Past and present outbreaks of the balsam fir sawfly in western Newfoundland: An analytical review

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Abstract

Historical data of defoliation and population density were examined to determine whether a sustained outbreak of balsam fir sawfly (Neodiprion abietis Harris) in western Newfoundland, Canada is unprecedented in severity and duration. Results indicate that the current outbreak departs substantially from historical trends, covering a surface area twice the sum of all infestations occurring in the preceding 50 years. The current outbreak is also of longer duration due to a northward expansion of the range usually subjected to severe defoliation by this insect. Time-series analysis indicates that balsam fir sawfly dynamics have a strong second-order component, providing testable hypotheses for future studies investigating the factors responsible for population fluctuations.

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The balsam fir sawfly (Neodiprion abietis Harris) (Hymenoptera: Diprionidae) is an eruptive defoliator indigenous to North America. The species has a transcontinental distribution (Ross, 1955; Wallace and Cunningham, 1995) and infestations have been recorded on many hosts. In Canada, larvae feed principally on balsam fir (Abies balsamea [L.] Mill) and occasionally on white (Picea glauca [Moench.] Voss) and black spruce (Picea mariana [Mill.] B.S.P) (Martineau, 1985).

Periodic outbreaks, usually 3–4 years in duration, have commonly been observed from central to Atlantic Canada (Cunningham, 1984).

Recently, a number of balsam fir sawfly outbreaks have occurred in young, managed stands of Atlantic Canada (Moreau, 2004; Piene et al., 2001). The extent of the defoliation attributed to this insect was such that significant efforts were involved in developing a biocontrol strategy for the management of this species (Moreau et al., 2005). Historically, balsam fir sawfly defoliation has been more conspicuous in Atlantic Canada than elsewhere in North America (Martineau, 1985) but the current outbreak on the west coast of the island of Newfoundland (Fig. 1) is apparently unprecedented in severity (Piene et al., 2001). As an integral part of studies on balsam fir sawfly ecology, a review of available time-series data from historical records was undertaken to examine and compare past outbreaks of this species with the current one. Through the use of a number of diagnostic techniques, certain time-series attributes were also examined to detect whether density-dependent processes (Royama, 1992) are responsible for balsam fir sawfly fluctuations, thus permitting inferences about the population dynamics of the species.

Balsam fir sawfly historical records for area defoliated, host-plant defoliation and population density for the west coast of Newfoundland were recovered from the annual reports of the Newfoundland Forest Protection Association (Anonymous, 1943–1996), from the Forest Insect and Disease Information Survey (Anonymous, 1943–1950; Anonymous, 1951–1995), from interim reports of the Forest Entomology and Pathology Laboratory of Corner Brook, Newfoundland, from district reports of the Forest Insect and Disease Survey (Clarke et al., 1968; Parrott et al., 1966) and from the Newfoundland Department of Natural Resources (Crummey, personal communication). A 65-year series of areas severely defoliated was extracted from these data for a zone of ~15,000 km² roughly delineated by Barachois Park in the south, Cormack in the north, Deer Lake in the east and Port-au-Port Bay in the west (Fig. 1). Yearly estimates of the area severely defoliated were based on a combination of aerial surveys and ground samples. Because forest stands in the study area are in the immediate vicinity of the mill in Corner Brook, they have been intensively...
surveyed for defoliation throughout the period of time covered by this review. Light (as opposed to severe) defoliation due to balsam fir sawfly feeding, or damage due to other insects, has been reported during the same period for most locations in the study area, suggesting that sampling intensity cannot explain the differences presented here. A complete 31-year continuous data series of host-plant defoliation (i.e., percent loss of old foliage) and an incomplete series of population density (i.e., larvae per standardized collection using the tree-beating method described in Harris et al., 1972) were also recovered for the Gallants–George’s Lake area (Fig. 1) where historical records are more extensive. Estimates of population density and host-plant defoliation in historical records were gathered using ground samples. All recovered data are presented in Figs. 1–3.

On an arithmetic scale, the 65-year record of areas severely defoliated by the balsam fir sawfly in western Newfoundland indicates that several outbreaks occurred throughout this period (Fig. 2). The three first outbreaks of the time-series (1944–1947, 1954–1956, 1960–1963) lasted 3–4 years and were relatively localized. In contrast, the subsequent outbreaks were extremely variable in duration and surface area. The last outbreak of the series is especially different from previous ones. Firstly, it covers a surface area twice the sum of all areas defoliated from 1940 to 1989, which is considerably outside the 95% confidence interval of the average size of the four previous largest outbreaks (one-sample t-test: $t = -21.65; \ P < 0.01$) (Fig. 2). Secondly, at the time this manuscript was written, this outbreak was in its 15th year, making it the longest outbreak ever reported. These differences may be due either to a larger area that is severely defoliated, or to longer periods during which individual stands are severely defoliated. Maps of the limits of severe defoliation during the five largest outbreaks described in historical records (Fig. 1) and evidence that balsam fir sawfly populations remain at high densities for only 2–4
years before collapsing at the stand level in the current outbreak (Moreau et al., in press), as in past outbreaks (Anonymous, 1943–1996), apparently support the idea that a larger area is impacted.

The logarithmic scale highlights an apparently cyclical pattern of defoliation, with peaks observed at 5–15-year intervals (Fig. 2). The apparent trough that occurred in the 1980s corresponds to a severe spruce budworm (*Choristoneura fumiferana* [Clemens]) outbreak that may have affected sawfly populations because it resulted in severe balsam fir mortality (Anonymous, 1951–1995). A comparison of the series of areas severely defoliated (Fig. 2) and the 31-year records of host-plant defoliation and balsam fir sawfly population density (Fig. 3) suggests that the large area defoliated from 1967 to 1975 is the result of two successive population eruptions. This indicates that the time-series of areas severely defoliated represents a combination of events at a regional scale and not the population fluctuations at any given location. Moreover, because quantitative data were not available when the area severely defoliated was less than 0.5 km², formal time-series analysis could not be carried out with these data. Similarly, missing data in the time-series of population density hindered the use of formal time-series analysis. A previous study has indicated that the relationship between sawfly density and defoliation is linear (Parsons et al., 2005) and thus, host-plant defoliation could be used as a population index. Indeed, a logistic regression between the estimates of host-plant defoliation and population density illustrated in Fig. 3 indicated that the two variables are strongly associated ($r^2 = 0.64$; $\chi^2 = 16.96$; d.f. = 1; $P < 0.01$). A Hosmer–Lemeshow test of goodness of fit for the logistic regression model showed no evidence of heterogeneity ($\chi^2 = 1.13$; d.f. = 7; $P = 0.99$).

To examine periodicity in balsam fir sawfly fluctuations and to detect whether density-dependent or -independent processes were responsible for such fluctuations, an analytical examination was carried out using the time-series of log-transformed values of host-plant defoliation as a population index. The time-series of host-plant defoliation was not detrended as there was no evidence of non-stationarity in the data. An autocorrelation function (ACF: Box and Jenkins, 1976) was plotted to measure the degree of association between the values in this series (Fig. 4a). Although the ACF plot suggested that fluctuations may be oscillatory in nature, with the number of lags between successive peaks or troughs indicating a periodicity of about 6 years, none of the autocorrelations were significant at any lag beyond lag 1 (Fig. 4a). Nevertheless, the negative spikes at lags 1 and 2 of the partial rate correlation function (PRCF: Berryman and Turchin, 2001), which provides information on the lag structure of the negative feedback mechanisms acting on the population, indicated that balsam fir sawfly fluctuations result from direct and delayed density-dependent feedbacks and not from some exogenous process(es) (Fig. 4b). The occurrence of delayed density dependence in balsam fir sawfly dynamics was also demonstrated by the circular orbits of the phase plot (Fig. 4c), by the selection of a non-linear, delayed density-dependent model by a response surface methodology (RSM: Turchin, 1996; Turchin and Taylor, 1992) ($r^2 = 0.45$) (Fig. 4d) and by the observation that 2–5 years of decline followed every major peak in oscillations (Fig. 3).

Direct and delayed density dependence may arise from the effects of a number of factors. The prevailing idea in the field is that both a pathogen (*NeabNPV; Neodiprion abietis* nucleopolyhedrovirus) and a complex of parasitoids are driving balsam fir sawfly fluctuations in density (Carroll, 1962; Martineau, 1985; Pardy, 1964; Smith, 1947; Struble, 1957). However, the parasitoids identified in those studies are multivoltine species that require alternate hosts to complete their development, making them likely candidates for direct,
but not delayed density dependence (Hassell and May, 1986). Conversely, NeabNPV, a specialist natural enemy that can cause severe epizootics in natural populations of balsam fir sawfly (Carroll, 1962; Brown, 1951; Moreau et al., 2005; Smith, 1947; Struble, 1957), could contribute to delayed density-dependent feedbacks as in other systems (Anderson and May, 1981; Dwyer et al., 2004). Host-plant effects were linked to fluctuations in another sawfly defoliator (Larsson et al., 2000) but have not yet been described in this system. Studies are currently under way in western Newfoundland to quantify the relative contributions of these and other factors to balsam fir sawfly dynamics and determine their roles in direct and delayed density dependence in this species’ fluctuations.

Thus, historical data suggest that the current outbreak of balsam fir sawfly in western Newfoundland is larger and longer than previous outbreaks in historical records due to an expansion of the range usually subjected to severe defoliation by this insect. Although the trend may be conjectural, each successive outbreak has generally occurred northward of previous ones (Fig. 1), perhaps due to increasing suitability of northern forests for balsam fir sawfly or to other factors. Contemporary studies have suggested that precommercial thinning, a silvicultural technique applied to reduce between-tree competition, has contributed to this expansion in range and to increases in balsam fir sawfly population density in individual stands (Moreau, 2004; Moreau et al., in press).

Since winter temperature appears to limit the range in another sawfly (Veteli et al., 2005), it may be speculated that climate change contributed also, or could contribute in the future, to this expansion of outbreak range. Historical data also indicate that balsam fir sawfly fluctuations are caused by direct and delayed density-dependent processes, providing valuable insights on the role of the different factors formerly associated with changes in density in this species.

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