



Fundamental ecological insights as a legacy of spruce budworm research in Canada

The study of forest insect ecology in Canada experienced a heyday of research following the Second World War. This was influenced by several important factors. First, men returning from the military were going to university and some trained in entomology and ecology. Planes were also increasingly available for monitoring

the defoliation caused by forest insects and for aerial spraying. In addition, knowledge and techniques for monitoring weather patterns and conditions were improving. Finally, with the increasing availability of computers, a new era of more complex data synthesis and biologically realistic models became possible.

As these developments in the potential for ecological studies occurred in the early 1940s, a periodic outbreak of eastern spruce budworm (SBW) (*Choristoneura fumiferana*) began (Figure 1). The univoltine SBW occurs in the Boreal Forest from the west to the east coasts of Canada and northern USA (Nealis 2016). Balsam fir, *Abies balsamea*, is the primary host tree of SBW, but white spruce, *Picea glauca*, black spruce, *P. mariana*, and red spruce, *P. rubens*,

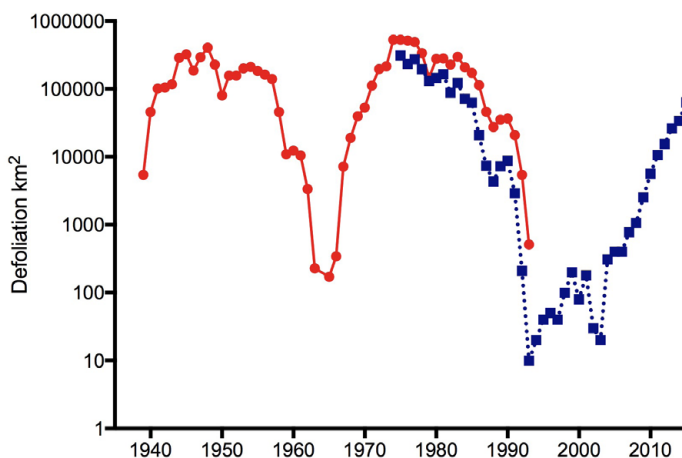


Figure 1. Defoliation predominantly by SBW in Quebec. Data provided by Barry Cooke (1940-1992) circles and from Canadian Forest Service and National Forestry Database (1975-2014) (<http://nfdp.ccfm.org/en/data/insects.php>) squares.

Judy Myers (myers@zoology.ubc.ca) is a professor emerita in the Department of Zoology and the Biodiversity Research Centre, University of British Columbia. Her Heritage Lecture was presented at the Joint Annual meeting of the Entomological Societies of Canada, British Columbia, and America, in Vancouver, November 2018.

Table 1. Major contributions to ecology from studies of Canadian forest insects arising particularly from studies on eastern spruce budworm. Citations based on Google (January 11, 2019).

Contribution	Early Authors	Status
Climatic release – warm dry conditions initiate population outbreak	Wellington et al. 1950 (69 citations)	Still being discussed but not supported as causing outbreaks. Dry conditions promote cone growth that provides good larval food.
Life tables and key factor analysis	Morris and Miller 1954 (333 citations)	Replaced by general linearized models and information theoretic approaches. Criticised by Royama (1996). Royama (2001) recommends using marginal mortality rather than the nominal mortality.
Functional responses to describe predation and parasitism	Holling 1959a, 1959b (3762 & 2873 citations)	Difficult to measure in the field with multiple predators and prey but used in models of population dynamics and widely discussed
Mathematical models for insect control	Watt 1961 (118 citations)	Further development on models of Thompson 1930, Nicholson 1933
Regression models of eruptive populations	Morris 1963 (570 citations)	Mathematics criticized by Royama (1971)
Stability, resilience and multiple stable states	Holling 1973 (12,335 citations)	Based on ideas about population eruptions that are not supported by cyclic population dynamics that show continuous change
Analytical models of eruptive population dynamics	Ludwig et al. 1978 (841 citations)	Output not realistic and depends on tree death that does not always occur
Second-order, density dependent, cyclic models – Oscillatory Hypothesis	Royama 1984 (441 citations)	Supported but improved by the addition of foliage quality and quantity and dispersal by Régnière and Nealis 2007
Innovative quantification of moth dispersal	Greenbank et al. 1980 (234 citations)	Dispersal still considered an important factor, but how it relates to synchronization of populations from “hotspots” and synchronizes populations remains under discussion
Development and application of ecologically based models to decision making in pest management	Baskerville 1975 (203 citations), Régnière and You 1991 (31 citations)	Still work in progress – “early intervention” programs to protect forests are now attempted.
Consideration of tree and insect quality, fecundity and mating success contribute to more realistic models of insect populations	Royama 1984 (441 citations) Régnière and Nealis, 2007 (56 citations)	Process driven models provide testable predictions as compared to earlier analytical models

are also acceptable host trees (Morris 1963). SBW became the focus for a unique and massive ecological study of the factors influencing population dynamics and resulted in numerous valuable contributions to insect ecology in general. Here I highlight some of the ecological advances that were made over the outbreak of SBW from the 1950s through 1970s and evaluate how these developments have held up over time as work has progressed (Table 1).

Weather and insect outbreaks

One of the first contributions from the study of SBW was the testing of the influence of weather on population dynamics. W.G. Wellington spent the war years as a meteorologist with the Canadian Air Force in Sault Ste. Marie, Ontario, which was also the location of the Forest Insect Laboratory founded in 1940. His combined interests in weather and insects culminated in his work on the influence of temperature and moisture on the behaviour of SBW larvae (Wellington 1949a, 1949b) and the association between June rainfall and SBW population increase (Wellington et al. 1950). This led to the “climatic release” hypothesis that proposed that warm and dry conditions are beneficial to larval survival and allow populations to escape the endemic period between population outbreaks. The potential association of weather and insect outbreaks continued to be an element in future work on SBW, but the generality of the association proposed by Wellington was later criticized as having been based on a small geographical region and a single outbreak (Royama 1984).

Further detailed analyses of weather and population growth and larval survival (Royama 1984) concluded that temperature and population dynamics of SBW were not related. Much later, Bouchard and Auger (2014) found that forest composition and average degree-days were not important to the initial development of SBW outbreaks, but did influence insect defoliation patterns within and between areas later in the outbreak process. In particular, dry weather in the previous summer which promotes the development of pollen cones, particularly in balsam fir, provides high quality larval food (Bouchard et al. 2018). Warm May temperatures are also related to larval survival and both low precipitation in the previous year and May temperatures were related to synchrony among SBW populations in Quebec.

Recently, interest in the influence of climate change on forest insects has stimulated a number of studies using data available on SBW to ask if the characteristics of the population cycles will change in the future. The results of these models have been contradictory, with some predicting increased duration of the outbreaks (Fleming and Volney 1995, Volney and Fleming 2000, Gray 2008), shorter duration of outbreaks (Gray 2013, Boulanger et al. 2016), or no change (Candau and Fleming 2011). Thus, climate change models don't predict how cyclic dynamics of SBW might change in the future. A current summary of SBW population dynamics on the NRCAN Website 2018 (<https://www.nrcan.gc.ca/forests/fire-insects-disturbances/top-insects/13383>) states that: “Although weather is often cited as an important factor, there is no consensus as to how weather may influence the beginning or end of outbreaks.”

Life tables

In 1944 the Green River Project was established in northwestern New Brunswick for the long-term study of SBW as related to forest management (Morris 1951). This project ran until 1960, at which time SBW had declined to low density (Figure 1). One approach used in this project was to study the relationship between population increase and mortality factors through the development of life tables (Deevey 1947) for each generation of moths in different forest stands. Morris (1955) discussed the history of life tables and, although life tables had been used for studies of humans, they had not been used for insects (Morris and Miller 1954). Life tables are a way to organize data by selecting appropriate age intervals such as larval instars, recording the number alive at the

beginning of the age interval, the number dying over the age interval, the proportion dying, the cause of death and the life expectation of individuals. If the population variation from generation to generation is determined by only one factor, the log of the density in the next generation should be determined by the log of the rate of increase plus the log of the initial population plus the proportion surviving (Morris and Miller 1954). Morris distinguished mortality factors that varied little from year to year from those that appeared to be responsible for the changes in the population density and showed that the factor causing the highest mortality was not necessarily that related to population density change.

The data collected in the Green River Project at different sites and over time became the basis of a key factor analysis of SBW reported in “The dynamics of epidemic spruce budworm populations” edited by Morris (1963). Parasitism was not a key factor for epidemic populations of SBW, but this study only included data from the outbreak phase of the populations and thus potential relationships for declining and low-density populations remained unknown.

More recent studies by Bouchard et al. (2018) of low-density populations using experimentally introduced sentinel larvae found that parasitism was compensatory between parasite species, varied among years and locations, and was higher in warmer areas; also temporal variation in parasitism was not related to temporal variation in SBW. An Allee effect related to reduced mate finding could also have an influence on reproductive success in low density populations (Régnière et al. 2013).

While key factor analysis has been widely used, Bellows et al. (1992) pointed out that the identification of a key factor does not necessarily identify the factor or factors that regulate population densities. A recent review of population studies of Canadian forest insects (Johns et al. 2016) found that 12 life table studies have been done on 7 species that involved key factor analysis. They concluded, however, that the approach has been largely abandoned after Royama (1996) showed statistical and logical issues with the technique.

Functional responses and endemic populations

In the same general time that Wellington was investigating the relationships between weather and SBW population dynamics, and Morris was developing the key factor analysis, C.S. Holling was describing the relationships between insect prey and vertebrate predators (Holling 1959a, 1959b), and insect hosts and parasitoids. Three basic patterns between prey capture and prey density were described both graphically (Type I, II, and III) (insert, Figure 2) and numerically. While these patterns are presented as being distinct, they represent a continuum (Denny 2014). Both Type I and Type II responses are described by equations that are special cases of the Type III expression. If predators followed the sigmoidal Type III functional response of Holling, the relationship between the number of larvae in N_t and N_{t+1} , the recruitment curve of Ricker (1954) (Figure 2), would indicate the possibility of a stable equilibrium at lower density associated with predation, a “predator pit”. A lower unstable equilibrium “release” point related to the effects of low parasitism, good weather or available host trees would be the point at which the outbreak begins, and a high density “stable” equilibrium related to defoliation of the food supply would occur if the trees responded to reduced larval density (Berryman 1987). If tree mortality reduces food availability, the larval population could fall back into the predator pit.

How well SBW dynamics fit this scenario is unclear. Although the impact of parasitoids could increase with host density following a Type 2 response, parasitism was not a key factor in the increasing phase of SBW dynamics described by Morris (1963). Royama (1984) recognized that what appears to be a sudden eruption of a population following a period of low density looks quite different if plotted appropriately on a log scale rather than an arithmetic scale (see Figure 1 for log scale). Thus, a long period of low density that might be predicted if a predator pit were operating does not seem to occur.

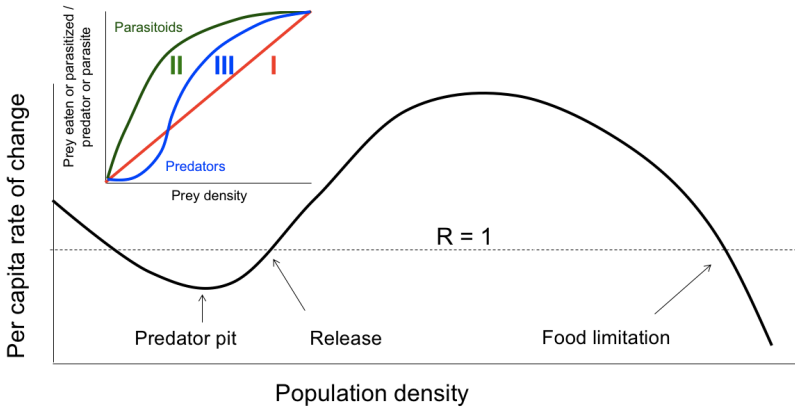


Figure 2. Recruitment curve after Berryman (1987) with the insert showing the functional responses described by Holling (1959a, 1959b).

Stability and resilience

The concepts of equilibrium theory and stability arose out of the field of forest insect ecology. The SBW dynamics described above clearly contributed to Holling's treatise on stability and resilience (Holling 1973). Holling proposed that SBW is highly unstable as indicated by its outbreak dynamics, but also the system is resilient because SBW defoliation prevents the forest from being dominated by balsam fir. Although fir suffers greater mortality from SBW attack than spruce, it also regenerates more rapidly than spruce and birch that are non-favoured host trees (Baskerville 1975). Even though SBW comes and goes, the forest composition is maintained over the long run.

While the details of budworm oscillations may not have been totally clear in 1973, the dramatic pattern of outbreaks of this defoliating insect certainly demonstrates that a simple equilibrium view of the world does not hold. But it is debatable as to whether regular population oscillations themselves equate to a form of ecosystem stability (Bouchard et al. 2006).

Models of population dynamics

The development of mathematical ecology and modelling of population dynamics was greatly advanced by forest insect ecologists. During the 1920s and 1930s deterministic models were developed for some insect systems (e.g., Thompson 1930, Nicholson 1933), but these were not realistic. With the availability of computers more realistic models of the interactions of predators, parasitoids, insects and host trees were feasible.

K.E.F. Watt, who was with the Statistical Research Service of the Canadian Department of Forestry, was a pioneer in developing models for insect pest control. His first mathematical model was published in 1959 (Watt 1959) and in the following years (Watt 1961, Watt 1962) he wrote about the use of mathematics in population ecology (but see Royama [1971] for a critique of this work). In the Memoir edited by Morris (Morris 1963), Watt developed a multiple regression model that showed that larval parasitism was not related to the level of larval survival during the epidemic phase of population growth.

Later computer models were designed to test the influences of various measures for SBW

control. Watt (1964) predicted that applying control measures as moth populations were increasing would be more effective than when populations were at peak density. This is the basis for the early intervention program now in place in New Brunswick (Rob Johns, personal communication, and Pureswaran et al. 2016).

Recently (Sturtevant et al. 2015), reviewed 15 models of SBW population dynamics. The early models, inspired largely by Morris and Watt (Morris 1963) and later Jones (1977) (cited by Sturtevant et al. 2015). These considered the population dynamics to be eruptive with multiple equilibria, for example, long periods of low density followed by SBW population outbreak, defoliation, tree death, and moth decline. One of the most highly cited models (Ludwig et al. 1978) had three main components: larval density, foliage density, and (mature) tree density. Larval density increased rapidly and tree recovery was slow. The population dynamics produced by this simulation model were cyclic but not realistic as the duration of the period of moth outbreak was very short as compared to the longer periods of outbreak in field data (Figure 1 and also Myers [1988]). The decline in larval survival in the model was attributed to tree death even though tree mortality is not a consistent characteristic of declining moth populations (Royama 1984). Ludwig et al. (1978) concluded that “the analytic model is likely to extend our understanding of the phenomena (SBW population dynamics), since the full armory of mathematical techniques is available”. No testable predictions were given to aid the understanding or predictability of SBW outbreaks although it would seem that if the model were correct, protecting forests with spray programs would prolong the outbreaks. History shows that this view is over simplified and other insect mortality factors during the decline must be considered (Pureswaran et al. 2016).

By 1984 Royama realized that the eruptive paradigm of SBW population dynamics was inaccurate and developed a second-order, density-dependent model that he proposed was a better description of SBW dynamics (Royama 1984). This model focused on mortality of the third to sixth instar larvae, with parasitoids, disease and an unknown mortality factor being the driving variables. Predation, weather, food shortage and larval dispersal are density-independent factors. This has been described as the “Oscillatory hypothesis” (Pureswaran et al. 2016).

In conclusion, without integrating defoliation and forest composition, as well as density related mortality as factors influencing SBW dynamics, models will be incomplete. Régnière and Nealis (2007) analyzed 15 years of sampling data from Ontario and Quebec and showed that defoliation influenced both moth fecundity and larval survival. Creating cyclic dynamics with mathematical models such as with the Ludwig et al. (1978) model is “not a predictive tool, nor could the assumptions be subjected to statistical tests” (Ludwig personal communication). Whether it promoted ecological understanding I think is debatable but the model is widely cited (Table 1). The process-oriented simulation of SBW feeding on white spruce and balsam fir by Régnière and You (1991) is a step in the right direction as it can be used to predict defoliation from SBW density. Thus, even to this day, more and more complex modelling of forest insect systems continues to attempt to explain the observed population dynamics.

Dispersal

The most difficult process to quantify in a population study is dispersal, yet it is key to understanding the dynamics of cyclic populations. Observations of the mass dispersal of SBW moths extend back to the 1912 outbreak in which additional street cleaners were required to sweep up dead moths in New Brunswick (Morris and Mott 1963). Dispersal of SBW can occur by adults, first instar larvae after emergence from the eggs, and by second instar larvae when they emerge from their hibernacula. Early studies showed dispersal of moths away from trees when defoliation was high (Morris and Mott 1963), little impact of dispersal of large larvae, but more more significant dispersal, related to egg density, of small larvae among plots. Greenbank (1963)

also recorded unexpected increases and declines in the number of egg batches in plots that could only be explained by immigration or emigration of moths. This phenomenon continues to be recognized as being important to the population dynamics (Régnière and Nealis 2007).

As technologies developed, studies of moth dispersal became more elaborate. Between 1970 and 1973 observations of moth flights were made from platforms, helicopters and fixed-wing aircraft (Greenbank 1973). This led to a much more extensive study using radar systems, a night-viewing telescope for observing moths taking off after dark, Doppler-equipped aircraft for the exploration of wind patterns, and aircraft with specially designed insect collecting nets to sample airborne moths (Greenbank et al. 1980). This work showed that moths emigrate from the forest canopy in vast numbers with dispersal flights at altitudes of 100-300 m and lasting for several hours between 7 and 10 PM. Moths were often concentrated by convergent wind fields and travelled from tens to hundreds of kilometers, depending on wind conditions. Landing sites tended to be localized and to change temporally. This expensive and unique project showed that dispersal varied temporally and, surprisingly, was greater on nights of widespread and heavy rain (Dickison et al. 1986).

The observed redistribution of moths may be an important factor in synchronizing outbreaks of SBW among areas, but Royama et al. (2005) concluded that because moth dispersal is not a diffusion process, as proposed by Williams and Liebhold (2000), a weather-driven Moran effect is required to synchronize populations. Based on pheromone trapping of male moths over 28 years, such weather associations have been shown to be related to the synchrony in variation among SBW populations in Quebec (Bouchard et al. 2018). Recent work reports genetic similarity among outbreak populations of SBW, indicating high gene flow (James et al. 2015).

In conclusion, moth movement, influenced by wind, temperature and forest conditions, is important for maintaining genetic homogeneity and potentially synchronizing population densities among sites with different forest characteristics (Candau et al. 1998, Nealis 2016). Models of dispersal of SBW are continuing to be developed (Sturtevant et al. 2013). Similarly, high dispersal and genetic homogeneity appear to be characteristics of all cyclic species that have been analyzed (Myers 2018).

Contribution of ecology to the control of spruce budworm

The focus on SBW as a study species stemmed from the need to develop management strategies for this outbreak species. Early work focused on the population ecology of SBW with the underlying idea that if the factors that influenced the density of populations could be understood, some clue to controlling populations might be revealed. The SBW system is an example of adaptations between forests and insects, and management aimed at disrupting the stability of this system is unlikely to be sustainable and thus “ecologic resilience does not imply economic stability” (Baskerville 1975).

The distribution of SBW in North America extends across the Boreal Forest from the west coast to the east coast. Thus, the areas attacked by SBW are heterogeneous in their histories and bioclimatic conditions. This is reflected in the spatial patterns of SBW outbreaks that show considerable geographic variation in their length and severity (Candau and Fleming 2005, Zhao et al. 2014). Heterogeneity among sites and the difficulties with scaling up models based on smaller spatial scales (Fleming et al. 2002) create a mismatch between results of detailed ecological studies and large scale projections of SBW dynamics. The dispersal of SBW moths that has been observed is a major factor in determining population dynamics but it remains unpredictable in when and where it will occur.

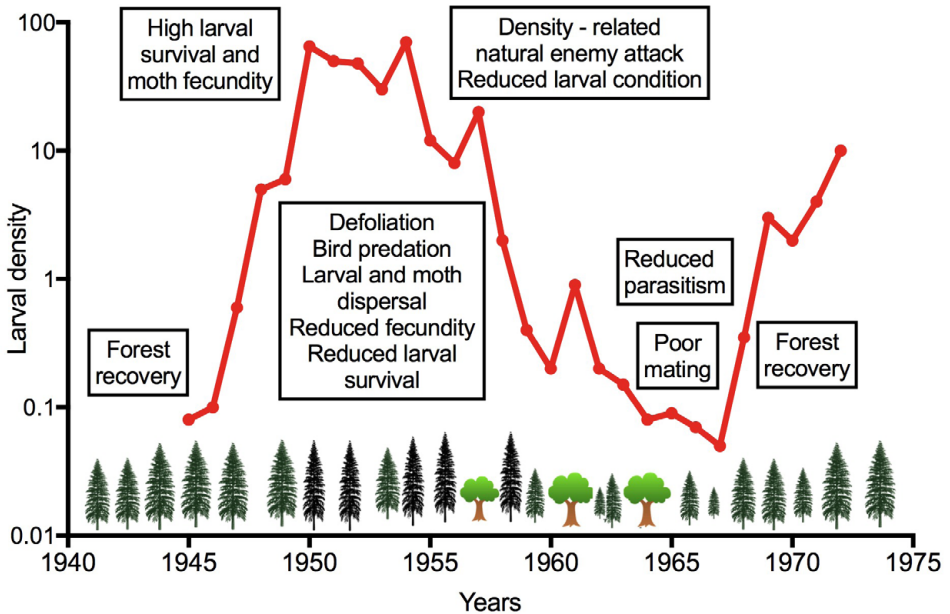


Figure 3. Summary of processes influencing SBW (Régnière and Nealis 2007; Royama et al. 2005) are outlined on a SBW population trend from Royama (1984).

Conclusion

For over 90 years the eastern spruce budworm has been the focus of ecological study in North America. The interactions between SBW, their myriad natural enemies (Eveleigh et al. 2007), and trophic interactions with their host trees (review in Nealis 2016) are well studied. While much is known about the details of SBW dynamics (Figure 3), the ecological principles developed from the extensive and innovative research have contributed to population ecology in general and to the study of cyclic forest Lepidoptera in particular. Table 1 outlines some of these advances and indicates through citations the relevance of particular work to further research on this species and others. Some of the ecological advances such as key factor analysis have not stood the test of time. Other advances such as functional responses and ideas about stability and resilience have continued to be developed and applied to many systems. There is no question that Canada has a proud heritage of insect ecology that has been particularly developed from the challenges of SBW outbreaks.

Acknowledgements

This paper is based on my presentation of the Heritage Lecture at the Joint Meeting of the Canadian, American and British Columbian Entomological Societies in November 2018. I wish to thank Barry Cooke, Vince Nealis, Richard Fleming, Brian Van Hezewijk and Jacques Régnière of the Canadian Forest Service for helpful comments and providing insights, and Barry Cooke for providing long-term defoliation data. I thank Jenny Cory for reviewing the manuscript and acknowledge the late Don Ludwig for interesting discussions.

References

- Baskerville, G.L. 1975. Spruce budworm: super silviculturist. *Forestry Chronicle*, **51**: 138-140.
- Bellows Jr, T., Van Driesche, R. and Elkinton, J. 1992. Life-table construction and analysis in the evaluation of natural enemies. *Annual Review of Entomology*, **37**: 587–612.
- Berryman, A. A. 1987. The theory and classification of outbreaks. *In* *Insect Outbreaks*. Edited by P. Barbosa and J. C. Schultz. Academic Press, New York. pp 3–30.
- Bouchard, M., and Auger, I. 2014. Influence of environmental factors and spatio-temporal covariates during the initial development of a spruce budworm outbreak. *Landscape Ecology*, **29**: 111–126.
- Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology*, **87**: 2319–2329.
- Bouchard, M., Régnière, J., and Therrien, P. 2018. Bottom-up factors contribute to large-scale synchrony in spruce budworm populations. *Canadian Journal of Forest Research*, **48**: 277–284.
- Boulanger, Y., Gray, D.R. Cooke, B.J., and De Grandpré, L. . 2016. Model-specification uncertainty in future forest pest outbreak. *Global Change Biology*, **22**: 1595–1607.
- Candau, J.-N., and Fleming, R.A. 2005. Landscape-scale spatial distribution of spruce budworm defoliation in relation to bioclimatic conditions. *Canadian Journal of Forest Research*, **35**: 2218–2232.
- Candau, J.-N., and Fleming, R.A. 2011. Forecasting the response of spruce budworm defoliation to climate change in Ontario. *Canadian Journal of Forest Research*, **41**: 1948–1960.
- Candau, J.-N., and Fleming, R.A., and Hopkin, A. 1998. Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Canadian Journal of Forest Research*, **28**: 1733–1741.
- Deevey, E.S. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology*, **22**: 283–314.
- Denny, M. 2014. Buzz Holling and the functional response. *Bulletin of the Ecological Society of America*, **95**: 200–203.
- Dickison, R.B.B., Haggis, M.J., Rainey, R.C. and Burns, L.M.D. 1986. Spruce budworm moth flight and storms: Further studies using aircraft and radar. *Journal of Climate and Applied Meteorology*, **25**: 1600–1608.
- Eveleigh, E.S., McCann, K.S., McCarthy, P.C., Pollock, S.J., Lucarotti, C.J., Morin, B., McDougall, G.A., Strongman, D.B., Huber, J.T., and Umbanhowar, J. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proceedings of the National Academy of Sciences*, **104**: 16976–16981.
- Fleming, R., and Volney W. 1995. Effects of climate change on insect defoliator population processes in Canada's boreal forest: some plausible scenarios. *Water, Air, and Soil Pollution*, **82**: 445–454.
- Fleming, R.A., Barclay, H.J., and Candau, J.-N. 2002. Scaling-up an autoregressive time-series model (of spruce budworm population dynamics) changes its qualitative behavior. *Ecological Modelling* **149**:127–142.
- Gray, D.R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. *Climatic Change*, **87**: 361–383.
- Gray, D.R. 2013. The influence of forest composition and climate on outbreak characteristics of the spruce budworm in eastern Canada. *Canadian Journal of Forest Research*, **43**: 1181–1195.
- Greenbank, D. 1963. The analysis of moth survival and dispersal in the unsprayed area. *Memoirs of the Entomological Society of Canada*, **95**: 87–99.
- Greenbank, D. 1973. The dispersal process of spruce budworm moths Canadian Forest Service Publications Information Report MX-39. 24 pp., Fredericton, NB.
- Greenbank, D., Schaefer, G.W., and Rainey, R.C. 1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. *Memoirs of the Entomological Society of Canada*, **112**: 1–49.
- Holling, C.S. 1959a. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**: 293–320.
- Holling, C.S. 1959b. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**: 385–398.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**: 1–23.
- James, P.M.A., Cooke, B., Brunet, B.M.T., Lumley, L.M., Sperling, F.A.H., Fortin, M.-J., Quinn, V.S., and Sturtevant, B.R. 2015. Life-stage differences in spatial genetic structure in an irruptive forest insect: implications for dispersal and spatial synchrony. *Molecular Ecology*, **24**: 296–309.

- Johns, R., Flaherty, L., Carleton, D., Edwards, S., Morrison, A., and Owens, E. 2016. Population studies of tree-defoliating insects in Canada: a century in review. *The Canadian Entomologist*, **148**(S1): S58–S81.
- Ludwig, D., Jones, D.D., and Holling, C.S. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *Journal of Animal Ecology*, **47**: 315–332.
- Morris, R. 1951. The importance of insect control in a forest management program. *The Canadian Entomologist*, **83**: 176–181.
- Morris, R., and Miller, C. 1954. The development of life tables for the spruce budworm. *Canadian Journal of Zoology*, **32**: 283–301.
- Morris, R., and Mott, D. 1963. Dispersal and the spruce budworm. *Memoirs of the Entomological Society of Canada*, **95**(S31): 180–189.
- Morris, R.F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. *Canadian Journal of Zoology*, **33**: 225–294.
- Morris, R.F. (ed.). 1963. The dynamics of epidemic spruce budworm populations, *Memoirs of the Entomological Society of Canada*. No. 31. 322pp. Ottawa, Canada.
- Myers, J.H. 1988. Can a general hypothesis explain population cycles of forest Lepidoptera. *Advances in Ecological Research*, **18**: 179–242.
- Myers, J.H. 2018. Population cycles: generalities, exceptions and remaining mysteries. *Proceedings of the Royal Society B*, **285**:20172841. <http://doi.org/10.1098/rspb.2017.2841>
- Nealis, V. 2016. Comparative ecology of conifer-feeding spruce budworms (Lepidoptera: Tortricidae). *The Canadian Entomologist*, **148**: 1–25.
- Nicholson, A. 1933. The balance of animal populations. *Journal of Animal Ecology*, **2**: 132–178.
- Pureswaran, D.S., Johns, R., Heard, S.B., and Quiring, D. 2016. Paradigms in eastern spruce budworm (Lepidoptera: Tortricidae) population ecology: A century of debate. *Environmental Entomology*, **45**: 1333–1342.
- Régnière, J., Delisle, J., Bause, E., Dupont, A., Therrien, P., Kettela, E., Cadogan, L., and van Frankenhuyzen, K. 2001. Understanding of spruce budworm population dynamics: development of early intervention strategies. *In Proceedings of the North American Forest Insect Work Conference, Information Report NOR-X-381*, Edmonton, AB. pp. 57-68
- Régnière, J., Delisle, J., Pureswaran, D.S., and Trudel, R. 2013. Mate-finding allee effect in spruce budworm population dynamics. *Entomologia Experimentalis et Applicata*, **146**: 112–122.
- Régnière, J., and Nealis, V. 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecological Entomology*, **32**: 461–477.
- Régnière, J., and You, M. 1991. A simulation model of spruce budworm (Lepidoptera: Tortricidae) feeding on balsam fir and white spruce. *Ecological Modelling*, **54**: 277–297.
- Ricker, W.E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**: 559-623.
- Royama, T. 1971. A comparative study of models for predation and parasitism. *Researches on Population Ecology*, **13**: 1–91.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs*, **54**: 429–462.
- Royama, T. 1996. A fundamental problem in key factor analysis. *Ecology*, **77**: 87–93.
- Royama, T. 2001. Measurement, analysis, and interpretation of mortality factors in insect survivorship studies, with reference to the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Population Ecology*, **43**: 157–178.
- Royama, T., MacKinnon, W., Kettela, E., Carter, N., and Hartling, L. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. *Ecology*, **86**: 1212–1224.
- Sturtevant, B.R., Achtemeier, G.L., Charney, J.J., Anderson, D.P., Cooke, B.J., and Townsend P.A. 2013. Long-distance dispersal of spruce budworm (*Choristoneura fumiferana* Clemens) in Minnesota (USA) and Ontario (Canada) via the atmospheric pathway. *Agricultural and Forest Meteorology*, **168**: 186–200.
- Sturtevant, B.R., Cooke, B.J., Kneeshaw, D.D. and MacLean, D.A. 2015. Modeling insect disturbance across forested landscapes: Insights from the spruce budworm. *In Simulation Modeling of Forest Landscape Disturbances. Edited by A.H. Perera, B.R. Sturtevant and L.J. Buse*. Springer International Publishing, Geneva, Switzerland. pp. 93-134.
- Thompson, W. 1930. The utility of mathematical methods in relation to work on biological control. *Annals of Applied Biology*, **17**: 641–648.

- Volney, W.J.A., and Fleming, R.A. 2000. Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems & Environment*, **82**: 283–294.
- Watt, K. 1959. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *The Canadian Entomologist*, **91**: 129–144.
- Watt, K.E. 1962. Use of mathematics in population ecology. *Annual Review of Entomology*, **7**: 243–260.
- Watt, K.E. 1964. The use of mathematics and computers to determine optimal strategy and tactics for a given insect pest control problem. *The Canadian Entomologist*, **96**: 202–220.
- Watt, K.E.F. 1961. Mathematical models for use in insect pest control. *Memoirs of the Entomological Society of Canada*, **93**(S19): 5–62. doi:10.4039/entm9319fv
- Wellington, W. 1949a. The effects of temperature and moisture upon the behaviour of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). I. The relative importance of graded temperatures and rates of evaporation in producing aggregations of larvae. *Scientific Agriculture*, **29**: 201–215.
- Wellington, W. 1949b. The effects of temperature and moisture upon the behaviour of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). II. The responses of larvae to gradients of evaporation. *Scientific Agriculture*, **29**: 216–229.
- Wellington, W., Fettes, J., Belyea, R., and Turner, K. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.)(Lepidoptera: Tortricidae). *Canadian Journal of Research*, **28**: 308–331.
- Williams, D.W., and Liebhold, A.M. 2000. Spatial synchrony of spruce budworm outbreaks in eastern North America. *Ecology*, **81**: 2753–2766.
- Zhao, K., MacLean, D.A., and Hennigar, C.R. 2014. Spatial variability of spruce budworm defoliation at different scales. *Forest Ecology and Management*, **328**: 10–19.
-



C. Sheffield

Andrena wilkella (Hymenoptera, Andrenidae) on Lupine (*Lupinus*), PEI