Relation of forest site and stand characteristics to Douglas-fir tussock moth (Lep. Lymantriidae) outbreaks in California[1]

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Outbreaks of the Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* MCDUNNOUGH, can be explosive and of short duration. The three phases of population change-release, outbreak, and decline-occur within a 3- to 4-year period. Outbreaks develop from a buildup of resident populations and are rarely affected by dispersal of larvae from other population centers. In large outbreaks, several population centers may coalesce through larval dispersion and behave as a single population.

Outbreaks are more likely to occur in forests with certain site and stand characteristics than in others. DFTM outbreaks in California have developed in relatively open white fir stands on poor sites, ridge tops and upper slopes. These site and stand characteristics can be noted for use in classifying forest areas that are most susceptible to outbreaks and defoliation damage. Detection and monitoring of Douglas-fir tussock moth populations is easier when these activities are focused on areas most susceptible to outbreaks.

The largest outbreak ever recorded of the Douglas-fir tussock moth (DFTM), *Orgyia pseudotsugata* MCDUNNOUGH, occurred from 1972 to 1974 in the Pacific Northwest portion of the United States. It provided an opportunity to study the population dynamics of epidemic DFTM populations and to devise methods for directly controlling such outbreaks. Some of the difficulties encountered in efforts to suppress this outbreak showed that early detection is an urgent need in any control plan. Observations during and after the outbreak indicated that DFTM population buildups and defoliation intensities may be associated with certain site and stand conditions within host forests. Identification of these conditions could facilitate early detection of population buildups and potential or imminent outbreaks.

The U.S. Department of Agriculture's Expanded Douglas-Fir Tussock Moth Research and Development Program, initiated in late 1974, provided much of the funding and the overall management of studies on the various impacts of the recent outbreak. The DFTM Program ended September 28, 1978, and many of the studies sponsored by the Program will soon be published. They will provide a partial information base for an understanding of the dynamics of epidemic DFTM populations, the impact of outbreaks on forest values, and the suppression of outbreaks. This paper summarizes some of the information on outbreaks and describes one of the DFTM Program studies on site and stand characteristics of California forests historically subject to DFTM outbreaks.

The DFTM is a forest-defoliating insect native to the Douglas-fir – true fir forests of western North America. The most economically important forest trees which the tussock moth larva defoliates are Douglas-fir *(Pseudotsuga menziesii)*, grand fir *(Abies grandis)*, subalpine fir *(Abies lasiocarpa)*, and white fir *(Abies concolor)*. These trees are considered the preferred hosts because DFTM population buildups occur in forests dominated by one or more of these tree species. However, mature DFTM larvae can feed and complete their development on ponderosa pine *(Pinus ponderosa)*, Jeffrey pine *(Pinus jeffreyii)*, sugar pine *(Pinus lambertiana)*, western hemlock *(Tsuga heterophylla)*, and western larch *(Larix occidentalis)* after the preferred hosts have been stripped (WICKMAN *et al.*, 1971).

There is one generation of DFTMs a year. Adults may be present from late July through mid-November, depending on the locality and the weather. Upon emerging from her pupal cocoon, the wingless female adult produces a pheromone that attracts male moths. After mating, the female lays up to 400 eggs in a single mass (generally 150 to 250 eggs per mass) on the surface of her old cocoon, and dies. The eggs overwinter and the tiny 1st-instar DFTM larvae begin hatching late in May and early June, shortly following the appearance of new foliage on their host trees. The freshly flushed new foliage is the only acceptable food for the newly hatched larve and they crawl from their egg masses upwards and outwards to the new foliage. This behavioral pattern leads the young larvae to where new foliage is abundant as well as to optimal off-tree dispersal sites (EDWARDS, 1965; MITCHELL, 1979). Their long hair, their light body weight, and the long silken threads they spin from the host tree allow young DFTM larvae to be easily wind-borne and dispersed for short distances throughout the forest. The major dispersal of DFTM populations occurs at this time.

The young larvae feed on the new or current year's foliage. They grow slowly at first, but during their 5 to 7 moults or instars they grow progressively faster and eat proportionately more (WICKMAN *et al.*, 1971). Most of the defoliation damage is caused by the 4th to 7th instars. These mature larvae can complete their development on foliage of any age of most conifers. Upon completion of their larval period, the larvae pupate inside a thin silken cocoon. Pupation occurs from late July to the end of August and the pupal stage lasts 10 to 18 days (WICKMAN *et al.*, 1971).

OUTBREAKS

Description

Major outbreaks of the DFTM in Oregon and California that occurred between 1935 and 1965 have been analyzed by WICKMAN *et al.* (1973). These outbreaks went through three phases of population change: release, outbreak, and decline, all occurring within a 3- to 4-year period (fig. 1). During its endemic phase, DFTM is a rare-to-uncommon insect within the forest, and population densities are generally less than 1.0 larvae/1000 in^2 (0.64 m^2) of foliated branch area at the midcrown of trees (MASON, R.R., 1977). Several years of inconspicuous population buildup are required before the DFTM becomes noticeable in the forest and reaches the sub-outbreak level (2 to 20 larvae/1000 in^2 foliated branch area). After

Fig. 1: Hypothetical model of an outbreak cycle of the Douglas-fir tussock moth (WICKMAN *et al.*, 1973).

this point, a sharp rise in population – the «release» phase – can result in an outbreak (MASON, R.R., 1977).

It is believed that release occurs within the span of a year. Population growth is rapid; this is the time when defoliation by the DFTM first becomes visible. The 2nd year, or the outbreak phase, is the period of greatest DFTM abundance and most conspicuous tussock moth defoliation (fig. 1). Population densities of DFTM larvae reached 360 larvae/1000 in^2 of foliated branch area in some forests of eastern Oregon in 1973 of the 1972–74 outbreak, and many trees were stripped of all foliage by mid-July. Some outbreaks may collapse naturally at the end of this 2nd year, but frequently the number of eggs laid that fall indicate a high population the next year. Populations usually collapse during summer of the 3rd year of the outbreak (WICKMAN *et al.*, 1973). New egg masses are rarely found the following fall.

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Past outbreaks have been terminated by starvation of the young DFTM larvae, virus disease, or both. Probably the most important natural control agent of DFTM outbreaks is the nucleopolyhedrosis disease. It usually appears in the DFTM larval populations at the end of the 2nd year of the outbreak, and many of the egg masses laid the fall of the 2nd year are infected. A high percentage of new larvae hatching in the spring become infected and the population generally collapses before most of the insects reach the fourth instar. When diseased larvae die, their internal organs liquefy and their bodies fall to the ground or lie smeared over the foliage. The disease is transmitted to other feeding larvae and commonly kills both larvae and pupae.

Spread

In the past there has been considerable speculation about the spread of DFTM outbreaks. Large spray programs have been justified on the assumption that outbreaks will spread extensively beyond a population center, or «hot-spot», unless controlled. An examination of the dispersal mechanism of the DFTM shows that this is unlikely. The female moth is flightless and oviposition always occurs at the site of female pupation. Dispersal is passive and is limited to the easily wind-borne newly hatched larvae. Mortality of dispersing larvae is very high, as many land on a flat surface and nonhost materials. Larvae landing on a vertical surface move upward towards a food source if on a suitable host or to a dispersal site if on a nonsuitable host (MITCHELL, in press).

The studies cited here on the dispersal process of the DFTM are relatively recent and are few compared to studies on dispersal of the gypsy moth, *Lymantria dispar* (L.) (Lep. Lymantriidae), a close relative of the DFTM (BURGESS, 1913; COLLINS, 1915; COLLINS, 1917; LEONARD, 1967; LEONARD, 1971; McMANUS, 1973a, b). Data from some of these studies have been used to help simulate the effect of terrain features on the dispersal of newly hatched gypsy moth larvae through modification of an advecting Gaussian puff dispersion model (McMANUS, 1973; MASON, C.J., 1977). The general conclusions determined from dispersal studies on the gypsy moth may be applicable to the DFTM and other passively dispersed organisms.

Generally, these studies have shown that in the absence of updrafts the larvae are deposited near the source. Long-range transport is impossible for dispersion taking place in the forest canopy. Most airborne larvae probably travel no farther than adjacent trees before they get hung up by their silken threads. They may redisperse. Only those larvae that are lifted above the canopy or are blown from the forest edge have a chance to be lifted by updrafts or eddies to heights where they can be dispersed for hundreds of meters. Two factors – the elevation of the source or hatching population, and the updraft/downdraft wind pattern (induced by the terrain) – determine the deposition pattern. Most notable in observed dispersion patterns in hilly terrain is the localization of heavy infestations to the tops of ridges: the infestation appears to spread from ridge top to ridge top. Model simulations indicate that dispersion in hilly terrain does show «hops» from ridge tops to ridge top (McMANUS, 1973a; MASON, C.J., 1977).

Although small larvae are dispersed from population centers and may enrich the gene pool of other nearby populations, they apparently do not invade new habitats in the concentrations required to cause significant 1st-year defoliation.

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Fig. 2: Distribution of Douglas-fir tussock moth in Western North America as determined by collecting and pheromone trapping (LIVINGSTON & DATERMAN, 1977).

Since most outbreaks collapse within 3 or 4 years of their inceptions, there is little chance for dispersed larvae to build to outbreak levels (WICKMAN et al., 1973). Dispersing larvae late in the outbreak cycle are of poor quality; many are weakened by starvation and disease and their chances of starting a new outbreak are low – even in areas of abundant food supplies (MITCHELL, in press).

In the 1972-74 outbreak that covered large geographic areas in the Pacific Northwest, several population buildups apparently occurred simultaneously throughout the suitable forest habitats in the area, so that the population peaks of most centers occurred within a year or two of each other. The most favorable habitats for population growth probably reached the release phase first and suffered the most severe defoliation during the outbreak phase. In large outbreaks there may be considerable mixing of larvae so that separate population centers coalesce and behave as a single population (WICKMAN et al., 1973). This could explain

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why most populations in a large outbreak, regardless of their abundance level, collapse the same year.

STUDY OF SITE AND STAND CHARACTERISTICS

A recent detection survey using the DFTM pheromone provided firm evidence that low DFTM populations persist throughout most of the host type (fig. 2) (LIVINGSTON & DATERMAN, 1977). Male DFTMs were captured in 829 of 1315 trapping sites throughout the host forests. Moths were found in areas where they had not been previously reported and where populations were so low that they could not be detected by other sampling methods. Historically the DFTM has been a problem in only a few concentrated areas. Its presence throughout the host forest types raises the question of why the moth is a problem in some areas but not in others. This is a question that has been investigated in California, through the DFTM Program (WENZ et al., 1978). Outbreaks have repeatedly occurred in some of our white fir mixed conifer stands but not in other stands which were nearby and similar in appearance.

The objectives of the study were to

(1) Describe the site conditions and the tree and stand variables in white fir stands of California which have historically had DFTM outbreaks, and in white fir stands with no previous history of tussock moth activity.

(2) Develop a model to classify stands and sites as «susceptible» or «nonsusceptible» to DFTM outbreaks.

An additional study, separate from the major objectives but related to them was a check on moth abundance by means of pheromone traps.

Methods

Study areas were in the Stanislaus, Eldorado, and Modoc National Forests, in the Central Sierra Nevada and northeastern region of California. Outbreak and non-outbreak areas were selected using forest type maps and records of past DFTM infestations. DFTM populations were very low during the period of this study and visible defoliation could not be used as a selection criteria of study areas. A total of 66 outbreak plots (198 1/10-acre subplots) and 67 non-outbreak plots (201 subplots) were eventually selected for study.

We recorded latitude, slope, elevation, aspect, and topography at each subplot and calculated annual radiation index from the latitude, slope, and aspect using tables by FRANK & LEE (1966).

We listed the tree species at each subplot and measured the following tree and stand variables: tree diameters at breast height (DBH) (4.5 feet high or 1.37 meters high), tree condition (live, dead, snag, stump, diseased), stand structure (one-story or multiple-story stand), average story height, percent crown cover, estimate of stand density, basal area, and site index. All trees 4 inches DBH (10.16 cm) and over in the subplots were measured. A site index was calculated for each plot using the DUNNING (1942) classification system for mixed conifers in the Sierra Nevada. The index was determined from the height-age measurements taken from six dominants (primarily) and codominants among four species: white fir, Douglas-fir, ponderosa pine and sugar pine.

These data were tested as independent variables by a full screen program. A dummy variable for outbreak versus non-outbreak served as the dependent variable in the analysis to screen the independent variables for linear discrimination. The adjusted coefficient of determination, $\bar{R}^2$, was used to eliminate less important variables. The remaining variables were more thoroughly evaluated by estimating numerous discriminant functions from a random half of the data. The remaining observations were then classified using each of the estimated discriminant functions. The final evaluation of each variable was based on the classification results.

Results and discussion

In the full screen analysis, topography was the single most important variable (table 1). Outbreaks tended to occur on ridge tops and upper slopes, whereas non-outbreak areas were more evenly distributed over the range of topography classes (table 2). This finding is consistent with observations in California and other areas, but does not imply that outbreaks occur on all within-type ridge tops and upper slopes. Similar findings were reported in defoliation studies of the 1972-74 DFTM outbreak in Idaho. Forest stands of grand fir and Douglas-fir in Idaho situated on ridge tops and upper slopes showed significantly higher defoliation by DFTM larvae than stands at midslope and lower slopes (STOSZEK, 1977). The association of high outbreak frequencies and defoliation damage intensities with forest stands on upper slopes and ridge tops may be the result of either or both of the following: (1) buildup of resident populations under favorable environmental conditions, and (2) concentration of larvae deposited through the dispersal process in hilly terrain as described by C.J. MASON (1977).

Topography and site class were the two most important combined variables (table 1). Outbreak plots tended to be associated with poor sites (about 70% on site III or worse), with approximately 73% of the non-outbreak plots in site class I or II (table 2). This finding is consistent, as ridge tops and upper slopes are often associated with poorer soils and less productive sites.

Basal area of white fir was the third most important variable in combination with topography and site index. Although there was little difference between the

Table 1: Nine best discriminant site and stand variables and combinations of variables associated with tussock moth outbreak, California, ranked by best adjusted R^2 value[1] (source: WENZ et al., 1978).

Number of variables	Variables									
	Best adjusted $\bar{R}^2$	Topo-graphy	Site index	Basal area white fir	Stand density	Crown cover	Stand structure	Eleva-tion	Total basal area	Species composi-tion
1	.3186	X								
2	.5042	X	X							
3	.5148	X	X	X						
4	.5216	X	X		X	X				
5	.5261	X	X	X	X	X				
6	.5303	X	X	X	X	X	X			
7	.5325	X	X	X	X	X	X	X		
8	.5296	X	X	X	X	X	X	X	X	
9	.5285	X	X	X	X	X	X	X	X	X

[1]X = variable included

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Table 2: Frequency distributions of selected site and stand variables associated with tussock moth out-breaks, California, 1976-77 (source: WENZ et al., 1978).

| Variable | Frequency | | | |
| | Outbreak area | | Non-outbreak area | |
	Plots	Pct of total	Plots	Pct of total
Topography:				
Ridge-top	73	36.9	28	13.9
Upper slope	125	63.1	75	37.3
Midslope	0	0	60	29.9
Lower slope	0	0	32	15.9
Bottom	0	0	6	3.0
Site class:				
I	7	3.5	103	51.2
II	53	26.8	43	21.5
III	84	42.4	22	10.9
IV	44	22.2	26	12.9
V	10	5.1	7	3.5
Stand density:				
Dense	41	20.7	45	22.4
Intermediate	85	42.9	99	49.3
Open	72	36.4	57	28.3
Stand structure:				
Single-storied	53	26.8	29	14.4
Two-storied	139	70.2	167	83.1
Multi-storied	6	3.0	5	2.5
Aspect				
N	74	37.4	41	20.4
NE	14	7.0	32	15.9
E	9	4.5	16	8.0
SE	13	6.6	13	6.5
S	16	8.1	28	13.9
SW	21	10.6	20	10.0
W	41	20.7	19	9.5
NW	10	5.1	32	15.8

Table 3: Species composition and basal area for the five most prevalent tree species on outbreak and non-outbreak plots, California 1976–77 (source: WENZ *et al.*, 1978).

Species	Percent species composition		Basal area, ft^2/10th acre		Percent basal area	
	Outbreak	Non-outbreak	Outbreak	Non-outbreak	Outbreak	Non-outbreak
	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE
White fir	57.6 ± 2.0	59.4 ± 2.2	12.3 ± 0.6	19.3 ± 1.1	52.7 ± 2.2	57.8 ± 2.2
Ponderosa pine	20.6 ± 1.6	21.4 ± 1.6	5.9 ± 0.5	6.8 ± 0.6	25.6 ± 1.7	23.0 ± 1.7
Jeffrey pine	17.0 ± 1.5	14.5 ± 1.5	4.4 ± 0.5	4.0 ± 0.4	16.4 ± 1.5	12.3 ± 1.3
Incense cedar	3.9 ± 1.5	1.5 ± 0.3	1.1 ± 0.2	0.8 ± 0.2	4.4 ± 0.7	2.1 ± 0.5
Sugar pine	0.6 ± 0.2	0.4 ± 0.2	0.2 ± 0.1	0.2 ± 0.1	0.8 ± 0.3	0.5 ± 0.2
Total			23.9 ± 0.8	32.7 ± 1.2		

outbreak and the non-outbreak plots in percent composition of the five most common species (table 3), white fir basal area and also total basal area were significantly higher in the non-outbreak plots.

The combination of topography and site class accounts for the biggest increase in $\overline{R}^2$ values. Inclusion of white fir basal area increased the $\overline{R}^2$ value by only 0.0106, less than one-fifth the gain from adding the second variable, site class. The remaining variables add little to our ability to discriminate between outbreak and non-outbreak plots.

Non-outbreak plots had a significantly higher mean upper story than the outbreak plots, averaging about 18 feet higher (table 4). This variable had a relatively high correlation with total basal area and basal area of white fir; results appear

Table 4: Means and standard errors for selected site and stand variables, California 1976–77 (source: WENZ *et al.*, 1978).

Variable	Outbreak	Non-outbreak
	$\overline{X} \pm$ SE	$\overline{X} \pm$ SE
Average upper story height	77.1 ± 1.7 ft.	95.1 ± 2.1 ft.
Elevation	5929 ± 22 ft.	5528 ± 48 ft.
Slope	17.6 ± 0.9%	20.6 ± 0.8%
Radiation index	0.4701 ± .0036	0.4664 ± .0039
Percent crown cover	43.9 ± 16.1%	55.1 ± 13.9%

consistent with the tendency of non-outbreak plots to occur on the better sites. Outbreak plots had less crown cover and averaged about 400 feet higher in elevation than the non-outbreak plots (table 4). Differences in slope and radiation index between outbreak and non-outbreak plots were not significant and did not have high correlations with other variables.

To develop a model to classify stands and sites as susceptible or not susceptible to outbreak, we eliminated all but six variables: topography, site index, basal area of white fir, stand density, percent crown cover and elevation. For the linear discriminant analysis, four runs were made: run one used the first three variables listed, and the three subsequent runs added one variable each in the order listed. All four runs resulted in more than 95% discrimination of outbreak sites (the main objective) and 73% discrimination of non-outbreak sites. Run one, using three variables (topography, site index, and basal area of white fir) gave the best classification of outbreak sites and stands, designating 97% of the outbreak plots correctly.

Pheromone trap catch analysis

Although DFTM populations were sparse throughout our outbreak and non-outbreak study areas, we wondered if pheromone traps could indicate different levels of DFTM population abundance among the outbreak and non-outbreak areas. We placed DFTM pheromone traps baited with two concentrations of the pheromone in 17 outbreak and 11 non-outbreak study sites. The relative mean trap catches in the outbreak plots were consistently higher than in the non-outbreak plots (table 5). Generally, traps in outbreak plots caught about twice the

Table 5: Mean adult male tussock moth catches in pheromone traps in outbreak and non-outbreak plots [1], by National Forest, California, 1977 (source: WENZ et al., 1978).

National Forest	Bait - 1		Bait - 2	
	Outbreak	Non-outbreak	Outbreak	Non-outbreak
	$\bar{X}$ + SE	$\bar{X}$ + SE	$\bar{X}$ + SE	$\bar{X}$ + SE
Stanislaus	121.0 + 21.7	80.4 + 48.2	47.3 + 7.6	61.9 + 40.6
Eldorado	207.8 + 29.8	57.6 + 14.9	150.4 + 23.2	36.1 + 12.1
Modoc	110.0 + 31.7	89.9 + 31.0	57.5 + 18.0	40.3 + 17.6
Total	148.4 + 18.6	74.7 + 18.7	86.7 + 15.1	47.3 + 16.9

[1]Based on 17 outbreak plots and 11 non-outbreak plots.

number of moths trapped in non-outbreak plots. The one exception was a trap with bait 2 on a non-outbreak plot on the Stanislaus National Forest, immediately down-slope from an outbreak site, on which we also trapped larger numbers of moths than on the other outbreak plots on the Stanislaus. The pheromone traps catch data, when combined with larval population estimates indicated also that DFTM populations in some outbreak areas were slightly higher in 1977 than 1976, although still at what are considered low densities. The trap catch data in general imply that even at low densities, there may be population differences between outbreak and non-outbreak areas.

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