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Predicting Pine Sawfly Population Densities and Subsequent Defoliation with Pheromone Traps

PÄIVI LYYTIKÄINEN-SAARENMAA[1,4], MARTTI VARAMA[2], OLLE ANDERBRANT[1],
MIKKO KUKKOLA[2], ERIK HEDENSTRÖM[3] AND HANS-ERIK HÖGBERG[3]

[1]Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
[2]The Finnish Forest Research Institute, Vantaa Research Centre, P.O.Box 18, FIN-01301 Vantaa, Finland
[3]Chemistry, Department of Chemistry and Process Technology, Mid Sweden University,
S-851 70 Sundsvall, Sweden
[4]Present Address: Faculty of Forestry, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland

ABSTRACT Field trials were conducted from 1989 to 1993 in Finland to develop a monitoring and prediction method using pheromone traps for European pine sawfly (*Neodiprion sertifer* Geoffr.) population densities and needle defoliation. Three traps per site were baited with 100 µg of (2*S*,3*S*,7*S*) - 3,7 - dimethyl - 2 - pentadecyl acetate (diprionyl) at sites representing advanced pine stands. The number of overwintering eggs per sample branch was used to evaluate the effectiveness of using pheromone traps to estimate sawfly populations. The relationships between the number of males in traps, the number of eggs per branch in the subsequent generation, and the number of needle-year classes after the subsequent growing season were highly correlated. The risk threshold for moderate to heavy defoliation was around 1,000 males/trap. Our results suggest that after some minor improvements, a pheromone-based monitoring system for the European pine sawfly would provide an effective tool for integrated pest management programs and successful forest management in coniferous pine-dominated forests.

THE EUROPEAN PINE sawfly (*Neodiprion sertifer* Geoffroy) (Hym., Diprionidae) is a common pest of pine in Eurasia and North America (Pschorn-Walcher 1982, Smith 1993). The species occurs in Finland up to the northern timberline, where the main host is Scots pine (*Pinus sylvestris* L.) (Viitasaari and Varama 1987). *Neodiprion sertifer* overwinters in the egg stage, larvae consume mature needles from June to July until pupation, and new adults emerge from August to early October. Outbreaks in Fennoscandia can reach over hundreds of thousands of hectares, including pine forests from seedlings to mature trees. Populations have extensive, large-scale peak densities every 20 to 30 years, but regional outbreaks can occur every 5 to 6 years. Scattered local outbreaks abound almost every year (Juutinen and Varama 1986, Hanski 1987).

Defoliation by European pine sawfly seldom kills trees, but it decreases tree increment considerably (Austarå et al. 1987, Lyytikäinen-Saarenmaa 1999). Tree mortality after an outbreak period was approximately 4% of the total number of trees in defoliated stands (Juutinen 1967, Tiihonen 1970), but the mortality level can be as high as 50% in young plantations (Austarå et al. 1987). Height growth decreased between 26% and 63%, volume growth decreased between 33% and 50%, and radial growth decreased between 20% and 84% after sawfly damage (Austarå et al. 1987, Britton 1988, Sanchez-Martinez and Wagner 1994). After moderate defoliation by *N. sertifer* in Finland, radial growth losses were estimated to be 20% on average (Tiihonen 1970) and height growth

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losses were 29% (Lyytikäinen-Saarenmaa 1999); however, there is a great need for a comprehensive examination of these questions. Defoliation is likely to reduce tree growth and timber yield, but these aspects have quite often been considered to be less important than potential tree mortality. However, economically significant reductions in increment might occur even after a single defoliation period and even when densities remain below those required to initiate a secondary attack by scolytid bark beetles. The grim reality is that *N. sertifer* causes serious consequences to forestry; in Finland alone, the estimated economic value of growth losses might reach up to 6.0 million USD (60 USD/ha) after a single-year, large-scale outbreak (P. Lyytikäinen-Saarenmaa and E. Tomppo, unpublished data).

The current sampling methods used to estimate European pine sawfly population densities include counting overwintering egg clusters in early spring or cocoons in mid summer. They may roughly detect population trends and predict damage but are time and labor consuming (Allen et al. 1986). It is essential to accurately predict the risk of sawfly epidemics and defoliation intensity in order to be prepared in time for outbreaks. Using pheromone traps to provide estimates of population trends and manage peak densities is available for many other insect pests, particularly within the orders Lepidoptera and Coleoptera (Howse et al. 1998). The most obvious aspect of pheromone-based sampling systems is to produce a quantitative relationship between trap catches and immature stages of the following generation(s) of pests. However, previous attempts to use pheromone-baited traps for monitoring purposes have provided contradictory results.

In the early 1990s, a new method for identifying and synthesizing the *N. sertifer* sex pheromone, (2*S*,3*S*,7*S*) -3,7 - dimethyl - 2 - pentadecyl (diprionyl) acetate or propionate (Högberg et al. 1990), launched development of monitoring and control programs in Scandinavia (Anderbrant 1993, Jönsson and Anderbrant 1993, Anderbrant et al. 1995, Wedding et al. 1995, Östrand et al. 1999). The first long-term monitoring study for predicting population densities of *N. sertifer* using pheromone traps was conducted in young pine plantations (Lyytikäinen-Saarenmaa et al. 1999). The development of a predictive tool that warns forest managers and forest owners of European pine sawfly outbreaks would be of considerable practical importance in pest management programs.

Our objective was to study the effectiveness of using pheromone-baited traps to estimate forthcoming population levels of the European pine sawfly and predict defoliation risks in naturally regenerated advanced Scots pine stands. This was done by comparing the number of sawfly males captured in traps in the fall with the number of eggs per pine branch of the subsequent generation. The correlation between trap catches and subsequent defoliation was also studied.

Materials and Methods

Sites and Sampling. The study was conducted from 1989 to 1993 in naturally regenerated forests representing the advanced stand development class (mid rotation and mature Scots pine stands) on dry or dryish forest sites in south and central parts of Finland. In 1989, mean tree age was 46.3 years (± 20.2 SD) and mean tree density was 1,888 stems/ha (± 1,015 SD). The estimated average annual height growth was 0.21 m (± 0.06 SD). The total number of sites for each year varied from 6 to 32 (Table 1); they were monitored for 1 to 4 years until local populations collapsed. Three monitoring traps were placed at each site in the form of a triangle. The distance between traps was approximately 50 m. The stand characteristics of experimental sites were, in most cases, measured after the growing season of the first monitoring year using a circular sample plot survey method. The position of each pheromone trap was used as the middle point for a circular plot for a total of three plots on each site. The plot radius was chosen depending on stand density and so that there were at least 20 pines in a plot. The data from the three circular plots were averaged for each site to produce an estimate of stand parameters (Table 1).

Table 1. Means of stand characteristics of the sites, numbers of males captured per trap, and numbers of subsequent overwintering eggs per branch in each year of the study. For details of stand characteristics, see the Materials and Methods section. Standard deviations of the stand characteristics are shown in parenthesis.

	1989	1990	1991	1992
Number of sites	32	31	6	7
Basal area (m^2ha^{-1})	16.9 (4.6)	17.0 (3.6)	20.6 (4.3)	19.7 (1.7)
Mean diameter (cm)	14.5 (4.6)	15.3 (4.7)	15.0 (4.6)	16.7 (5.7)
Mean height (m)	11.8 (3.4)	12.1 (3.4)	13.0 (4.7)	13.8 (4.4)
Number of males/trap	186.0 (160.5)	446.0 (593.8)	132.2 (174.8)	203.9 (160.6)
Number of eggs/branch	37.8 (52.6)	91.6 (221.7)	5.4 (8.3)	3.7 (4.3)

Diameter at breast height was measured for all trees; every fourth tree was chosen for height measurement to an accuracy of ±0.5 m using a Suunto hypsometer. The diameter and height of each tree were projected for other years of the monitoring period using a diameter increment model developed by Pukkala (1989) and a height increment model developed by Nyyssönen and Mielikäinen (1978). Tree basal area per hectare was then calculated for each year as well as mean diameter and mean height, both weighted by basal area.

Branch samples (0.5 m) were collected early each year from 2 to 4 sample trees per site at about the middle point of the triangle in order to count the number of overwintering egg clusters and eggs and to estimate the degree of defoliation. Nine branch samples were collected per tree (three samples each from the upper, middle, and lower third of the crown) and placed in sealed plastic bags in an outdoor shelter. Egg-bearing shoots were kept in water at room temperature for approximately 1 to 2 weeks before the number of eggs was counted. The eggs represented the subsequent generation and were compared to trap catches. The degree of defoliation was determined by estimating the number of remaining needles to an accuracy of a quarter of a needle-year class one year after each trap catch. Scots pine has approximately 2.5 to 4 needle-year classes in southern and mid Finland.

Sawfly Monitoring. The population density of sawfly males was measured by placing three Lund-I sticky traps about 2 m above ground. Traps were baited with (2*S*,3*S*,7*S*) - 3,7 - dimethyl - 2 - pentadecyl acetate (Högberg et al. 1990) applied on dental cotton roll dispensers. The substance was of a high stereoisomeric purity (> 99 %) and contained less than 0.01% of the antagonist (2*S*,3*R*,7*R*) - isomer (Anderbrant et al. 1992b). The traps were baited with 100 μg diprionyl acetate that gave an average release rate of 2.8 μg/d from the cotton roll dispensers over a 30-day period and, on average, a double release rate for a 2-week period (Anderbrant et al. 1992a). The trapping period started in early August each year and extended to mid October. Baits and sticky bottoms were renewed either every second week (1989) or every fourth week (1990 to 1992).

Data Processing. Data were processed applying analysis of variance (ANOVA) and linear regression analysis (BMDP Statistical Software 1994). A square root transformation (Sokal and Rohlf 1981) was applied to improve normality and homoscedasticity of the parameters when necessary. The figures present the original, untransformed data. The average trap catch of three traps was used in analyses. The differences between years in number of eggs per branch and trap catch were tested by one-way ANOVA. The relationships between trap catch and number of eggs in the subsequent generation and stand parameters were determined by linear regression analyses.

Results

Both trap catch and the number of eggs per branch reached peak values in 1990 (Table 1). ANOVA revealed significant differences in trap catch between years (F = 2.96; df = 3,72; P = 0.038), but not in egg number (F = 0.99; df = 3,72; P = 0.404). When trap catch was regressed linearly with number of eggs per branch in the subsequent generation, using combined data from all years, the coefficient of determination was high (76%) (Fig. 1). The relationships were never significant within a single year.

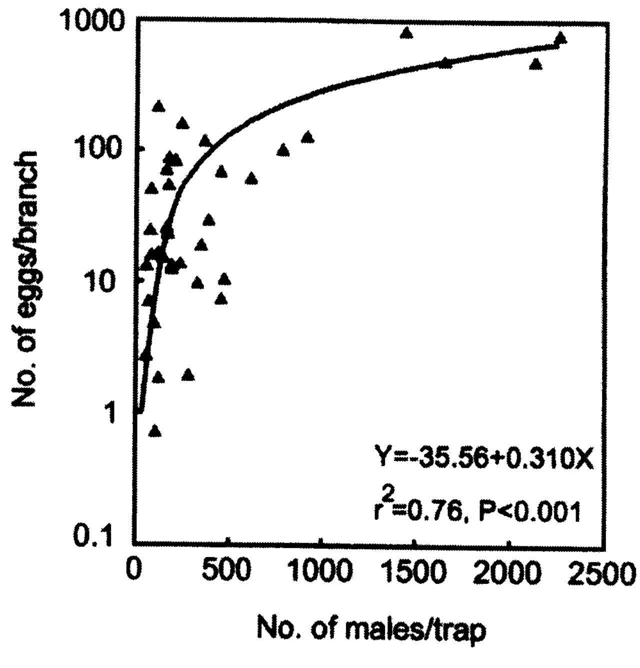

Figure 1. Relationship between the number of *Neodiprion sertifer* males captured in traps baited with 100 μg diprionyl acetate and the number of eggs per branch in the subsequent generation.

Trap catch data were divided into two groups before analyzing relationships with the number of needle-year classes after a subsequent growing season: low male density (< 400 males/trap) and high male density (> 400 males/trap). When male density was low, the relationship between trap catch and number of needle-year classes was not significant (Fig. 2A). However, the regression line indicated a negative relationship trend between these factors. On the contrary, a different pattern was revealed at high male densities. The relationship between trap catch and number of needle-year classes after the subsequent growing season had a highly significant negative correlation. It is obvious that a risk threshold for moderate to heavy defoliation (and thus a loss of almost all but current year needles) may occur when the number of males caught exceeds 1,000 per trap (Fig. 2B). However, the data from the four sites with the highest male densities should be regarded with caution. These four sites were heavily defoliated in 1990. Nuclear polyhedrosis virus (NPV) was applied in the summer of 1991 prior to the last estimation of the number of needle-year classes in winter. This might have caused a drop in defoliation intensity. Without NPV application, defoliation levels would have been even higher.

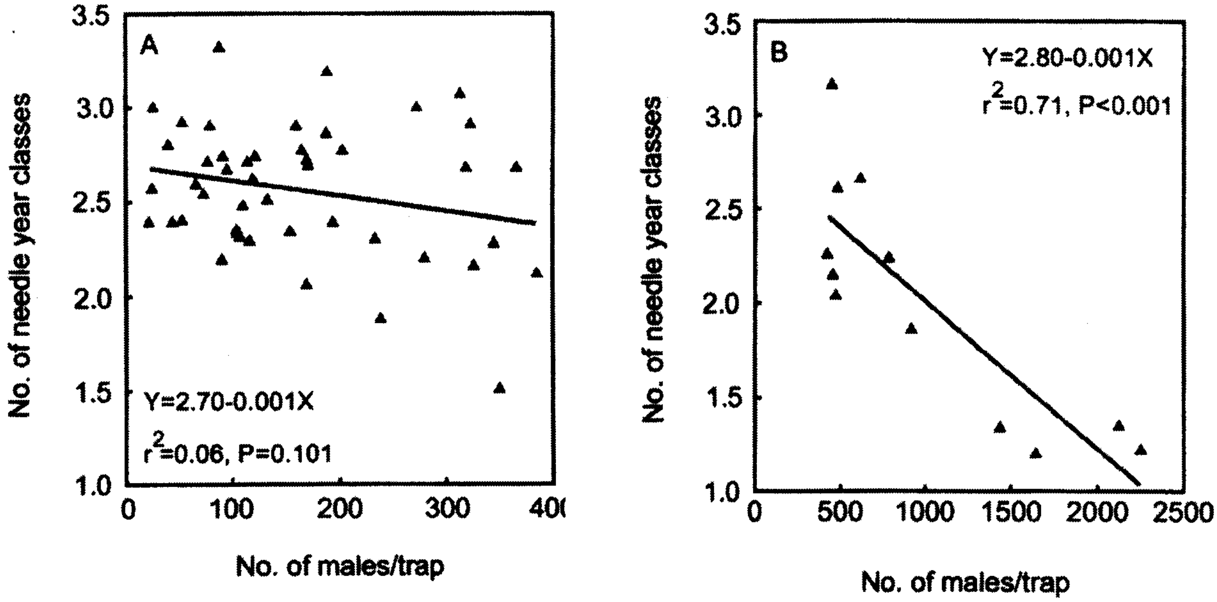

Figure 2. Relationship between the number of *Neodiprion sertifer* males captured in traps baited with 100 µg diprionyl acetate and the number of needle-year classes after the subsequent growing season from 1989 to 1993. (A) male density < 400 males/trap; (B) male density > 400 males/trap.

Discussion

European pine sawfly populations had one peak year (1990) and afterwards rapidly declined toward endemic levels. However, our study period was relatively short and resulted in an inability to follow long-term population trends. The number of males in traps was still quite high despite the low number of eggs per branch in the subsequent generation (Table 1). This relatively high level in male numbers could be a consequence of an immigration of males from nearby forest stands (Sweeney et al. 1990) or the termination of a prolonged diapause after high population densities associated with epidemics (Juutinen and Varama 1986). Moreover, virus epizootics may alter the sex ratio of the surviving population to create a male biased population (Lyons 1964).

The number of eggs per branch in the subsequent generation showed a strong relationship with the number of males in traps, indicating the ability of traps to give a proper estimate of future population densities. Generally, the accuracy of the prognosis would be better if several sites with moderate to high sawfly densities were available, particularly when densities are increasing (Lyytikäinen-Saarenmaa et al. 1999). Egg parasitism might hamper European pine sawfly density estimates in some years because egg mortality can be as high as 90% after the population's peak (Juutinen and Varama 1986). The number of eggs per sample branch was used to estimate needle damage risks. During the early stage of epidemics, when stands have only suffered slight defoliation, about 250 to 300 healthy eggs per branch (length 0.5 m) are needed for almost all mature needles to be consumed during the subsequent growing season (Juutinen and Varama 1986). The corresponding egg number during the second outbreak year is only around 100 healthy eggs per branch. Several of our sites included those risk threshold densities of eggs, particularly in 1989 and 1990. Therefore, when predicting the number of eggs and forthcoming defoliation using the number of males caught in pheromone traps, we can be one (or even more) step ahead and have more time to prepare and plan for control measures. These results are promising, suggesting that pheromone traps can be applied as part of integrated pest management programs after some improvements of the method.

Trap catch correlated well enough with the number of eggs in the subsequent generation, and obviously with larvae causing the damage, as also observed earlier (Lyytikäinen-Saarenmaa et al. 1999). It is generally accepted that the amount of growth loss after defoliation is roughly proportional to the amount of foliage defoliated (Sanchez-Martinez and Wagner 1994, Lyytikäinen-Saarenmaa 1999). Defoliation of pines early in the growing season usually causes a reduction in current growth, but in some cases even higher reductions will follow a year or several years later (Lyytikäinen-Saarenmaa 1999). Increment losses, including height, radial, and volume growth, could be estimated by knowing the number of remaining needle-year classes. It is possible to predict the degree of defoliation using the average number of males caught, which represents pine sawfly population density in an area.

Searching for a threshold value of defoliation risks is the main question in pest management programs. According to our results, having less than 400 males per trap does not create risks for remarkable needle damage, but at higher male densities (> 400 males per trap), considerable forest damage is likely. Our results suggest that having at least 1,000 males per trap implies a need for control methods, e.g. virus application and intensive observation of a pest situation. If the number of sawfly males greatly exceeds 1,000 per trap, loss of all old needles (and, in some cases, part of the current needles) can be expected. Our data contained only a few sites with such high population levels, which normally appear in epidemics. It is likely that additional observations from sites with high population levels would indicate a lower threshold value than mentioned above. The pheromone trap method may help to predict defoliation in the near future, providing more accurate damage estimates than traditional methods. Our method could also very easily be included into the framework of integrated pest management and modern decision support systems, linking pest and forest ecosystem management.

When pest densities are at a risk threshold, the value of growth loss and killed trees normally equals the maximum amount of money spent on control measures to prevent insect damage (Austarå et al. 1987). The risk threshold fluctuates depending, for example, on the geographic location of the area, stand age, price of standing timber, transport costs of timber, and domestic and international trade. It is possible to estimate the economic value of growth losses based on the proportion of tree species in the area, timber volume in the stand, annual increment, average intensity of insect defoliation, percentage of killed trees, and timber value. A model that predicts defoliation and increment losses and evaluates the losses using pheromone trap catches would be highly practical for forest managers and forest owners. After improvements, our pheromone-based monitoring system for the European pine sawfly would provide an effective tool for integrated pest management programs and successful forest management in coniferous pine-dominated forests.

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References Cited

Allen, D.C., I.P. Abrahamson, D.A. Eggen, G.N. Lanier, S.R. Swier, R.S. Kelley and M. Auger. 1986. Monitoring spruce budworm (Lepidoptera: Tortricidae) populations with pheromone-baited traps. Environ. Entomol. 15: 152-165.

Anderbrant, O. 1993. Pheromone biology of sawflies. In: Wagner, M.R. and K.F. Raffa, (eds.) Sawfly life history adaptations to woody plants. San Diego: Academic Press: 119-154.

Anderbrant, O., M. Bengtsson, J. Löfqvist and P. Baeckström. 1992a. Field response of the pine sawfly *Neodiprion sertifer* to controlled release of diprionyl acetate, diprionyl propionate and trans-perillenal. J. Chem. Ecol. 18: 1707-1725.

Anderbrant, O., J. Löfqvist, H.-E. Högberg and E. Hedenström. 1995. Development of mating disruption for control of pine sawfly populations. Entomol. Exp. Appl. 74: 83-90.

Anderbrant, O., J. Löfqvist, H.-E. Högberg, E. Hedenström, A.-B.Wassgren, G. Bergström, M. Bengtsson and G. Magnusson. 1992b. Field response of the pine sawfly *Neodiprion sertifer* to the pheromones (2S, 3S, 7S)-diprionyl acetate and its stereoisomers. Entomol. Exp. Appl. 62: 169-181.

Austarå, Ø., A. Orlund, A. Svendsrud and A. Weidahl. 1987. Growth loss and economic consequences following two years defoliation of *Pinus sylvestris* by the pine sawfly *Neodiprion sertifer* in West-Norway. Scand. J. For. Res. 2: 111-119.

BMDP Statistical Software. 1994. BMDP new system for Windows. Version 1.0. Los Angeles: BMDP Statistical Software, Inc.

Britton, R.J. 1988. Physiological effects of natural and artificial defoliation on the growth of young groups of lodgepole pine. Forestry 61: 165-175.

Hanski, I. 1987. Pine sawfly population dynamics: patterns, processes, problems. Oikos 50: 327-335.

Högberg, H.-E., E. Hedenström, A.-B. Wassgren, M. Hjalmarsson, G. Bergssröm, J. Löfqvist and T. Norin. 1990. Synthesis and gas chromatographic separation of eight stereoisomers of diprionol and their acetates, components of the sex pheromone of pine sawflies. Tetrahedron 46: 3007-3018.

Howse, P.E., I.D.R. Stevens and O.T. Jones. 1998. Insect pheromones and their use in pest management. London: Chapman & Hall.

Jönsson, P. and O. Anderbrant. 1993. Weather factors influencing catch of *Neodiprion sertifer* (Hymenoptera: Diprionidae) in pheromone traps. Environ. Entomol. 22: 445-452.

Juutinen, P. 1967. Zur Bionomie und zum Vorkommen der roten Kiefernbuschhornblattwespe (*Neodiprion sertifer* Geoffr.) in Finland in den Jahren 1959-65. Communicationes Instituti Forestalis Fenniae 63: 1-129. (In German with Finnish summary)

Juutinen, P. and M. Varama. 1986. Occurrence of the European pine sawfly (*Neodiprion sertifer*) in Finland during 1966-83. Folia Forestalia 662: 1-39. (In Finnish with English summary)

Lyons, L. A. 1964. The European pine sawfly, *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae). A review with emphasis on studies in Ontario. Proceedings of Entomological Society of Ontario 94: 5-37.

Lyytikäinen-Saarenmaa, P. 1999. Growth responses of Scots pine (Pinaceae) to artificial and sawfly (Hymenoptera: Diprionidae) defoliation. Can. Entomol. 131: 455-463.

Lyytikäinen-Saarenmaa, P., O. Anderbrant, J. Löfqvist, E. Hedenström and H.-E. Högberg. 1999. Monitoring the European pine sawfly population densities with pheromone traps in young pine plantations. For. Ecol. Manage. 124: 113-121.

Nyyssönen, A. and K. Mielikäinen. 1978. Estimation of stand increment. Acta For. Fenn. 163: 1-40. (In Finnish with English summary)

Östrand, F., R. Wedding, E. Jirle and O. Anderbrant. 1999. Effect of mating disruption on reproductive behavior in the European pine sawfly, *Neodiprion sertifer* (Hymenoptera: Diprionidae). J. Insect Behav. 12: 233-243.

Pschorn-Walcher, H. 1982. Underordnung Symphyta. In: Schwenke, W. (ed.) Die Forstchädlinge Europas. Bd. 4: Hautflügler und Zweiflügler. Parey, Hamburg, Berlin: 4-234.

Pukkala, T. 1989. Predicting diameter growth in even-aged Scots pine stands with a spatial and non-spatial model. Silva Fennica 23: 101-116. (In Finnish with English summary)

Sanchez-Martinez, G. and M.R. Wagner. 1994. Sawfly (Hymenoptera: Diprionidae) and artificial defoliation affects above- and below-ground growth of ponderosa pine seedlings. J. Econ. Entomol. 87: 1038-1045.

Smith, D.R. 1993. Systematics, life history, and distribution of sawflies. In: Wagner, M.R. and K.F. Raffa, (eds.) Sawfly life history adaptations to woody plants. San Diego: Academic Press: 3-32.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition. San Francisco: W.H. Freeman and Company.

Sweeney, J.D., J.A. McLean and R.F. Shepherd. 1990. Factors affecting catch in pheromone traps for monitoring the western spruce budworm, *Choristoneura occidentalis* Freeman. Can. Entomol. 122: 1119-1130.

Tiihonen, P. 1970. Ruskean mäntypistiäisen (*N. sertifer* Geoffr.) tuhojen vaikutuksesta männiköiden kasvuun Etelä-Pohjanmaalla, Pohjois-Satakunnassa ja Länsi-Uudellamaalla vuosina 1960-1967. Metsäntutkimuslaitoksen julkaisuja 71: 1-21.

Viitasaari, M. and M. Varama. 1987. Sawflies 4. Conifer sawflies (Diprionidae). University of Helsinki. Department of Agricultural and Forest Zoology. Reports 10: 1-79. (In Finnish with English summary)

Wedding, R., O. Anderbrant and P. Jönsson. 1995. Influence of wind conditions and intertrap spacing on pheromone trap catches of male European pine sawfly, *Neodiprion sertifer*. Entomol. Exp. Appl. 77: 223-232.

Effects of Gypsy Moth Defoliation in Oak-Pine Forests in the Northeastern United States

R.M. MUZIKA[1] AND A.M. LIEBHOLD[2]

[1]Department of Forestry, University of Missouri, Columbia, MO 65211 USA
[2]United States Department of Agriculture, Forest Service, Northeastern Research Station, 180 Canfield St., Morgantown, WV 26505 USA

ABSTRACT Dendrochronology data from two oak-pine (*Quercus-Pinus*) forests in the northeastern United States (New Jersey and Massachusetts) were examined to understand the influence of defoliation on radial ring width of highly preferred trees (*Quercus*) and slightly less preferred trees (*Pinus*). Over a 5-year period, defoliation from gypsy moth (*Lymantria dispar* L.) ranged from 2.4% to 86.4% and mortality was nearly 50% of *Q. alba* stems in Massachusetts. The effect of individual tree defoliation, although generally negative, differed slightly among all the oak species. Stand-level defoliation negatively influenced growth of oaks and pines on both sites. There was no compensatory response apparent in the radial growth of pitch pine. The effect of defoliation was also evident in the relative production of earlywood and latewood with a pronounced dominance of earlywood production in host trees during the same year as defoliation and often in the following year.

AS A NON-NATIVE, polyphagous species in North America, the gypsy moth (*Lymantria dispar* L.) can negatively influence many forest types. Its preferred host are oaks (*Quercus* spp.), the dominant overstory tree species in the eastern United States. Pines (*Pinus* spp.) generally are considered less likely to be defoliated by gypsy moth than oaks (Liebhold et al. 1995), although defoliation of pines has been widely observed and documented (Brown et al. 1988, Gottschalk and Twery 1989, Montgomery et al. 1990). When gypsy moth larval densities are high and defoliation is widespread, shifting to a less preferred host is common. Oak-pine forests, therefore, may be classified as susceptible to gypsy moth. Oak-pine forests are also typically found on the most xeric portion of the landscape capable of supporting forests.

Site factors may exacerbate defoliation-related stress and may account for increased mortality in forests with high defoliation. Although some research findings support this assumption, Davidson et al. (1999) suggest that the evidence is contradictory, and that at least an equal number of studies have demonstrated that trees growing on poor sites have less mortality than those on good sites. Gansner (1987) suggested that poor quality trees were physiologically adapted to stress conditions and therefore could endure defoliation.

Dendroecological techniques can be useful in assessing the effect of insect outbreaks, but have been used primarily to reconstruct historic patterns of outbreaks (Fritts and Swetnam 1989). In western North America, western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak histories have been developed through many studies (Thomson and VanSickle 1980; Swetnam and Lynch 1989, 1993; Weber and Schweingruber 1995). Extensive chronologies have been developed to determine the long-term impact of defoliation, such as radial growth losses of trees and forests (Brubaker 1978, Wickman 1980, Mason et al. 1997).

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Few studies have used dendrochronology to examine the effects of hardwood defoliators in the eastern United States. With the exception of research by Baker (1941), Campbell and Garlo (1982), and Muzika and Liebhold (1999), there is a noticeable absence of dendrochronological research examining the effects of defoliation on deciduous trees. In this paper, we use data from a study conducted in the 1970s to examine the effect of gypsy moth defoliation on both pines and oaks in two areas of the northeastern United States.

Methods

The data used in this study were collected as part of the USDA Forest Service Intensive Plot System (IPS) from 1972 to 1978 (Reardon 1976). Data were collected in six areas throughout the northeastern United States. For this study, however, we focused on the two areas that were dominated by oak-pine forests. Area 1 was located on Cape Cod, Massachusetts, and Area 2 was located along the Atlantic coast in New Jersey. These areas contained coastal stands that were dominated by white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), and pitch pine (*Pinus rigida*). Each area consisted of five to eight sites that were relatively homogenous in soil type and overstory species composition. Within each site, there were five 0.04-ha plots from which data were collected on a wide array of parameters relative to gypsy moth populations, individual tree defoliation, and crown condition. All trees within the plots were identified, height and diameter were measured, and vigor and defoliation were evaluated. Defoliation was measured as a percentage loss of canopy and was estimated following gypsy moth feeding in the summer (Table 1).

Table 1. Defoliation estimates (%) of overstory trees for the two study areas for each of 5 years. Defoliation estimates represent averages across the sites at each area.

Year	Massachusetts	New Jersey
1972	79.7	67.3
1973	56.3	86.4
1974	10.6	21.9
1975	4.7	15.0
1976	2.4	3.4

In the winter of 1976-1977, an increment core was taken from each living tree on every plot. Ring widths were measured at Virginia Polytechnic Institute and State University soon after the cores were extracted. Most of the cores were measured through the most recent 25 years, although a few had longer series. Only species with at least 10 individuals per site were retained for analysis. Total radial increment was measured on all trees and earlywood and latewood were differentiated.

All cores consisted of at least 25 annual growth rings; the most reliable chronologies existed for the years from 1952 to 1976. We graphically cross dated each series and eliminated series that may have had missing rings. The raw tree-ring series were standardized to correct for an age-related growth trend. Because of the relative shortness of the series, we fit unique linear regressions for each tree and used the residuals as the standardized increment. Detrending eliminated the effect of individual tree age and resulted in a series that represented the relative growth level for each year.

Detrended ring widths were used for analysis of defoliation effects; we used averages for each species at each site. Defoliation data were available for only the last five years of each series (1972 to 1977). Overall, there were five species used in the analysis (white oak, scarlet oak, chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), and pitch pine). Stepwise linear regression was used to test the effect of defoliation on radial increment. The dependent variable was normalized, detrended increment for each tree in each year. Increment was normalized by dividing the detrended (residual) increment by the standard deviation of the detrended values. Normalization was performed in order to remove among-tree variation in increment variance. Independent variables used in the stepwise regressions were: (1) individual tree defoliation in the same year as increment (defoliation), (2) individual tree defoliation in the prior year (lag defoliation, or defoliation (t-1)), (3) average stand-level defoliation in the same year as increment (stand defoliation), and (4) stand-level defoliation in the previous year (lag stand defoliation, or stand defoliation (t-1)). A *P* value of 0.05 was used as the criterion for including either defoliation or lag defoliation in the regression model.

Using earlywood and latewood measurements, we calculated the proportion of earlywood and used it as the dependent variable in stepwise regression for all trees of a given species pooled across all sites. We used the same independent variables as described above. The proportion of earlywood was transformed, then detrended because of the influence of age on early and latewood width (Zhang et al. 1994).

Results and Discussion

Previous research indicated that both study areas were dominated by oak with 10 to 15% of their basal area in pitch pine (Montgomery et al. 1990). Defoliation estimates were comparable between the two areas and reflected gypsy moth populations in outbreak years (1972 and 1973) with a dramatic decline in populations within a few years following extensive defoliation. The temporal sequence in defoliation suggests that the outbreak occurred in Massachusetts initially and a year later in New Jersey. Among all six areas in the original study, these two oak-pine forests incurred the greatest amount of defoliation.

Mortality within each area was determined as a percentage of dead stems by species. Mortality of pine was comparable at both areas. In Massachusetts, nearly half of the white oak stems died over the 5-year period, but only 9% died in New Jersey (Table 2). As a group, the red oaks (*Q. velutina* and *Q. coccinea*) had greater mortality than white oaks in New Jersey. Overall, mortality was greater in Massachusetts than in New Jersey, despite higher levels of defoliation in New Jersey.

Stepwise regression results indicated the specific influence of each of the identified variables on ring width of each species (Table 3). Predictably, individual-tree defoliation and stand-level defoliation in a given year negatively influenced growth of pitch pine in Massachusetts and New Jersey. While that negative effect persisted in Massachusetts, previous year's defoliation did not influence pine growth in New Jersey. Similarly, stand-level defoliation in the previous year was inversely related to growth in Massachusetts but not New Jersey. As a less preferred host, pitch pine may be expected to benefit from

Table 2. Cumulative percent mortality from *L. dispar* defoliation for overstory trees over a 5-year period (1973 to 1978) at Cap Cod, Massachusetts, USA, and New Jersey, USA. "NA" indicates that no individuals of that species were present at the study area.

Species	Massachusetts	New Jersey
Pinus rigida	16.1	15.6
Quercus alba	46.3	8.7
Quercus rubra	20.4	NA
Quercus velutina	29.5	37.8
Quercus montana	NA	14.3
Quercus coccinea	NA	23.4

Table 3. Results of stepwise regression of radial increment on defoliation. Each tree had four observations corresponding to defoliation data from 1972 to 1976. See text (page 119) for an explanation of the variables. This table lists parameter estimates from the stepwise regression that indicate the direction of the relationship. A *P* value of 0.05 was used as the criterion for retaining a variable in the regression.

Species	Variables	Massachusetts	New Jersey
Pinus rigida	Defoliation	-2.201	-1.359
	Defoliation (t-1)	-0.767	*ns*
	Stand Defoliation	-1.323	-1.138
	Stand Defoliation (t-1)	-0.381	*ns*
Quercus alba	Defoliation	0.203	-0.548
	Defoliation (t-1)	-0.328	*ns*
	Stand Defoliation	0.449	-0.666
	Stand Defoliation (t-1)	-0.538	*ns*
Quercus coccinea	Defoliation	*ns*	-0.588
	Defoliation (t-1)	-1.138	-0.175
	Stand Defoliation	*ns*	-0.710
	Stand Defoliation (t-1)	-1.564	-0.216
Quercus montana	Defoliation	-	-0.793
	Defoliation (t-1)	-	*ns*
	Stand Defoliation	-	-1.045
	Stand Defoliation (t-1)	-	*ns*
Quercus rubra	Defoliation	0.227	-
	Defoliation (t-1)	-0.615	-
	Stand Defoliation	*ns*	-
	Stand Defoliation (t-1)	-0.840	-
Quercus velutina	Defoliation	*ns*	-0.417
	Defoliation (t-1)	-0.479	*ns*
	Stand Defoliation	*ns*	-0.668
	Stand Defoliation (t-1)	-0.785	*ns*

defoliation of oak species; therefore, stand-level defoliation could result in a positive influence on pitch pine growth, as has been demonstrated with non-host species (Muzika and Liebhold 1999). In the present study, increased growth in less preferred species (pitch pine) was not observed, but this most likely resulted from the high intensity of defoliation that included less preferred species themselves and depressed their growth.

Oak species were predictably, but variously, influenced by defoliation. Only scarlet oak demonstrated a consistent and negative effect of defoliation, but only in New Jersey. Defoliation in the year of growth and the previous year, both at the individual-tree and stand level, affected scarlet oak growth increment in New Jersey. The fact that defoliation positively influenced white oak increment in Massachusetts may be explained by the high mortality rate of that species. With nearly 50% white oak mortality, the individuals that did not die also did not reduce increment, likely reflecting a different cohort, i.e. the survivors may have been considerably younger than those that died. Reductions in radial growth are uncommon in younger trees. Furthermore, stand-level defoliation positively affected white oak growth in Massachusetts, suggesting enhanced or compensatory growth of the remaining cohort. In New Jersey, where white oak mortality was lower (Table 2), individual tree defoliation and stand defoliation both negatively influenced radial growth.

Most other oak species were negatively affected by defoliation in either study area. Unexpected findings include a positive influence of current-year, individual-tree defoliation on red oak and white oak growth. The previous year's individual-tree defoliation and previous year's defoliation at the stand level both negatively affected red oak increment, however. It is possible that some mortality occurred in red oaks in the first year of defoliation, but survivors responded with increased growth. In subsequent years, however, growth was negatively influenced by defoliation from the year previous. The delayed, but negative, response in growth increment the year following defoliation was also evident in scarlet and black oaks in Massachusetts.

To further assess the influence of defoliation on radial increment, we examined the proportion of earlywood to latewood as a dependent variable using stepwise regression for the oak species only. We anticipated that defoliation effects on earlywood would be minimal since earlywood production is well underway by the time defoliation by gypsy moth occurs. Contrary to our expectations, there were significant positive effects of defoliation on the proportion of earlywood in all oak species in the year of defoliation and, for most oaks, in the year following defoliation (Table 4). Since total increment was often reduced in these trees, a positive effect on earlywood proportion indicated a relatively severe negative effect on latewood. Latewood production would be directly influenced by both current and previous year's defoliation, corresponding to the results of the stepwise regression. The proportion of earlywood in chestnut oak was significantly related to defoliation in the current year only.

Our findings are in general agreement with previous studies describing how defoliation by gypsy moth and other insect species affects tree growth and production of latewood. Earlier research characterizing the influence of gypsy moth on tree growth indicated that increment loss was proportional to defoliation. There is variation in the timing of the significant relationships, however. Minott and Guild (1925) found that the effect of defoliation on increment appeared to be greatest in the same year as defoliation, but noted that there may also be a decline in growth in the year following defoliation. Similarly, Baker (1941) demonstrated that throughout a 10-year period of repeated gypsy moth defoliation, reductions in growth were strongest in the year during defoliation; there was a noticeable, although less pronounced, lag effect, i.e. reduced increment in the year following defoliation.

Table 4. Results of stepwise regression of earlywood proportion of total increment on defoliation. This table includes trees from both study areas.

Species	N	Variable	Parameter Estimate	P
Quercus alba	1,905	Defoliation	0.074	0.0001
		Defoliation (t-1)	0.047	0.0001
Quercus coccinea	955	Defoliation	0.100	0.0001
		Defoliation (t-1)	0.025	0.0005
Quercus montana	1,225	Defoliation	0.118	0.0001
Quercus rubra	1,495	Defoliation	0.107	0.0001
		Defoliation (t-1)	0.046	0.0023
Quercus velutina	360	Defoliation	0.102	0.0001
		Defoliation (t-1)	0.056	0.0004

In this study, we have shown that gypsy moth defoliation negatively influences radial increment in hosts irrespective of the quality of that host. Overall, the more highly preferred oaks were negatively influenced, but the strength of the relationship differed among species. The intermediate host, pitch pine, was negatively affected by defoliation, but the lag response varied between the two areas. The consistent relationships between the two sites indicated that generalizations about the susceptibility of oak-pine forests to gypsy moth can be established and predictions about anticipated losses in radial growth or tree mortality can be made to benefit forest management efforts.

References Cited

Baker, W.L. 1941. Effect of gypsy moth defoliation on certain forest trees. Journal of Forestry 39: 1017-1022.

Brown, J.H., V.B. Cruickshank, W.P. Gould and T.P. Husband. 1988. Impact of gypsy moth defoliation in stands containing white pine. Northern Journal of Applied Forestry 5: 108-111.

Brubaker, L.B. 1978. Effects of defoliation by Douglas-fir tussock moth on ring sequences of Douglas-fir and grand fir. Tree Ring Bulletin 38: 49-60.

Campbell, R.W. and A.S. Garlo. 1982. Gypsy moth in New Jersey Pine-Oak. Journal of Forestry 80: 89-90.

Davidson, C.B, K.W. Gottschalk and J.E. Johnson. 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. Forest Science 45: 74-84.

Fritts, H.C. and T.W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. Advances in Ecological Research 19: 111-188.

Gansner, D.A. 1987. Site productivity and tree mortality following gypsy moth defoliation on new frontiers of gypsy moth infestation. U.S. Dep. Agric. For. Serv. Res. Note NE-340. 3 p.

Gottschalk, K.W. and M.J. Twery. 1989. Gypsy moth impacts in pine-hardwood mixtures. In: Pine-hardwood mixtures: a symposium on management and ecology of the type. U.S. Dep. Agric. Gen. Tech. Rep. SE-58: 50-58.

Liebhold, A.M., Gottschalk, K.W., Muzika, R.M., Montgomery, M.E., Young, R., O'Day, K. and Kelley, B. 1995. Suitability of North American Tree Species to the Gypsy Moth: A Summary of Field and Laboratory Tests. USDA For. Serv. Gen. Tech. Rep. NE-211.

Mason, R.R., B.E. Wickman and H.G. Paul. 1997. Radial growth response of Douglas-fir and grand fir to larval densities of the Douglas-fir tussock moth and the western spruce budworm. Forest Science 43: 194-205.

Minott, C.W and I.T. Guild. 1925. Some results of the defoliation of trees. Journal of Economic Entomology 18: 345-348.

Montgomery, M.E., M.L. McManus and C.W. Berisford. 1990. The gypsy moth in pitch pine-oak mixtures: predictions for the south based on experiences in the north. In: Pine-hardwood mixtures: a symposium on management and ecology of the type. U.S. Dep. Agric. Gen. Tech. Rep. SE-58: 43-49.

Muzika, R.M. and A.M. Liebhold. 1999. Changes in radial increment in host and non-host tree species with gypsy moth defoliation. Canadian Journal of Forest Research 29: 1365-1373.

Reardon, R.C. 1976. Parasite incidence and ecological relationships in field populations in gypsy moth larvae and pupae. Environmental Entomology 5: 981-987.

Swetnam, T.W. and A.M. Lynch. 1989. A tree-ring reconstruction of western spruce budworm history in the southern Rocky Mountains. Forest Science 35: 962-986.

Swetnam, T.W. and A.M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworms outbreaks. Ecological Monograph 63: 399-424.

Thomson, A.J. and G.A. VanSickle. 1980. Estimation of tree growth losses caused by western spruce budworm defoliation. Canadian Journal of Forest Research 10: 176-182.

Weber, U.M. and F.H. Schweingruber. 1995. A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the front range, Colorado, from 1720 to 1986. Trees 9: 204-213.

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. Journal of Forestry 78: 31-33.

Zhang, S.Y., G. Nepveu and R. Eyong Owoundi. 1994. Intratree and intertree variation in selected wood quality characteristics of European oak (*Quercus petraea* and *Quercus robur*). Canadian Journal of Forest Research 24: 1818-1823.

Modeling Seasonal Development of the Gypsy Moth in a Novel Environment for Decision Support of an Eradication Program

VINCENT NEALIS[1], JACQUES RÉGNIÈRE[2] AND DAVID GRAY[3]

Natural Resources Canada, Canadian Forest Service
[1]Pacific Forestry Centre, 506 W. Burnside Rd., Victoria, British Columbia V8Z 1M5 Canada
[2]Laurentian Forestry Centre, P.O. Box 3800, Ste-Foy, Québec G1V 4C7 Canada
[3]Atlantic Forestry Centre, P.O. Box 4000, Fredericton, New Brunswick E3B 5P7 Canada

ABSTRACT Observations of field-caged egg masses of the European gypsy moth (*Lymantria dispar* (L.)) on Vancouver Island, British Columbia, Canada, indicate that overwinter survival of the insect is very high in this area. Emergence of larvae in the spring occurred over a period of 4 to 5 weeks. These observations were used to validate a process-oriented phenology model that was, in turn, used to time pesticide applications during an eradication program against the gypsy moth. Based on a digital elevation model and climate normals, the phenology model was used to examine heterogeneity of seasonal development within the eradication zone and to identify areas where successful completion of the insect's life history might be unlikely because of climate.

THERE HAVE BEEN repeated introductions of gypsy moth (*Lymantria dispar* (L.) (Lepidoptera: Lymantriidae)) into British Columbia, Canada, since 1978. In many cases, capture records of single male moths in pheromone traps in one year have not been repeated in the following year despite an intensification of trapping effort. These cases indicate the population did not persist and no eradication programs were undertaken. However, there have been several occasions when detected populations have persisted and apparently increased for at least 2 years. These infestations have been treated, mostly through multiple aerial applications of *Bacillus thuringiensis* var. *kurstaki* (*Btk*) (Humble and Stewart 1994).

The introduction of exotic insects such as the gypsy moth to a new geographic area presents unique challenges for pest managers. At minimum, resource managers will want to intensify monitoring to delimit the area of actual infestation. With gypsy moth, this monitoring is done with pheromone traps and so it is necessary to know the period of male adult flight so traps can be deployed and retrieved at appropriate times. If a decision is made to eradicate the incipient population, there is then the more demanding practical problem of predicting the timing of treatment of susceptible life stages. Susceptibility to *Btk*, for example, is greatest for early larval stages. In the situation of recently introduced exotic insects, there is no historical record of seasonal development for the area and the insect is too rare to sample reliably at all life stages. Moreover, the environmental conditions in the newly infested area may be significantly different from areas where historical information is available. The result is that the phenomenological approach often used by pest managers is either unavailable or unreliable for decision making.

This paper describes a modeling approach to these problems using the recent experience involving the European gypsy moth on southern Vancouver Island in British

Pages 124-132 in Liebhold, A.M.; McManus, M.L.; Otvos, I.S.; Fosbroke, S.L.C., eds. 2001. **Proceedings: integrated management and dynamics of forest defoliating insects**; 1999 August 15-19; Victoria, BC. Gen. Tech. Rep. NE-277. Newtown Square, PA; U.S. Department of Agriculture, Forest Service, Northeastern Research Station.

Columbia, Canada, as a case study. We analyzed the phenology of all life stages of the gypsy moth using a temperature-driven model of gypsy moth development. This model was validated with field observations from southern Vancouver Island. The phenology model was then used to develop area-wide forecasts of target events in the seasonal life history of gypsy moth as described by Régnière and Sharov (1999). The results were mapped to visualize spatial variation in the timing of specific phenological events such as egg hatch and moth flight at the landscape level. These events were then used to support timing decisions made in an eradication program in 1999.

Methods

Models. Régnière and Sharov (1998) linked models of gypsy moth egg hatch (Johnson et al. 1983), early instar development (Logan et al. 1991), and late instar and pupal development (Sheehan 1992) into a composite, full-season model of gypsy moth development. They then used this composite model to demonstrate a method of simulating temperature-dependent ecological processes over a large geographic area (Régnière and Sharov 1999). For our purposes, we compared the output of three egg-hatch models: that of Johnson et al., that of Lyons and Lysyk (1989), and that of Gray et al. (1991, 1995, In press). These egg-hatch models were run using on-site temperature records, and their output was compared to observed gypsy moth egg hatch to determine the best-fitting egg-hatch model to include in the composite seasonal model.

The best-fitting egg-hatch model and the composite seasonal model were then linked to BioSIM, a system designed to generate area-wide phenology simulations based on digital elevation models, climatic normals, real-time weather observations, and temperature-dependent phenology models (Régnière 1996). BioSIM generates forecasted temperature traces that drive the phenology model to predict target events such as the date of egg hatch or moth flight. Daily air temperature records starting in 1997 for a range of locations in southern Vancouver Island and Vancouver and regular, 5-day forecasts for Nanaimo, Victoria, and Vancouver were provided by the Victoria Weather Office, Environment Canada. Standard air temperature normals (mean monthly and extreme minimum and maximum) from 1961 to 1990 were obtained from the Canadian Monthly Climate Data and 1961-1990 Normals and Monthly Averages CD-ROM (1993 issue; Climate Information Branch, Environment Canada, Ontario, Canada). A 3-arc-second digital elevation model of southern Vancouver Island was obtained from D. McKenney (Canadian Forest Service, Sault Ste Marie, Ontario). The digital elevation model was projected to Universal Transverse Mercator and the horizontal resolution was decreased to 150 m by re-sampling.

In the process of generating maps of phenology model outputs, BioSIM must simulate phenology for points other than the location of weather stations. This is done by adjusting temperatures for differences in elevation, latitude, and longitude between stations and simulation points. These adjustments were based on thermal gradients obtained by a method developed by M. Gignac (pers. comm., Department of Geomatics, Laval University, Quebec, Canada) and involve a general linear model that includes latitude, longitude, elevation, month of year, and an index of either minimum or maximum temperature.

Validation. To compare and validate predictions of the three available models of egg hatch, 76 locally collected egg masses were obtained from survey crews of the Canadian Food Inspection Agency (CFIA), Victoria, B.C., between December 1998 and February

1999. Each egg mass was placed in an individual plastic petri dish and housed outside in a ventilated cage at ground level under partial shade. Because gypsy moth egg masses are laid mostly in sheltered locations at ground level (Leonard 1972), this was our best effort to provide ambient overwintering and spring conditions for the eggs. A temperature probe (Optic Stowaway, Onset, MA) was placed among the petri dishes and provided temperature records hourly. Egg masses were observed daily for eclosion and hatching larvae were counted and removed. This gave the seasonal distribution of egg hatch for both individual egg masses as well as the population as a whole. After the emergence of larvae was completed, all egg masses from which no larvae had emerged and a random subsample of 20 egg masses from which at least some larvae had emerged were examined and the status of unhatched eggs (uneclosed but fertile, infertile or parasitized) was determined. This provided an estimate of survival of the gypsy moth eggs in the area.

An independent check on the composite seasonal model was made by comparing model predictions of the timing of adult male moth flight in 1998 to actual observations made by survey crews of the CFIA from pheromone traps monitored daily in that year. This composite model predicts seasonal appearance of the adult stage. Pheromone traps record moth flight. Therefore, we imposed an arbitrary linear relationship between air temperature and moth flight activity, with a lower activity threshold of 15°C for graphical comparison of predicted and observed male flight activity (inset, Fig. 2).

Forecasts. Area-wide forecasts of egg hatch and adult moth flight were mapped to visualize spatial heterogeneity of gypsy moth phenology on southern Vancouver Island and to advise pest managers on the timing of critical target events at specific locations. These maps also allow identification of areas where seasonality is biologically impossible for the gypsy moth on southern Vancouver Island as has been done for this same insect in northeastern North America (Régnière and Sharov 1999).

Results

Egg Hatch: Observations and Model Validation. Seventy-six unhatched gypsy moth egg masses were collected and assessed between December 1998 and May 1999. Twelve of these egg masses contained only infertile eggs and could have been from either 1998 or previous years. There was no evidence of egg parasitism. At least 1 larva hatched from each of the remaining 64 egg masses. The mean (standard error) number of gypsy moth larvae emerging per egg mass was 317.8 (±26.0). Examination of a subsample of these egg masses after hatch was complete indicated that mean survival in viable egg masses was 90%. Given that some mortality of individual eggs could be expected from handling, as these egg masses were in many cases scraped off the substrate with a knife, this is a conservative estimate of survival for gypsy moth eggs in Victoria. Thus, the gypsy moth survived the relatively warm and wet winter in Victoria at least as well as they did in climatically dissimilar places where populations have persisted for decades (Nealis et al. 1999).

The distribution of hatch within individual egg masses was protracted with larvae eclosing from the same egg mass over a 10- to 26-day period for egg masses containing more than 100 eggs. Hatch of the population as a whole, of course, was even more protracted, occurring over a 38-day period in 1999. Of the three egg-hatch models compared to this observed distribution, Gray's model fit by far the best (Fig. 1).

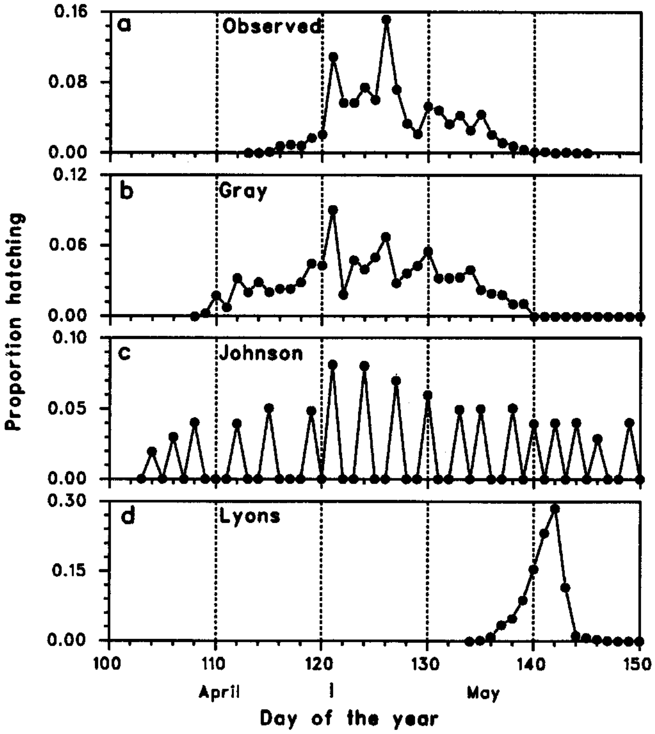

Figure 1. Comparison of observed and predicted egg hatch rates in Victoria, British Columbia, in 1999. (a) Observed. Note that individual egg hatch was not recorded for the first 6 masses to hatch. Hatch rate predicted by (b) Gray's, (c) Johnson's, and (d) Lyons and Lysyk's models.

The models developed by both Johnson et al. (1983) and Lyons and Lysyk (1989), although validated in the areas for which they were developed originally, were inadequate in forecasting phenology in the novel environment of southern Vancouver Island. In contrast, Gray's model is based on a detailed description of egg developmental physiology and, if valid, should be relatively robust to changes in regional climate. Parameters were developed from carefully controlled laboratory experiments and the model makes an explicit distinction between the phases of embryonation, diapause, and post-diapause development. Gray's model requires the date of peak oviposition as input, but is relatively insensitive to this parameter. Preliminary simulation studies suggested that early September was a likely date of peak oviposition for the south of Vancouver Island. By itself, this model permitted accurate forecasts for egg hatch in 1999 using the date of observed peak moth flight in 1998 as the peak oviposition date. When combined with sub-models for the remaining life stages compiled by Régnière and Sharov (1998), it contributed to a very good prediction of observed flight of male gypsy moths in 1998 (Fig. 2).

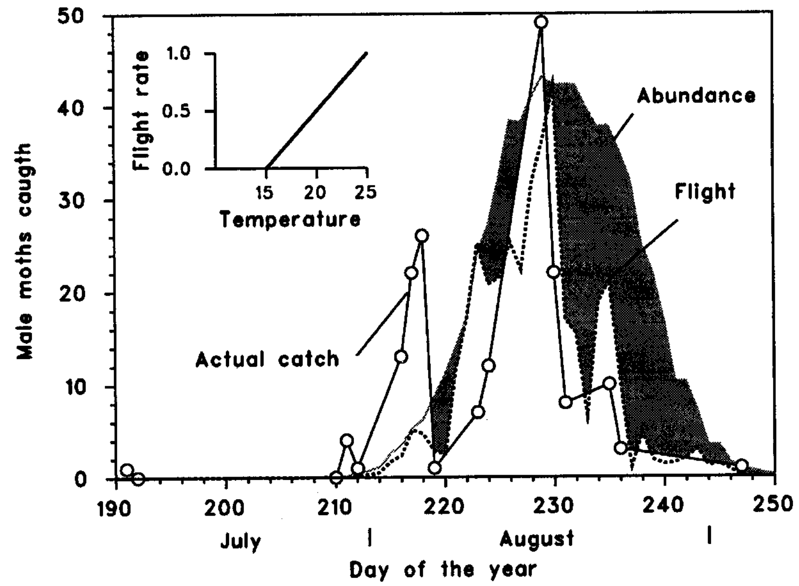

Figure 2. Comparison of predicted and observed male moth flight in 1998. Grey-shaded curve: predicted moth abundance; dotted line: predicted flight activity, the product of male abundance by the linear relationship of mean air temperature illustrated in the inset; solid line and open circles: observed daily moth catch in pheromone traps. Egg hatch simulated using Gray's model.

The importance of substituting available real-time weather observations for normal weather records when predicting target events for specific pest control operations is illustrated in Figure 3. Our reliance on 30-year normal temperatures to predict the occurrence of peak first instars or first moth flight on Vancouver Island would have been very inaccurate in both 1998 and 1999 because of specific weather patterns in those years. In 1998, a relatively warm spring and summer led to phenology that was much earlier than would have been expected from climate normals (peak first instar was 14 days in advance and the first moth flight was 20 days in advance). In 1999, spring temperatures were below normals and peak first instar was reached 8 days later than expected on the basis of normals. The remainder of the summer was near normal, so that moth flight also started nearly one week later than would have been predicted by climate normals. Had the timing of control operations in 1999 been based on 1998 phenology, the first application would have been made 20 days too early.

Maps. Maps of the date on which first instar and male moth frequency are predicted to be maximum were generated for southern Vancouver Island (Figs. 4a and b). These maps were generated using the first week of September as the peak oviposition date (day 250) for all locations and illustrate the wide range of phenology expected for gypsy moth in this relatively small geographic area. Areas where male abundance (approximately synchronous with peak oviposition) would occur after November are unlikely to permit persistence of the population for reasons of seasonality alone. Such maps provide pest managers with a means of identifying areas were gypsy moth populations are most likely to persist as well as provide specific guidelines for timing *Btk* applications and the deployment and recovery of pheromone traps.

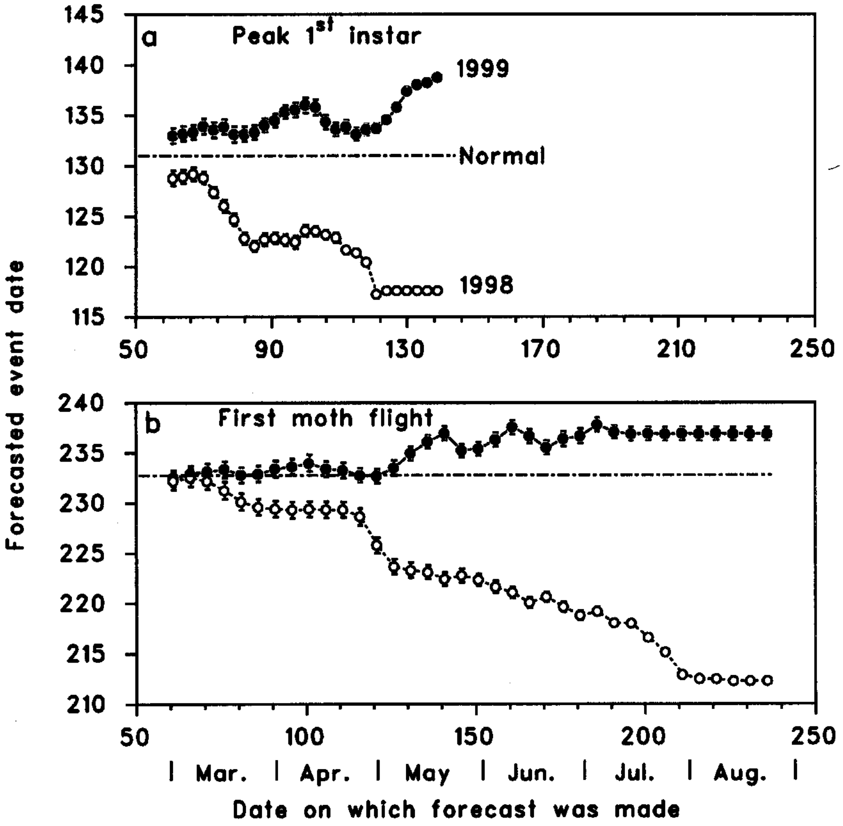

Figure 3. Evolution of the predicted date of peak abundance of (a) first instar larvae and (b) male moths in 1998 (open circles) and 1999 (closed circles) as time in the season progressed and an increasing amount of actual (real-time) data accumulated. The horizontal lines represent the predictions based solely on climatic normals. Egg hatch simulated using Gray's model.

Discussion

Phenology models provide a critical basis for a generalized approach to forecasting insect seasonality at the landscape level (Schaub et al. 1995, Régnière 1996, Régnière and Sharov 1999). The process-oriented model of egg development constructed by Gray et al. (1991, 1995, In press) provided an accurate prediction of observed hatch in Victoria in the spring of 1999. The advantage that this model has over others is its explicit description of temperature-dependent processes occurring between the time of oviposition in year *t*-1 and the time of egg hatch in the spring of year *t*. This distinction allowed the egg-hatch model to be far more sensitive to the warm winter conditions characteristic of the area of interest and was therefore important for forecasting specific target events within the unique climatic environment of southern Vancouver Island. Comprehensive modeling of diapause also permitted a biological, rather than a calendar, definition for initiating the seasonal model, namely, the actual time of oviposition the previous season.

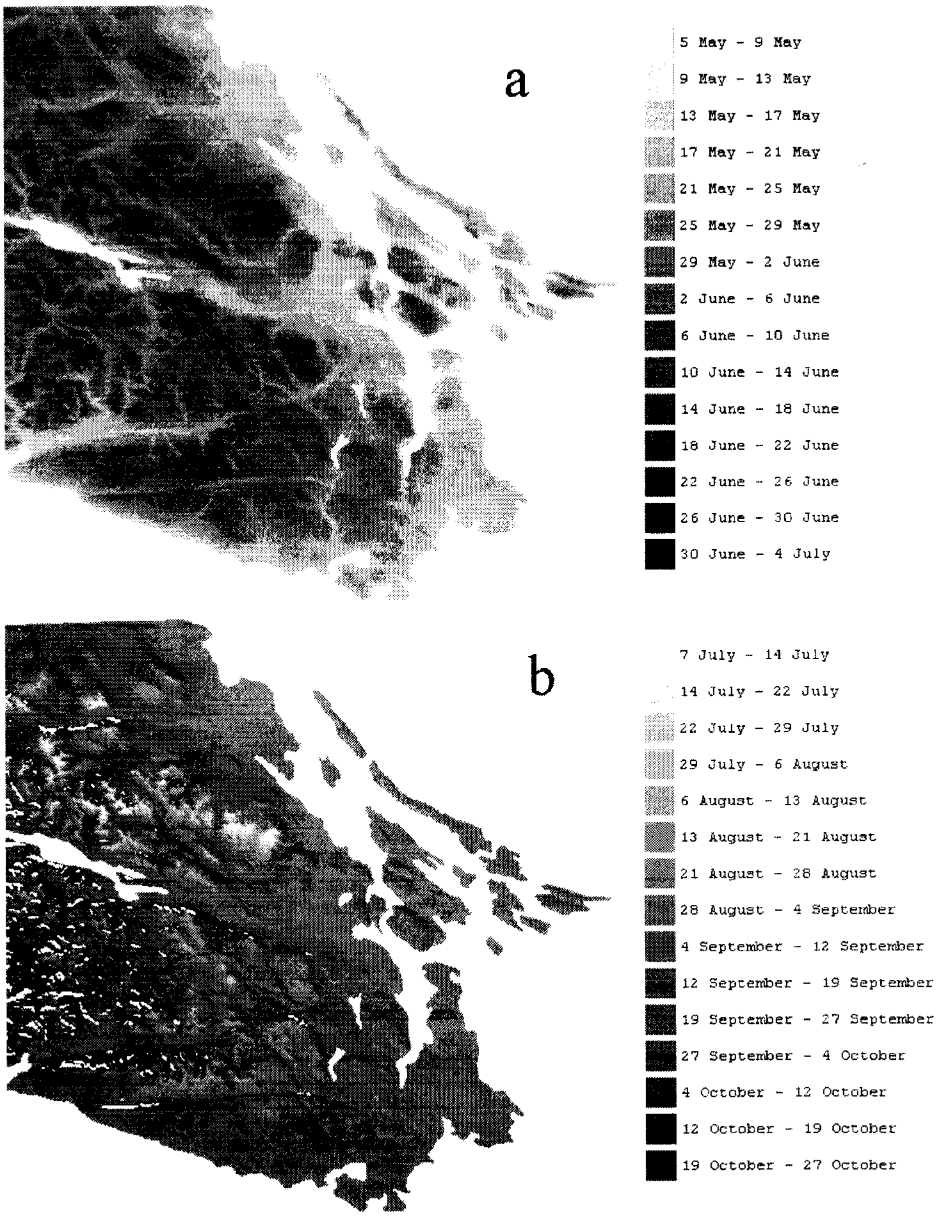

Figure 4. Maps of the predicted dates of peak frequency of (a) first instars and (b) male moths on southern Vancouver Island, based on climatic normals. Maps prepared with the BioSIM system. Egg hatch simulated using Gray's model.

Gypsy moths survived the 1998-1999 winter very well on southern Vancouver Island. The relatively mild coastal climate imposes no direct source of mortality during diapause unlike the cold winter climate in eastern Canada (Nealis et al. 1999). This climate, however, does influence the timing and distribution of critical life stages. The timing of egg hatch in the spring varies considerably over the region because of dominating maritime and topographical influences on air temperatures in the spring. This spatial heterogeneity is further modified during the summer months as a result of pronounced vertical thermal gradient inversions related to cooling near the cold ocean waters, especially in the Victoria area. Development in low-lying areas near the sea is retarded, and the most pronounced influence of topography becomes exposure to sunshine (slope and aspect) rather than elevation. Annual weather patterns typical of Vancouver Island (relatively warm winters and relatively cool summers) can lead to a seasonal biology in which oviposition is so late that egg hatch the following spring is delayed. This further retards oviposition to the point where the population is eventually unable to maintain a viable seasonality and cannot persist.

The use of this model for decision support by pest managers has already been tested, in part. In British Columbia, recommended timing of aerial applications of *Btk* in 1999 was established from output of the composite model. The spray window was opened when the population was predicted to be mostly in the first or early second larval stages and was closed as the population approached the end of the third larval stage. Within the spray window, the three applications of *Btk* were timed individually based on daily updates of the simulations rather than on an arbitrary 10-day schedule as had been the practice in the past. Pest managers also used the forecast of moth activity to deploy and recover over 5,000 pheromone traps for timely reporting of results bearing on evaluation of the eradication program and planning the future course of action.

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References Cited

Gray, D.R., J.A. Logan, F.W. Ravlin and J.A.Carlson. 1991. Toward a model of gypsy moth egg phenology: using respiration rates of individual eggs to determine temperature-time requirements of pre-diapause development. Environ. Entomol. 20: 1645-1652.

Gray, D.R., F.W. Ravlin and J.A. Braine. [In press.] Diapause in the gypsy moth: a model of inhibition and development. J. Insect Physiol.

Gray, D.R., F.W. Ravlin, J. Régnière and J.A. Logan. 1995. Further advances toward a model of gypsy moth (*Lymantria dispar* (L.)) egg phenology: respiration rates and thermal responsiveness during diapause, and age-dependent development rates in postdiapause. J. Insect. Physiol. 41: 247-256.

Humble, L. and A.J. Stewart. 1994. Gypsy Moth. Forest Pest Leaflet 75, Cat. No. Fo29-6/75-1994E.

Johnson, P.C., D.P. Mason, S.L. Radke and K.T. Tracewski. 1983. Gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), egg eclosion: degree-day accumulation. Environ. Entomol. 12: 929-932.

Leonard, D.E. 1972. Survival in a gypsy moth population exposed to low winter temperatures. Environ. Entomol. 1: 549-554.

Logan, J.A., R.A. Casagrande and A.M. Liebhold. 1991. Modeling environment for simulation of gypsy moth (Lepidoptera: Lymantriidae) larval phenology. Environ. Entomol. 20: 1516-1525.

Lyons, D.B. and T.J. Lysyk. 1989. Development and phenology of eggs of gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), in Ontario. In: Wallner, W.E. and K.A. McManus, (eds.) Proceedings, Lymantriidae: a comparison of features of New and Old World tussock moths. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-123: 351-365.

Nealis, V.G., P.M. Roden and D.A. Ortiz. 1999. Natural mortality of the gypsy moth along a gradient of infestation. Can. Entomol. 131: 507-519.

Régnière, J. 1996. Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environ. Entomol. 25: 869-881.

Régnière, J. and A. Sharov. 1998. Phenology of *Lymantria dispar* (Lepidoptera: Lymantriidae), male flight and the effect of dispersal in heterogeneous landscapes. Int. J. Biometeorol. 41: 161-168.

Régnière, J. and A. Sharov. 1999. Simulating temperature-dependent ecological processes at the sub-continental scale: male gypsy moth flight phenology as an example. Int. J. Biometeorol. 42: 146-152.

Schaub, L.P., F.W. Ravlin, D.R. Gray and J.A. Logan. 1995. Landscape framework to predict phenological events for gypsy moth (Lepidoptera: Lymantriidae) management programs. Environ. Entomol. 24: 10-18.

Sheehan, K.A. 1992. User's guide for GMPHEN: Gypsy Moth Phenology Model. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-158.