, b), (2) demonstration of transovum transmission by means of contaminated egg surfaces and hair of the egg mass (Doane 1969, 1970, 1971b, 1975), (3) determination that NPV-killed-first-instar larvae are the major source of inoculum for transmission of NPV to other larvae within the same generation, (4) demonstration of the importance of debris mats (silk webbing, larval exuviae, pupal cases, and dried cadavers) as a source of intergeneration NPV contamination in the field, (5) development of a method of forecasting epizootics by measuring the virus load in overwintering egg masses (1971b), and (6) development of the modified density-dependent hypothesis, which explains, in part, the frequency and duration of gypsy moth outbreaks by taking into account the amount of virus in the environment (Doane 1976).

Bacterial pathogens Two bacterial pathogens have been studied extensively. One is the naturally occurring *Streptococcus faecalis* Andrewes and Horder and the other is the commercially available *Bacillus thuringiensis* Berliner (*Bt*). Doane (1970) reported *S. faecalis* as a primary pathogen capable of reaching epizootic levels under field conditions. Its morphological, biochemical and serological characteristics as well as its effects on larvae were described by Doane and Redys (1970). Subsequently, Doane (1971a) suggested the disease be called "brachyosis" because of the shrunken, shortened appearance of infected larvae. Ground-application tests by Doane (1971a) showed that outbreaks of this disease could be produced in populations in the field and that defoliation of trees could be prevented, even in dense populations. A method of producing the bacterium in the laboratory was described.

Experiments to determine the effectiveness of *Bt* against the gypsy moth were begun in the early 1960s and continued periodically for about a decade. Doane and Hitchcock (1964) obtained inconclusive results with aerially-applied Thuricide 90T, a liquid suspension. The same formulation, however, protected foliage when applied from the ground with a mistblower (Doane 1966). The addition of boric acid to *Bt* formulations enhanced its effectiveness in laboratory and field tests (Doane and Wallis 1964, Doane 1965); commercial formulations containing *Bt* and boric acid

have not been developed. When commercial formulations containing a more potent strain of *Bt* became available, further tests were made. Dunbar and Kaya (1972) showed that high rates of *Bt* (e.g., 0.4 pint Thuricide HPC/gallon of spray) applied with a mistblower were required to reduce gypsy moth populations to low levels. Aerial tests demonstrated that *Bt* reduced larval numbers and gave foliage protection, but large numbers of larvae survived and egg masses were often more numerous in the following generation (Dunbar et al. 1973, Kaya et al. 1974).

Laboratory culture of the gypsy moth and its parasites The gypsy moth and its natural enemies were difficult to rear in the laboratory prior to the mid-1960s because of the necessity of supplying large quantities of oak, apple, or other leaves for the larvae to feed on. This difficulty was overcome when Leonard and Doane (1966) developed an artificial wheat germ diet containing linolenic acid that was suitable for rearing larvae to adulthood. The authors also reported that disinfecting the surface of eggs with sodium hypochlorite greatly reduced mortality from disease, particularly NPV. These developments greatly enhanced the research effort on the gypsy moth which was to follow. Parasites and pathogens could finally be studied and produced in large quantities with a minimum of effort spent on rearing the caterpillars.

Hatchable eggs from the field are not conveniently available during part of the year, and despite surface disinfection, virus disease continues to be a problem. Hoy (1977) began a program to genetically select a nondiapausing strain of the gypsy moth while at the Station in 1974. By selecting and rearing only those larvae which developed without diapause, a nondiapausing, essentially disease-free strain was developed in about eight generations. Using this strain it should be possible to rear host specific natural enemies in large quantities at any time of the year.

Weseloh has attempted to rear the parasite, *Apanteles melanoscelus* Ratzeburg, in artificial culture media. Parasite eggs aseptically dissected from hosts and placed in heat deactivated sterile host hemolymph hatch and will develop to the late first instar before dying. When perfected, this approach may result in a more efficient means of culturing the insect.

Exotic parasite introduction and establishment The gypsy moth parasite introduction program in North America began in 1905 when the USDA and the State of Massachusetts introduced natural enemies from Europe and Asia where the gypsy moth is a native insect. Collaborative efforts between the USDA and The Connecticut Agricultural Experiment Station resulted in the introduction into Connecticut of a number of natural enemies. Species introduced and their status are shown in Table 11. Ten insect parasites and one predator from Europe and Asia are established in the State.

Table 11. Insect parasite and predator species introduced into Connecticut for the control of the gypsy moth.

Species	Family	Host stage attacked	Year first released or recovered in Connecticut	Establishment status	Reference
<i>Monodontomerus aereus</i> Walker	Torymidae	Pupae	1911	Established	Britton, 1916
<i>Compsilura concinnata</i> (Meigen)	Tachinidae	Small-large larvae	1912	Established	Britton, 1916
<i>Calosoma sycophanta</i> L.	Carabidae	Larvae and pupae	1914	Established	Britton, 1916
<i>Anastatus disparis</i> Ruschka	Eupelmidae	Eggs	1917	Established	Britton, 1921
<i>Ooencyrtus kuvanae</i> (Howard)	Encyrtidae	Eggs	1921	Established	Britton, 1922
<i>Apanteles melanoscelus</i> (Ratzeburg)	Braconidae	Small larvae	1922	Established	Britton, 1923
<i>Blepharipa pratensis</i> (Meigen)	Tachinidae	Larvae	1922	Established	Britton, 1923
<i>Brachymeria intermedia</i> (Nees)	Chalcididae	Pupae	1963	Established	Dowden, 1969
<i>Phobocampae uncinatus</i> (Gravenhorst)	Ichneumonidae	Small larvae	Unknown	Established	Personal observation
<i>Exorista larvarum</i> (L.)	Tachinidae	Larvae	Unknown	Established	Personal observation
<i>Parasetigena silvestris</i> (Robineau-Desvoidy)	Tachinidae	Larvae	Unknown	Established	Personal observation
<i>Apanteles fulvipus</i> (Haliday)	Braconidae	Larvae	1922	Not established	Britton, 1923
<i>Exorista segregata</i> (Rondani)	Tachinidae	Larvae	1963	Not established	Dowden, 1969
<i>Apanteles porthetriae</i> Muesebeck	Braconidae	Larvae	1965	Not established	Dowden, 1969
<i>Exorista vossica</i> Mesnil	Tachinidae	Larvae	1968	Not established	Dowden, 1968
<i>Rogas indiscretus</i> Reardon	Braconidae	Larvae	1968	Not established	Dowden, 1968
<i>Brachymeria lasus</i> (Walker)	Chalcididae	Pupae	1979	Not established	Weseloh and Anderson, (in preparation)
<i>Coccygomimus disparis</i> (Viereck)	Ichneumonidae	Pupae	1979	Not established	Weseloh and Anderson, (in preparation)

Of the 10 gypsy moth parasites presently established in North America, only one, *Brachymeria intermedia* (Nees), was not known to be established by 1930. This parasite had been released in North America periodically from 1911 to 1927 (Dowden 1935), but there were no reports that it had become established except for Burks' (1960) publication of the recovery of one adult from a pupa of *Cacoecia* collected in Massachusetts in 1942. More releases were made by the USDA in 1963. Leonard (1966) recovered this parasite from gypsy moth pupae in five Connecticut towns in 1965, thereby confirming its establishment in North America. Leonard suggested that *B. intermedia* maintained itself at low population levels following its early release in North America and that its appearance in 1965 was not a result of the 1963 release. The incidence of parasitism in 1966 was less than 5% (Leonard 1967), although 4 years later, Doane (1971c) reported a parasitization rate of 51% from one locality.

More recently, two exotic pupal parasites from Japan, *Brachymeria lasus* (Walker) and *Coccygomimus disparis* (Viereck), have been released in Windham and Fairfield counties (Weseloh and Anderson, ms. submitted). There is no evidence that either has become established (overwintered successfully and parasitized gypsy moths in succeeding years). Both were shown to have multiple generations each year, thus

suggesting their need for alternate hosts when gypsy moth pupae are not present.

Field cage evaluation of exotic parasites Anderson et al. (1977) used field cages to study a promising but unestablished exotic parasite. *Rogas indiscretus* Reardon, a parasite of *Lymantria obfuscata* Walker in India, was selected because it readily parasitized gypsy moth larvae in the laboratory and was thought to have only one generation a year in India. Studies showed that this species, which originally had been colonized in the laboratory in the 1960s and reared in various laboratories before being placed in field cages, produced three generations per year and overwintered successfully. Adult emergence the following year was synchronized with the appearance of small gypsy moth larvae. The data show that the limiting factor for successful establishment in North America of this strain of *R. indiscretus* is the availability of suitable alternate hosts.

Field cages were also used to evaluate the overwintering potential of *Brachymeria lasus* and *Coccygomimus disparis* (Weseloh and Anderson, ms. submitted). There was no evidence that *B. lasus* could overwinter, but *C. disparis* successfully overwintered as an immature stage in greater wax moth, *Galleria mellonella* (L.), pupae. It had four generations per year. So, like *R. indiscretus*, it requires suitable alternate hosts to survive in the field. These studies

demonstrate the effectiveness of field cages for evaluating the potential for establishment of exotic parasites.

Inundative release of parasites Few efforts have emphasized inundative releases of parasites already established. Weseloh and Anderson (1975) reared and released 1000-7000 adults and cocooned immatures of *Apanteles melanoscelus* per 4 ha plot in three towns over 2 years (1973-74) in both low and high density gypsy moth infestations. In all cases, % parasitism of caterpillars collected in five release plots was significantly greater (up to 40%) than in eight check plots.

Hoy (1975b) released a triple hybrid of *A. melanoscelus* from France, Yugoslavia, and Connecticut in three plots (6000/plot) in 1974 under conditions similar to the above and also obtained significantly greater % parasitism in the test plots than in three check plots. This triple hybrid had a greater fecundity in laboratory tests than did the Connecticut strain released, but no evidence in the field showed it to be more effective in parasitizing larger numbers of caterpillars.

These releases suggest that *A. melanoscelus* has the potential to become a more effective parasite. The development of an efficient rearing procedure would aid greatly in improving its usefulness.

Behavior of natural enemies Studies of the behavior of natural enemies have relevance in understanding parasite effectiveness and other aspects of their ecology. Diel periodicities of parasites were investigated by Weseloh (1972b, 1976b). All parasites studied (*Ooencyrtus kuvanae* (Howard); *Blepharipa pratensis* (Meigen); *Parasetigena silvestris* (Robineau-Desvoidy); and the hyperparasite, *Brachymeria compsiluræ* (Crawford), which attacks tachinid parasites) were active during daylight hours. *O. kuvanae* females were also seen to oviposit on gypsy moth egg masses until around 2 a.m.

Weseloh (1977a) found that courtship behavior in *Apanteles melanoscelus* was similar to that of other ichneumonoids. Old males did not mate readily, but old females were as receptive as young ones to young males. Environmental conditions under which females were not disturbed easily when contacted by males were conducive to mating. A sex-pheromone in *A. melanoscelus* and *A. liparidis* (Bouche) was found to be produced in paired glands on the female's abdomen (Weseloh 1976d, 1980b).

Doane and Schaefer (1971b) showed that adults of *Calosoma sycophanta* (L.) are strong and capable fliers, thus enhancing their dispersal.

Responses of *O. kuvanae* to abiotic environmental factors were studied by Weseloh (1971). This parasite oriented to low relative humidities at moderate temperatures but to high relative humidities at high temperatures. Females were negatively geotactic in both dark and light. Their preferred temperature was be-

tween 20 and 30°C. The parasites were positively phototactic under almost all conditions tested. This species appears to have broad behavioral responses to abiotic environmental factors, which may explain its wide distribution in the field. Adults responded to white- and blue-colored sticky panels that reflect wavelengths of light between 500 and 600 nm (Weseloh 1972c). This response may indicate that the parasite disperses upward toward openings in the forest canopy.

A study of comparative responses of other parasites in humidity and temperature gradients (Weseloh, 1979b) demonstrated that *Brachymeria intermedia*, *B. lasus*, and *B. sp.* (the last two not established in North America) preferred dryer air and higher temperatures than the other gypsy moth parasites tested, including *Apanteles melanoscelus* and *Compsilura concinnata*, and the hyperparasites *Eurytoma appendigaster* (Swederus) and *Gelis tenellus* (Say). *B. intermedia* is known to prefer sunny areas. The responses to humidity and temperature would be compatible with such a microhabitat preference. Because the preferences of *B. lasus* and *B. sp.* were similar to those of *B. intermedia*, it seems likely that their field microhabitat preferences and their impact on gypsy moth populations will be similar. Indeed, parasitization in the *B. lasus* release plots was highest in pupae collected from sunny locations (Weseloh and Anderson, ms. submitted).

Parasite responses to different microhabitats in the field were also investigated. *Parasetigena silvestris* attacked tethered hosts more readily on the exposed trunks of trees, no matter what the height, than hosts placed under burlap bands or on leaves (Weseloh 1974a). *Compsilura concinnata*, on the other hand, preferred tethered hosts on leaves (Weseloh, ms. in preparation). *Ooencyrtus kuvanae* oviposited in egg masses without respect to height or aspect on tree trunks, but did not attack eggs placed in a sunny clearing (Weseloh 1972a, d). Adults were caught most often on sticky panels near the top of trees, probably while they were dispersing. *Apanteles melanoscelus* adults were caught on sticky panels most often at 4 m above ground level and above, probably due to responses to tree foliage. *Brachymeria intermedia* was found predominantly in sunny areas, such as the edges of clearings (Doane 1971c) and tops of trees (Weseloh 1972d).

Parasite host selection and interrelationships with hosts have been investigated in a number of studies. *Parasetigena silvestris* attacked parasitized hosts as readily as unparasitized ones in field studies, but did not lay eggs on tethered, dead, freeze-dried caterpillars unless these were moving in the wind. Most probably, this parasite responds to host shape and especially movement. No evidence for response to host chemicals (kairomones) was found (Weseloh 1976b).

Apanteles melanoscelus was studied extensively. This

parasite examined and oviposited more often in non-parasitized larvae than in parasitized hosts, but superparasitism was common when host numbers were restricted. Supernumerary parasitoid larvae were eliminated by active combat if all were first instars, but larger larvae eliminated younger ones by more subtle means (Weseloh 1976a). *Apanteles melanoscelus* recognized gypsy moth larvae as hosts by their hairiness and a lipid-soluble kairomone on their integument (Weseloh 1974b). Females responded specifically to gypsy moth silk, using their antennae to examine areas where silk was laid down. Silk retained its activity when heated, when held 1 week at room temperature, or when placed in non-polar solvents, but water deactivated it by dissolving an active substance. Extracts and smears of the silk glands were active, especially when presented with water-deactivated silk. Results show that there is on gypsy moth silk a water soluble, stable kairomone(s) that influences the parasite's behavior and enables it to more readily find host larvae. Response of *A. melanoscelus* decreased when it was continually exposed to the silk kairomone. This habituation occurred over about 15-20 minutes. The response to silk is intimately associated with the response to hosts; parasites habituated to one (silk or hosts), had decreased responses when subsequently presented with the other. Habituation to silk insures that the parasite does not remain unduly active (for long periods) when in the presence of silk (Weseloh 1980a).

If this kairomone can be identified it may be useful for manipulating *A. melanoscelus* in the field, especially in conjunction with mass-releases (Weseloh 1976e, 1977b).

Parasite diapause An understanding of diapause is important in rearing parasites, evaluating their overwintering capabilities, and in understanding their biology. Weseloh (1973a) found that diapause in *Apanteles melanoscelus* is terminated by exposure of field-collected cocoons to 5°C for eight or more weeks. Different photoperiod lengths after chilling are unimportant. Induction of diapause is dependent on photoperiod. Older parasite larvae inside the host are most sensitive to photoperiod and almost always enter diapause when reared at photophases of less than 16 hrs.

Hoy (1975a) expanded this work by investigating diapause induction in various strains of *A. melanoscelus*. Strains from France (F) and Yugoslavia (Y), which had been reared for many generations in laboratory culture, and their hybrid (F × Y) had a critical photophase of 12.5-13.5 hr light/day. In contrast, a Connecticut strain (C) had a critical photophase of 16-17 hr. The triple hybrid's (F × Y × C) critical photophase was 15 hr. Strain differences in diapause intensity were maintained under natural day-length conditions in June. Hoy's work shows that the diapause response is genetically controlled and that

it can be changed by genetic manipulations, including inadvertent laboratory selection.

Evaluation of parasite effectiveness The effectiveness of parasites is an important but difficult matter to assess. Some progress has been made by comparing sampling procedures for parasites, the predator *Calosoma sycophanta*, and the gypsy moth (Weseloh 1972a, 1973b, 1974c). The % parasitism of eggs by *Ooencyrtus kuvanae* (which ranged from 10-60%) was negatively correlated with egg mass size in some but not all locations sampled. Adult numbers of *Apanteles melanoscelus* and *Blepharipa pratensis* were negatively correlated with immature parasite numbers and gypsy moth larval numbers; however, the sampling procedure may have been monitoring adult activity rather than numbers. The abundance of *C. sycophanta* adults was not correlated with larval numbers or gypsy moth abundance.

The number of generations per year of parasites can affect their ability to reproduce on hosts. Hitchcock (1959) found that percent parasitism of gypsy moth egg masses by *O. kuvanae* did not change throughout the fall, which suggested that this parasite had only one generation in the late summer and fall. Hitchcock (1972) showed that *O. kuvanae* has two generations in summer but eggs laid after September 1 did not produce adults. He also documented that the parasite successfully oviposits in the spring in egg masses laid the previous year.

More recently, Weseloh (1976c) found that *A. melanoscelus* is not synchronized properly with its host. Adults, as measured by sticky panel catches and % parasitism of laboratory reared hosts exposed weekly in the field, were most abundant in mid to late June when most gypsy moth larvae were 4th instars or larger. In laboratory studies, 4th instars were much less acceptable hosts than earlier instars because of their long body hairs and vigorous defensive movements. Thus, most second generation *A. melanoscelus* must attack instars which are too large for them, resulting in low parasitism rates in June although most *A. melanoscelus* adults are present at this time.

Hyperparasites Hyperparasites annually destroy up to 99% of *A. melanoscelus* larvae overwintering in cocoons. Many *A. melanoscelus* cocoons also fall prey to predators. Van Sickle and Weseloh (1974) found that hidden cocoons were attacked more readily than exposed ones and that percent hyperparasitism increased as the season progressed. More recently, Weseloh (1978a) found that at least 13 species of hyperparasites attacked *A. melanoscelus* cocoons. *Eurytoma appendigaster*, the most abundant species, attacked cocoons on tree trunks more often than those on tree leaves. Other species usually did not exhibit the same degree of preference for cocoons on trunks because *E. appendigaster* destroys the immature stages of other hyperparasite species when eggs of both spe-

cies were laid within the same *A. melanoscelus* cocoon (Weseloh 1979a).

Protecting *A. melanoscelus* from hyperparasites might result in a substantial increase in numbers of parasitized gypsy moth caterpillars. One approach was to cross an *A. melanoscelus* strain from India with the strain established in North America. The Indian strain has a thick "halo" of silk surrounding its cocoon, a possible protection against hyperparasites; but it does not have a photoperiodically-induced diapause and so would not likely become established in North America. The "halo" trait is genetically controlled and could probably be transferred to the North American strain (Weseloh 1978b). Field and laboratory experiments by Weseloh (ms. submitted) showed, however, that cocoons with the "halo" were as susceptible to hyperparasites as those without.

Careful screening of imported parasites can also be helpful in preventing the introduction into North America of new hyperparasites. Weseloh et al. (1979) found that an imported egg parasite, *Anastatus kashmirensis* (Mathur), from India also attacks *A. melanoscelus* and *Rogas indiscretus*, usually to a greater extent than they do gypsy moth eggs. Therefore, *A. kashmirensis* was judged too dangerous for release.

Effects of insecticides on natural enemies It has long been recognized that pesticides also influence beneficial insects. Several studies have examined the effects of pesticides on natural enemies of the gypsy moth. Doane (1968a) reported that egg parasitism by *Ooencyrtus kuvanae* was greater outside than within plots treated with Gardona® (2-chloro-1-(2,4,5-trichlorophenyl) vinyl dimethyl phosphate), but the difference was not attributed to a direct effect of the insecticide on the parasite. Tachinids and sarcophagids were found to be reduced significantly in Dylax® (2,3 dimethyl (2,2,2-trichloro-1-hydroxyethyl) and Gardona®-treated plots in comparison to untreated and Sevin® (1-naphthyl N-methylcarbamate) treated plots (Doane and Schaefer 1971a). *Calosoma frigidum* Kirby and *C. sycophanta* were susceptible to residues of Sevin. The three insecticides did not directly affect birds, although the available food (insects) was depleted and bird activity altered.

The effects of *Bt* sprays on natural enemies were evaluated by Doane and Hitchcock (1964), Dunbar et al. (1973), and Kaya et al. (1974). In general, the spray applications had no apparent adverse effects on small mammals, birds, predaceous insects or parasites, and may have increased the activity of *Apanteles melanoscelus*.

When the new insecticide Dimilin® (1-(4-chlorophenyl)-3-(2,6-difluorobenzoyl)-urea) was recognized to be effective against the gypsy moth (Granett and Dunbar 1975), studies were initiated to evaluate its effect on *Apanteles melanoscelus*. These authors found that the parasite within the gypsy moth host was affected by the insecticide. Granett and Weseloh (1975)

showed that Dimilin-treated leaves fed to parasitized gypsy moth caterpillars killed *A. melanoscelus* larvae during their 2nd-3rd larval molt but not later in development. Granett et al. (1976) then reported that properly timed sprays of Dimilin could minimize effects on the parasite and still be effective against the gypsy moth.

Two juvenile hormone analogues were lethal to *Ooencyrtus kuvanae* at 100 ppm (Granett et al. 1975). *Apanteles melanoscelus* survived treatments, although development took longer.

Gypsy moth sex pheromone Work at the Station on the gypsy moth sex pheromone began in 1961 when Doane published his field results with a material known as gyplure. Later studies on mating behavior revealed that only virgin female moths with the abdominal sex pheromone gland exposed (calling females) attracted males downwind (Doane 1968b); mated females did not call and did not attract males. Copulation usually lasted about 1 hr, but only about 8 minutes was necessary for sperm to be successfully transferred. In the presence of pheromone and at close range, males oriented to females visually.

Doane also investigated mating behavior in cooperation with other scientists. They observed that males would touch wings when arriving simultaneously near a "calling" female, causing one of the males to leave the area (Doane and Carde 1973). Apparently, this mechanism prevents aggregation of males near any one receptive female, thereby insuring a greater number of successfully-mated females. In a related study, males were found to respond to pheromone-baited traps mainly from 11:00 a.m. to 3:00 p.m. (Carde et al. 1974).

With the goal of improving sampling procedures for gypsy moth males, Granett (1973) developed a large-capacity pheromone trap using the synthesized pheromone, disparlure, which caught more moths than the normal, sticky-coated survey traps. He was able to relate the number of captured males to pupal density and length-of-time-to-mating of receptive females (a measure of mating potential). Therefore, these traps might be useful in estimating population size as well as detecting moths (Granett 1974).

The possible use of disparlure in controlling the gypsy moth was explored in a number of tests. An olefin hydrocarbon, 2-methyl-cis-7-octadecene, in the female's pheromone gland was discovered and shown to depress numbers of males caught in traps; however, it seemed to increase male searching behavior (Carde et al. 1973, 1975). When tested in the field along with the pheromone as a "confusant," the pheromone, in contrast to the olefin, inhibited males from finding females. Granett and Doane (1975) sprayed microencapsulated disparlure into relatively small plots from the ground using a mistblower. The pheromone disrupted mating even at high populations. This sug-

gests that ground application in small plots may be useful for further testing of the confusion method; other pheromone batches, however, did not give such promising results.

Station scientists have also been involved in investigations of the (+) enantiomer of disparlure, which may be the actual pheromone. By testing racemic disparlure (which contains equal quantities of the (+) and (-) optical isomers, or enantiomers) and various analogues of the pheromone, Carde et al. (1977a) demonstrated that only the (+) enantiomer was attractive. In field tests, the (+) enantiomer was shown to initiate long range orientation better and to be more effective at trapping males than was the racemic mixture (Carde et al. 1977b). Finally, Carde et al. (1978) compared three methods of synthesizing the (+) enantiomer and found them equivalent in attractancy in field tests. The (+) enantiomer of dispar-

lure is now used extensively in survey and detection work.

Summary Extensive studies have been and are continuing to be carried out on natural enemies in an attempt to better understand their biology, behavior, and interrelationships with their hosts; to improve their effectiveness; and to establish new exotic species. We conclude with two of Britton's observations (1906): *There are several species of parasitic Hymenoptera, Diptera and predaceous insects that attack . . . the gypsy moth . . . , and they are also devoured by birds, toads and other insectivorous animals. But all of these working together do not control the pest.* He says further of importations, . . . *parasites may not be able to thrive, or even to live, in this country, but it is an experiment worth trying, and we certainly hope for much benefit from it.* **Our experimentation will continue.**

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About the maps

The following maps show the location and the intensity of defoliation experienced in Connecticut during 1975-1980. Although Table 1 shows four categories of defoliation, the 10-25% and 26-50% categories have been combined on the maps for this period.



Fig. 1 Defoliation, 1975

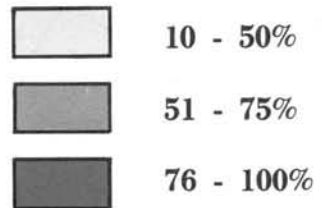






Fig. 2 Defoliation, 1976




	10 - 50%
	51 - 75%
	76 - 100%





Fig. 3 Defoliation, 1978



10 - 50%



51 - 75%



76 - 100%





Fig. 4 Defoliation. 1979







	10 - 50%
	51 - 75%
	76 - 100%





Fig. 5 Defoliation, 1980

	10 - 50%
	51 - 75%
	76 - 100%