Forests with animals eating their trees

A chapter in: *Trees of the people,* by Alan R. Walker

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Woodlands remain in place decade after decade, each tree resisting storms and hungry animals that would invade them and eat them. Leaves, stems and roots are attacked by bacteria and fungi, by insects and mammals. These plant-eating microbes and herbivorous animals can benefit from the effects of fire and storm as gaps are created in the tree cover and nutrients are recycled as ash or the end products of fungal decay.

Balsam fir, *Abies balsamea*. Credit: R.A.Nonenmacher, Wikimedia.

Gaps in the canopy allow more light and space for seedlings of a wide variety of plants to flourish: grasses, herbs, and the offspring of the surrounding mature trees. Herbivores, from insects to large species of deer, are likely to benefit from the flush of new green growth, here more accessible, palatable and nutritious. In the long life of a tree this pressure on it of being eaten by insects or deer is part of the continuous cycling of energy and nutrients. This goes in a fluctuating balance between growth of the population of trees and the population of the herbivores. Numbers of herbivores are kept in check by combinations of non-living factors such as winter harshness or summertime drought. Herbivores are also kept in check by other living organisms, from microbes to small predators such as insects through to predatory mammals.

Adult moth of genus *Choristoneura*. It is the larval stage of these moths that feeds on trees, see page 10. Credit: Jeffrey J. Witcosky, USDA, Wikimedia.

This large and varied topic needs to focus on a few examples of herbivores. Good examples will be animals that cause major damage to forests as localised outbreaks of severe damage to trees. Other examples will be herbivores that exert a continuous pressure of loss of foliage of forest trees that is measured as tonnes of lost production of a commercial forest. Damage to woods and forests by herbivores is often well studied and documented by foresters and botanists seeking understanding of how to contain or reduce damage to woods and forests from herbivory.

In North America some forests have a combination of two herbivores that serve the purpose here. One is an insect, a species of moth called eastern spruce budworm, *Choristoneura fumiferana*. This particular species lives in north eastern Canada, and similar budworm species are distributed westwards across northern USA and southern Canada. “Budworm” derives from the worm-like immature stage of the moth. This eastern species, during its immature stage, prefers to feed on balsam fir, *Abies balsamea*, but also feeds on white spruce, *Picea glauca*, and black spruce, *Picea mariana*. Spruce budworms are well studied because of the large losses they cause to commercial forestry.

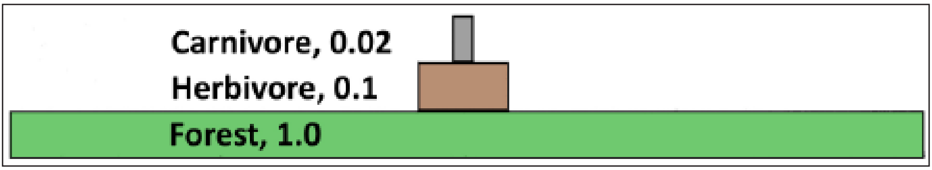
In the same forests lives the largest species of deer: moose, *Alces alces*. This impressive animal of the forest browses on needle-leaves of firs and spruces, particularly during winter, but prefers to browse and graze on more palatable, low lying herbage during summer. Moose are distributed in boreal forests all around the north polar region. They are well studied in relation to the direct damage they cause to forests, and as examples of the relationships between deer and large predator mammals.

Adult male moose (or elk) *Alces alces*. Moose damage forest by using tree seedlings as winter forage. Only males grow antlers and only during breeding season. Antlers are boney and for mating display. Credit: USDA, Wikimedia.

Energy flows in forests.

Plants are fundamental to life on Earth and in our present times grasses and trees are the most important by their colossal mass of vegetation. These and all other plants are the primary producers of the carbon based materials that comprise the substance of plants, and store energy available for the work of growth and reproduction. Photon particles arriving as sunlight deliver intense energy to the chemical reactions of photosynthesis, driving the production of the materials that the plant will use to grow. Enzymes and reagents working in the leaves capture carbon from gaseous carbon dioxide in air, together with the hydrogen of water, to make simple carbohydrates, firstly as glucose. This sugar is the key molecule providing the energy needed for most living things. It is used in living tissues by a cold wet type of burning reaction, an oxidation. This releases the energy embodied in glucose to drive the chemical activity of bodily maintenance and growth, collectively called respiration.

All organisms wear out as mechanisms for repair and replacement become faulty during constant turnover of new cells replacing old cells. Dead plants pile up and would smother everything but for the activity of bacteria, fungi, and the small animals of soil that feed on the detritus of dead plants and animals. The mass, as tonnes of active microbes, fungi and other decomposers in soil is only a little less than the mass of green vegetation above. Trees with their huge foliage are attractive to many herbivores and winter-green trees are an essential resource for some herbivores. Insects gnaw at leaves or tap into the sap as a source of food. Some insects, as grubs, bore into the stems of trees and digest their woody food with the aid of bacteria in their guts. Voles, rabbits, hares, squirrels, deer, sheep, cattle, antelope, elephants will live partly by eating leaves and stems of trees. Which may seem a devastating range of threats to the plants, except that the mass of these many types of animal herbivores is always small compared to the mass of plants. Much smaller, as tonnes of living things, because of fundamental constraints on the ability of herbivores to gain energy. So rather than mass, access to energy is the key driver: as shown below.



Trophic levels diagram as relative access to **energy**. Width of the bars represents amounts of energy available to do work for organisms at each level. Forest has full access to Sun's photon energy. Herbivores have direct access to 10% of the forest's embodied energy as they feed on leaves. Carnivores have indirect access to 2% of the forest's embodied energy as they feed on herbivores.

Compared to all other forms of life, plants grow and reproduce by using an intense form of energy that comes direct to them. Energy available to plants is limited by night-time, seasonal levels of light, and shade from clouds and other plants. A tree seedling may only grow to maturity if its parent trees and others nearby are wind-thrown by storm or consumed by fire, leaving a gap into which sunlight pours. Ample energy is available to maintain something as big as a forest, but for each tree of the forest there is a loss of photon energy during the process of growth from seedling to reproductive tree. For every unit of energy, a joule or calorie as sunlight into leaves, all that is left as the energy embodied in new plant tissue is a minute fraction. From our perspectives, plant life seems extremely wasteful. (An example for trees, using joule as a standard unit of energy, is: 9.5 megajoules/square-metre/day of sunlight energy onto the canopy diminishing down to 0.05MJ/m2/day of energy embodied in leaves and stems. See 'Photosynthesis' chapter for details.)

The simple but strange laws of energy, of thermodynamics, operate here. Specifically the second law of thermodynamics: when energy is transformed from one form to another there is always a dilution of energy. Energy is never destroyed, but it becomes more disordered and thus less useful for doing work. During that transformation, work can be done, molecules can be put in place as plant tissues are formed and the plant.

Animal herbivores, such as beetle grubs boring into stem wood or deer chewing on needle-leaves, have far less energy available from this plant source than the tree does as is raises its leaves into sunlight. Other factors add greatly to the difficulties for animals to obtain enough energy. Insects need to grow fast and search continuously for plant food that is edible, that will not poison them. They need to produce a new generation within the summer season or overwinter by hibernation. Deer and other mammals need to burn much food by respiration just to keep their body temperature warm enough to remain functional. They need to walk far to find better food and shelter and avoid predators. As for the carnivores, from blood-sucking insects through to bears, they in turn are subject to these same unavoidable constraints on the availability of energy. The larger these carnivores are the rarer they are: they cannot gain sufficient energy by hunting herbivores to reproduce rapidly.

Nearly all living things, everything except possibly viruses, need defences against all those other living things that would eat them. These defences have a cost, as energy expended to maintain and operate them. Even bacteria have defences against some types of viruses, named bacteriophages – eaters of bacteria. Insects and similar animals have an immune system, with blood containing mobile cells that can engulf and consume invading microbes. Our blood works in similar way with white blood cells that find and kill invading pathogens. Without an immune system functioning correctly life is at severe risk. Plants do not have an immune system of this animal type, but defend themselves in many ways from the great range of microbial, fungal and animal life that would use them as food.

Relations between feeding levels of plants and animals.
The diagram above, illustrating a type of food chain, is called a trophic pyramid. Much written in textbooks of ecology about which way these feeding relationships work. Do top predators rule an ecosystem as influences of death by predation cascading down? Or do the plants rule by their stubbornly rooted vast quantity of greenery and supply of photon energy, of which only small fractions of energy and nutrients move up to animals?

Relative to large carnivores, deer are common and widespread. They are ruminant animals, as are the closely related sheep, goats and cattle. Their digestive system has four chambers followed by a very long intestine. The first two in line of these chambers are termed the rumen. These allow fermentation of leafy food with the aid of bacteria. Some of these animals regurgitate material from their rumen for further chewing of the cud – ruminants ruminate. These major adaptations to eating plants have been one of evolution's successes. There are many ruminant species populating most land masses of the world and the deer of this chapter – moose, elk, red deer, roe deer – all have populations known to be increasing in density or expanding their range.

> Vernacular names in English of these deer species are confusingly variable between countries.
> • Moose (*Alces alces*) are known also as elk in Norway, Sweden and Finland.
> • Elk, or wapiti, of North America are *Cervas canadensis*; they also inhabit central Asia and Siberia.
> • Red deer are *Cervas elaphus*; they inhabit Eurasia, and are similar to the larger elk of North America.
> • Caribou are *Rangifer tarandus* of North America, and this species is called reindeer in Eurasia.

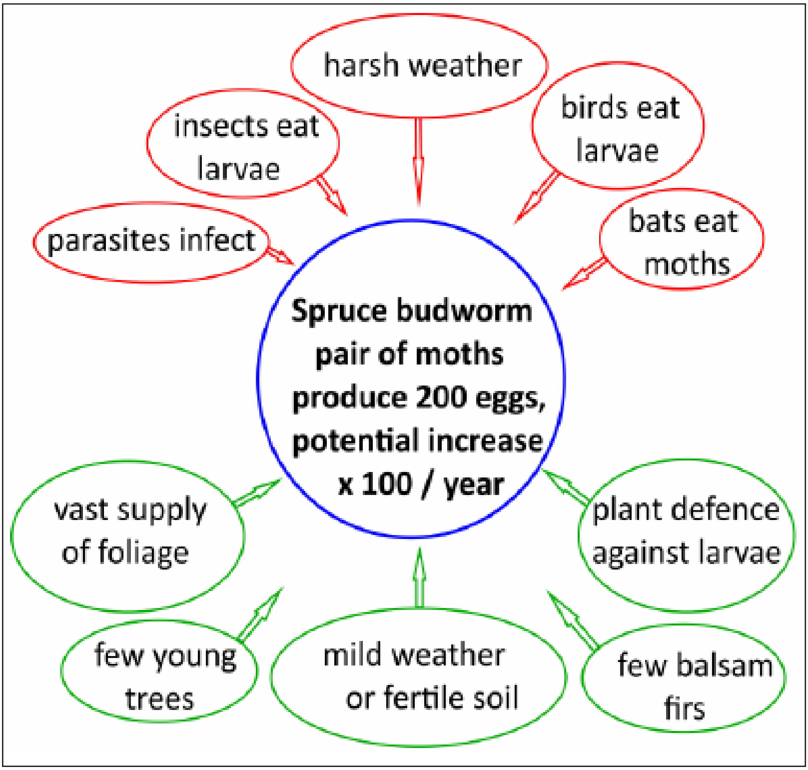
Is the direct effect of predation and fear of it a strong influence on the long term and wide-ranging health and productivity of the forest? For any population of deer of any species it is the young, the old, and the diseased that are most likely to succumb to predators. In that population of prey those individuals in their prime of life are likely to be robust and agile enough to escape their enemy by learnt alertness, speed, and in the case of moose, by sheer size. Full grown moose defend against a pack of wolves by kicking their attackers. Male moose in the breeding season have large antlers for sexual display – also useful to scare wolves. Predator threats and consequent changes of behaviour toward feeding in safer places will reduce the impact of the deer on the forest. The question for foresters is how much benefit to the forest is such reduction in herbivory?

Red deer *Cervas elephas*, hind, in Europe; one of commonest and widespread deer across a wide range of woodland habitats in Eurasia. They have substantial effect on condition of woodlands. Credit: Charles J. Sharp; Wikimedia.

This type of ecological influence is called top-down. The effect flows down through the food chain of a forest, it cascades through the trophic levels. There is another direction of ecological influence that goes the other way: bottom-up. Growth and condition of a forest depends greatly on the non-living (abiotic) conditions of soil nutrients, water supply, aspect of the forest relative to sunshine and exposure to wind and avalanche. On soil rich with mineral nutrients and the right level of water supply the trees will have sufficient materials and energy to build strong defences against herbivores. Commonly these are chemical compounds derived from the usual processes of growth and reproduction but are not directly involved in the core metabolism, the essential chemical workings, of the tree. They are termed secondary metabolites and work for the tree as repellents and poisons. This pathway from nutrient supply to good defence against insect or deer herbivores is a typical bottom-up process.

Arguments about relative importance of top-down versus bottom-up influences often take up much effort and printed space. These assemblages of living organisms are so complex and varied that better understanding of them requires much data collected over long times and wide areas: less theory, more facts.

Other non-living influences can have massive effects on forests that initially and suddenly are devastating but in the slow life of a forest are of great benefit to its health. Fire opens up the canopy and enriches the soil with nutrients from ash and freshly weathered rocks. Seedlings rapidly colonize these areas as seed blows in from surrounding trees. The seedlings are likely to thrive but remain at high risk from many species of herbivore, insects to mammals. These herbivores thrive on the plentiful, fresh and palatable vegetation. Younger trees growing fast are likely to have a denser complement of needle-leaves that are more edible for insects than the foliage of older and taller trees. The question of how bottom-up processes may influence forest structure and health is a matter of many different factors and is hard to predict. Nevertheless, important for foresters making decisions on how to manage their trees.

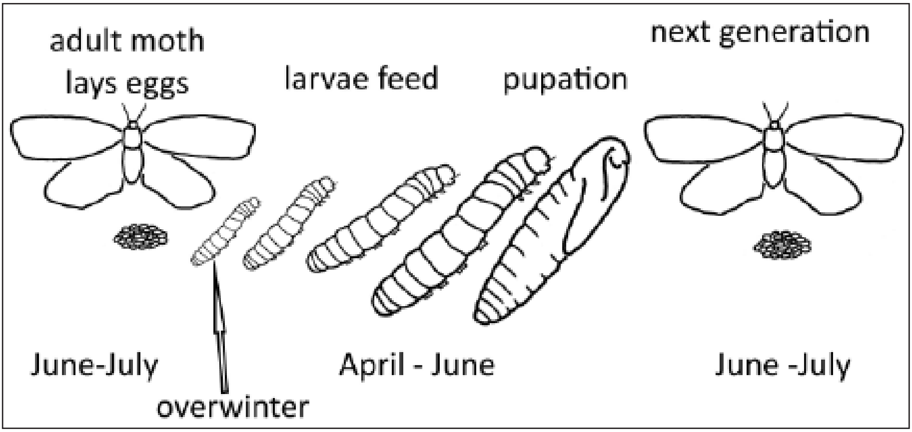


Typical factors affecting the population dynamics of spruce budworms. Red items a represent **top-down** factors; green items represent **bottom-up** factors. Note that abiotic factors: harsh weather and mild weather, fertile or infertile, soil are interchangeable here.

Spruce budworm: life-stages and damaging effects.

A budworm is an immature stage of a species of moth. The eastern spruce budworm is the focus here, *Choristoneura fumiferana*, but there are other important species such as western spruce budworm. Spruce budworms are confined to North America, but trees of the boreal forests of Eurasia have numerous species of insects feeding on them.

The immature stages, the damaging ones, are ordinary caterpillars familiar to us as creatures that develop into butterflies or moths. This immature stage is called larva. They grow rapidly, so need to shed their skin, usually four times. Spruce budworms feed on needle-leaves and freshly developing male cones of spruce and fir trees (see 'Reproduction' for photograph of cones of spruce, soft at this stage.) Where the larvae feed depends greatly on where an adult female moth has laid a batch of eggs, and when balsam fir is available this tree is preferred. When fully grown a larva develops into a stage called pupa. This then transforms into the adult stage, a female or male moth. The change is fundamental – a metamorphosis – of the insect's structure. What emerges from the outer case of the pupa is a female or male moth, ready to fly, find a mate, then reproduce. Adults are small, cannot feed, but are well adapted for strong flight and females are fussy about where they lay their eggs. Males are similar to females but once their role of mating and fertilization is done they die.



Life stages of eastern spruce budworm from an adult female moth laying eggs in mid-summer to another moth laying eggs one year later. (Adults and egg batches at smaller scale than larvae and pupa.)

During June to July a female moth lays about 200 eggs in total, as several batches glued onto needle-leaves. Ten days later larvae hatch then migrate as a group to a site on the bark of branches and stems. Here they spin silken threads as a collective shelter whilst they over-winter in a dormant state. In spring reactivated larvae seek feeding sites where they group together on needle-leaves.

Two white batches of eggs of spruce budworm moth laid on needle-leaves. Credit: USDA, Wikimedia.

Larva (a caterpillar) of an early stage of eastern spruce budworm on needle-leaves. Credit: Jerald E.Dewey, Wikimedia.

These budworm larvae feed voraciously and to protect themselves they collectively spin a covering of silk over their feeding sites. The larvae need to protect against threat of birds, carnivorous insects, and a type of insect known as parasitoid wasps that lay their eggs within living caterpillars. By mid-summer the larvae are fully grown. Pupation and emergence as adults takes one week, by August adult moths are flying, seeking mates and laying eggs.

Adult and pupa of eastern spruce budworm. Speckled adult moth is above the dark brown pupa. Credit: USDA, Wikimedia

Typically the density of a local population of spruce budworms remains low relative to resources of the conifers they feed on. Few of the eggs laid by one female will survive through to another adult moth. Detailed counts of these life-stages under typical conditions in a forest have revealed counts as shown on the table below.

Life-table of eastern spruce budworm (assumes sex ratio is 1:1)
[Data from Morris, 1957]

* Eggs: 200 of which 30 die due to predator/other = 15% stage mortality
* Early larvae: 170 of which 136 die due to dispersal = 80% stage mortality
* Later larvae: 34 of which 30.6 die due to predator/other = 90% mortality
* Pupae: 3.4 of which 0.9 die due to predator/other = 25% mortality
* Adult: 2.5 of which 0.5 die due to miscellaneous causes = 20% mortality

Generation survival = 2 adults (1%)

A life-table like this shows a stable population of an insect or other animal. That stability of population density usually comes from a relationship with the resource of the insect's food and the risks of death before production of another batch of offspring. Those risks are predators and adverse climate. (The term other in this table includes defences that the tree will deploy.)

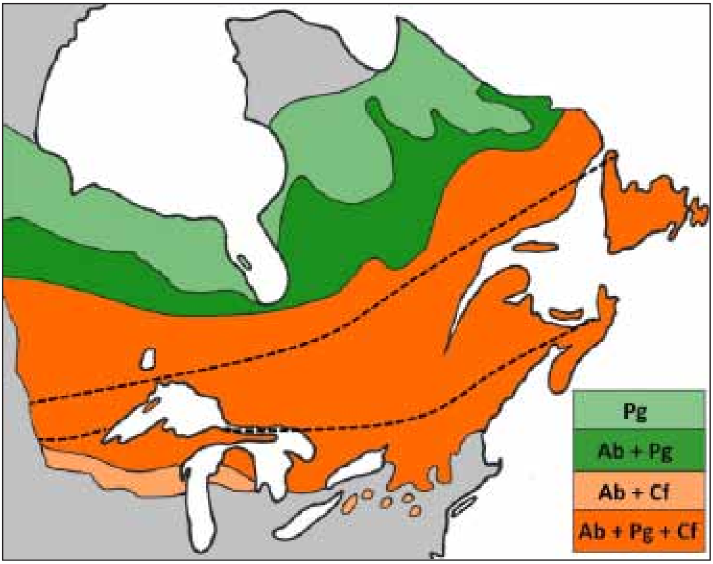
Stable populations of budworm are not an immediate problem here. This insect is a serious pest of timber trees and historical records from the 1800s show that before modern forestry eastern spruce budworm was capable of expanding local populations into size and density that were witnessed as huge numbers of larvae on huge areas of forest. An insect with a breeding system of each new female (together with the male that fertilized it) in the one year of her life laying 200 eggs and each of these new insects with the potential of either laying eggs or being a male, has a powerful mechanism for exponential growth of numbers of the population.

If, instead of only 2 of a batch of 200 eggs surviving to adults (as in life-table above) 150 out of 200 survive. Several years of favourable climate and foliage might be sufficient to start a trend. That survival rate gives a population growth rate of 1.75 per yearly generation of moths instead of 1.0 of the stable population. (For comparison our human rate globally is 1.09, with a generation time measured in decades). Now a mated pair of budworm moths will produce descendants expanding each year in the following sequence of population numbers:

200 x 1.75 = 350, thereafter 613; 1072; 1876; 3283; to 5745 by year 6 of an exponential increase of numbers of moths.

The danger for forest managers lies in the difference between the last two or three numbers of a population expansion like this. Who will notice the build-up in one area of a large forest, from a density of just several budworm larvae per tree to many thousands per tree in six years, before an outbreak becomes obvious?

Environmental conditions that produce outbreaks of budworm infestation at intervals of several decades are difficult to study in forests and remain poorly understood. Some crucial combination seems necessary: starting population of moths; condition of forest; severity of previous winter; temperature and humidity during spring and summer; others unknown. One distinctive factor leading to an outbreak is the ability of these moths to fly vigorously in search of fresh areas of forest to lay their eggs, specially the females. Female spruce budworm moths are robust flyers and take flight in unison, at night, to form large migrating swarms. They become active between 15°C to 30°C and start to fly in the evening as humidity rises with falling temperature. They ascend into the layer above the forest canopy and there can continue to fly by the kilometre in search of new, leafier, forest on which to lay their eggs. Strong winds will blow them further.



Distributions in north eastern USA and Canada of: white spruce (*Picea glauca*, **Pg**), balsam fir, (*Abies balsamea*, **Ab**) eastern spruce budworm (*Choristoneura fumiferana*, **Cf**) and the zone between dashed lines in which outbreaks of budworm infestation have been recorded, from minimal to severe levels. Zone of outbreaks includes Lake Superior and Newfoundland, but not Nova Scotia. Redrawn from: Gray & McKinnon, 2006; Neilis, 2015; USDA in Wikimedia.

During an outbreak tens of millions of hectares of forest, mostly in the Canadian provinces of Ontario, Quebec, New Brunswick and the island of Newfoundland, are severely damaged by loss of needle-leaves, also loss of pollen from male cones that in turn leads to poorer seed production (1 hectare is a square with sides of 100 metres; 1 hectare = 2.47 acres). The most recent outbreak at time of writing started in Quebec in the northern side of the St Lawrence River in 2006 with 3,000 hectares of forest defoliated severely. By 2019 over 9.6 million hectares of forest had suffered moderate to severe defoliation. Infested trees become a dull brown colour as the remains of damaged leaves dry out. Trees can withstand a single year of heavy infestation but repeated seasonal infestations will weaken a tree to where it can no longer grow, even after the outbreak has ceased. Balsam fir will die after four successive years of infestation as defoliation reduces its supply of new materials from photosynthesis. Under conditions of a large forest over many decades there is likely to be a stabilizing influence between density of the budworm population and number and health of the trees they feed on. This long-term stability, interrupted by outbreaks every twenty to thirty years, is liable to be put out of balance by forestry methods that create more open patches in the forest canopy. Such open patches areas are formed by storm and fire and here regenerating saplings provides good feeding for the budworm. Also commercial forestry methods provide many patches as the clear-cut areas with regeneration on seedlings.

Defoliation of conifers caused by spruce budworm infestation. Credit: USDA, Wikimedia.

We people take leaves as food for granted but would need a different type of teeth and digestion to survive on leaves alone. Herbivores eating grass need digestive systems adapted for large volumes and ability to nurture bacterial fermentation. Needle-leaves are meagre and difficult food for mammals. The taste and digestibility of conifer foliage are reason enough to avoid them if there is alternative vegetation available. However, any insect adapted to this source of food will rarely be short of it and have few competitors for it – moose at their low population density perhaps.

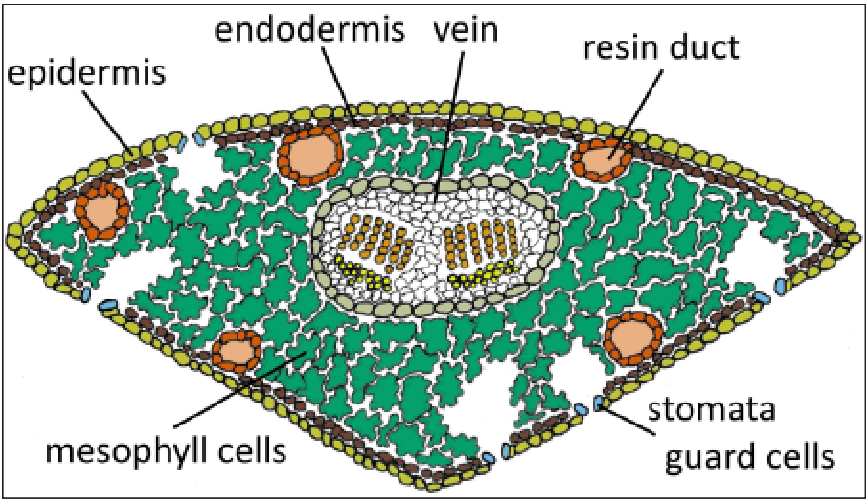
Mouthparts of a larva of a herbivorous insect are formidable at their tiny scale. A pair of massive jaws work sideways, as serrated mandibles constructed of a specially hard form of the structural polymer called chitin. The larvae of woodworm beetles gnaw through beams of dry oak, digesting this food as they go safely hidden from predators. Digestion of plant food is a complex and inefficient process that costs time and energy for these insects.

Many plants produce chemical compounds that are poisonous, as toxins of potent effect toward insects. Tasty spices we use in cooking are, for the plant, usually repellents against herbivores. Some of the most potent of these toxins are alkaloid chemicals, such as nicotine with its strongly insecticidal effect protecting tobacco plants. However, alkaloids are not produced by conifers.

A parasitoid wasp next to its prey, the caterpillar of a cinnabar moth (similar size to a budworm). Parasitoid insects like this commonly attack budworm caterpillars by laying their eggs within the budrowm to feed and develop there - fatally to the budworm. Credit: Peter O'Connor, Wikimedia.

Trees make it difficult for any animal intent on eating any part of them. Trees have a range of adaptations to defend against herbivores and these can be grouped into two broad types. The simplest are preformed within the tree and technically known as constitutive. Also there various rapid response chemicals directed against herbivores. They are induced directly by the feeding attempts of herbivores. Both preformed and rapid response defences can work either as physical blocking mechanisms such as toughness of needle-leaves, or as chemical mechanisms such as release of a poison produced within the tissue of the plant.

Constitutional defences are costly for the plant to produce and maintain long-term, standing ready for defensive action. There is a potential advantage for a plant also to have defences deployed only when herbivores are attacking. The herbivore will induce a defensive reaction by the plant. The stimulus to a leaf of the first cutting action of an insect's jaws, or of the saliva of the insect, may suffice to trigger deployment of a rapid defence. But such a mechanism will be more complicated for the plant's physiology than a preformed defence, already in place within the leaf.



Diagrammatic cross section of a typical needle-leaf showing five resin ducts. Resin is a preformed defense against insects and larger herbivores that chew into bark of stems and branches, or on leaves, The resin is tree-wide defence system.

Simple toughness of leaves, specially needle-leaves, is a basic constitutive defence against budworms. Cellulose, as the bulk of a leaf, is a polymer molecule, a chain of simple elements that bundle tightly together as long fibrils that form the walls of most of the cells of a leaf.

Within the needle-leaves of spruce trees there are two closely related phenolic compounds that act powerfully against feeding of budworms and other insects. These are piceol and pungenin. They act as induced responses to the saliva of a larva as it chews into the leaf. This rapid response within a leaf is made by a specific network of communication chemicals in the cells of the leaf for rapid mobilization of these two polyphenol toxins.

Typical species of conifers are well known for producing resin: sticky, slowly flowing, and containing toxins. Resin is produced in ducts by leaves, branches, stem and roots of conifers. Resin works as both constitutive and induced defence against herbivores. It contains a type of chemical called terpene. This technical name is derived from turpentine, a liquid of many industrial uses. Terpenes are common in many plants. The distinctive pine scent that we enjoy during a summer's day walk under conifers is from a terpene called beta-pinene. Terpenes are available as defences in needle-leaves. Ducts run lengthwise along each leaf: into them resin rich in terpenes is secreted and stored. These preformed stores are typical constitutive defences.

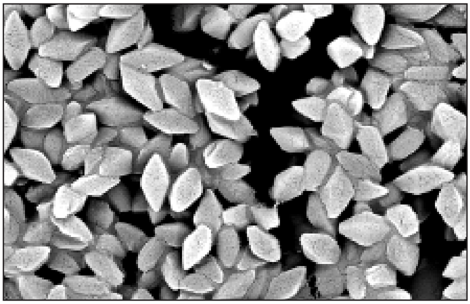
Not only insects but leaf-eating mammals are also deterred by these types of plant defences. Moose surviving on bunches of leaf and twig of conifers as their main food during winter later gain weight as they feed on the soft herbaceous leaves of open swampy areas during summer. In the evolutionary history of a tree species this herbivory has delivered a strong imperative to grow from seed rapidly to outreach hungry deer. This is specially important for conifers. They depend on the activity of the core growing tissue at the top of the main stem that can keep growing throughout the long life of the tree. Here is the apical meristem of conifers, the growing point that dominates the tree and produces the typical shape of a steep cone. Every fully thriving spruce, pine and fir tree needs its core of a single central stem to reach the light at the forest canopy. A deer that nips off the topmost bud of a seedling, one mouthful, condemns that tree to side branching only, not the necessary upward thrust. Hence most of the problems associated with high population densities of deer, of which moose have the biggest jaws and appetites.

Control of budworm at the scale of forest.
Against the background of problems of attempting to suppress outbreaks of budworm, researchers continue to experiment with methods of managing the structure and dynamics of forests to reduce risk of infestations. Their aim is to combine commercial forestry operations with knowledge of what leads to outbreaks of budworm.

Responsiveness of resin ducts to attack by herbivores is a heritable trait in particular genetic strains of conifers. This provides opportunity for foresters using nursery stock for regeneration of trees. White spruces of different provenance have varying ability for induced responses of defensive piceol and pungenol, active against budworm. This genetic variation has potential for breeding trees for heritable ability to produce defences against herbivores. Using the same silvicultural process there lies potential for application of a chemical compound that works naturally on plants as a signal or alarm for induced defence. This molecule is methyl jasmonate, readily available as a synthesized chemical. When applied to seedlings in a nursery the defence response induced in seedlings will last the growing tree into its mature size.

Balsam fir is more susceptible to attack by budworm than are spruce trees, in descending order of white, to red to black spruce. Balsam fir is less valuable as timber than the spruces, so felling management to change the proportion of these species will reduce forest susceptibility to budworm over the large scale. Older stands of trees are more susceptible to severe damage than younger fully grown trees, so managing proportions of these age classes is an additional approach. A focus of danger for high infestation levels is felling coupes where regeneration has reached the size and relative freshness of vegetation most favourable to expansion of budworm populations. Here are the sites to monitor budworms using a standardized detection method, with the intention to spot-treat these areas when a threshold of infestation is reached.

When foresters detect the start of an outbreak of budworm they often use the control method of applying insecticide onto the affected trees. The bulk sort, made in a factory by chemical synthesis, similar to those used for protecting arable crops against insects. Insecticide in liquid form needs to be applied from aircraft over large areas previously identified as hot-spots of infestation, with the expectation that this will suppress the spread and damage of a developing outbreak. The types of spraying equipment and logistics of treatment are derived from routine spraying from low flying aircraft over agricultural crops. Anywhere but over large fields this style of pest control is difficult, dangerous, and requires logistic support of great complexity and cost. But how else to reach these pests within forests?



Left: culture of bacteria, species *Bacillus thuringiensis*, stained purple for microsopy at high magnification. Credit: Wikimedia
Right: spore form of these bacteria as insecticide; spores are about 0.5 micrometres lengthwise. Credit: Jim Buckman, Wikimedia.

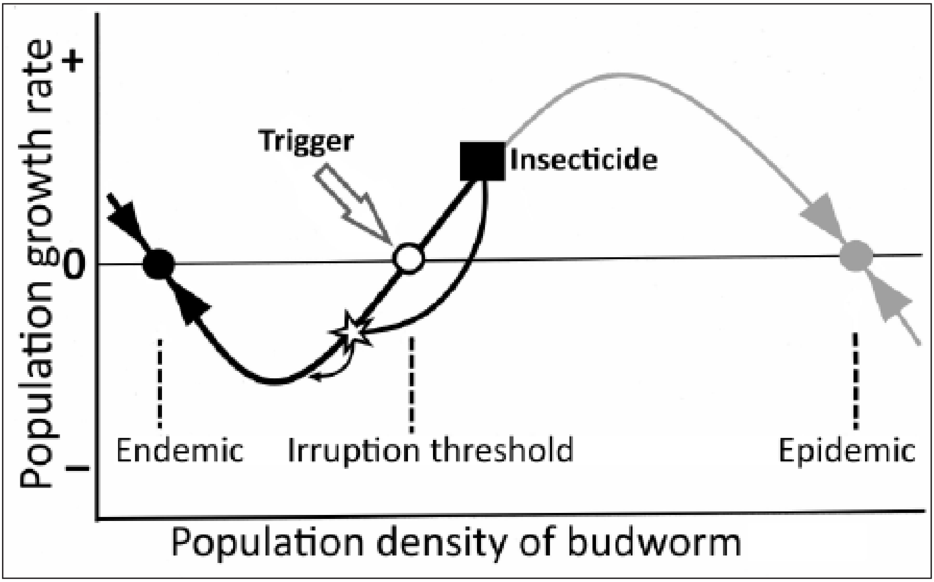
Insecticide is directed at larvae of budworm, using materials with high specificity for this species of insect. The synthetic pesticide, of common chemical name tebufenozide, is the one licenced for use against this insect. It acts as if a moulting hormone of larval insects, necessary for them to go stage to stage through their life-cycle. When applied to budworm tebufenozine disrupts their ability to moult, so larvae cannot grow to become adult moths. Another insecticide of potent effect when sprayed against larvae of moths is derived from a bacterium. This type of bacteria was first found as a devastating parasite of the larvae of silk-worm moths. The bacteria are cultivated in factories to produce a natural pesticide, formulated as spores of the bacteria for spraying from aircraft. This bacterium is *Bacillus thuringiensis* (well known simply as BT), now of wide use for controlling many types of insect infestation. Its spores are highly specific for insects, of minimal danger to vertebrate animals, and they degrade rapidly in the environment. A strain called *B.t.kurtsaki* is used against budworm because of its high specificity against this species of moth larvae.

Spraying insecticide from the air onto forests is very expensive so it is crucial that site and timing of spraying is has maximum effect on the budworms below in the forest. How populations of spruce budworm grow and decline over large areas of forest and over several decades between major outbreaks is a difficult problem for forest ecologists. Starting spraying insecticide when an outbreak is obvious is likely to be too late. But how to find the area in which a local population of budworm has started to expand rapidly? Where are the hot-spots of infestation?

Spraying an infestation of spruce budworm with a suspension of *Bacillus thuringiensis* (BT). Credit: USDA, Wikimedia.

Local populations of budworm can be monitored by on-ground surveys for the overwintering second stage larvae, the *L2* stage, when they cluster together under a protective web. The trees are checked by regular ground surveys for signs of defoliation. Also moth traps are used to attract males lured by synthetic versions of the mating pheromone produced by female moths.

The ecological understanding of the growth of budworm populations from such data has led to a concept of oscillating populations that rise and fall as the density of the population, as number of budworms per area of forest. (See diagram next page.) This oscillation is driven by the effects of predation on the budworms by parasitoid wasps and birds, by influence of swarms of adult moths migrating into a particular area, and probably other factors. Any local population of budworm in a large area of forest will be, in terms of budworm infestation as a disease, in an *endemic* state of minimal damage or in transition to an *epidemic* state of maximal damage: an outbreak. Standard terminology of disease outbreaks – malaria, covid – is used here. The transition through to the epidemic state of an obvious outbreak can be triggered variously, with moth migration suddenly expanding a local population being one example. A precise way to control budworm is to detect in advance this transition between endemic to epidemic conditions in an area of forest, then to apply insecticides intensively by area and time. This method is named *Early Intervention Strategy*, as it applied in the eastern provinces of Canada. Intervention of this design requires application of pesticide over as large an area of forest where the signs of transition to outbreak are found.

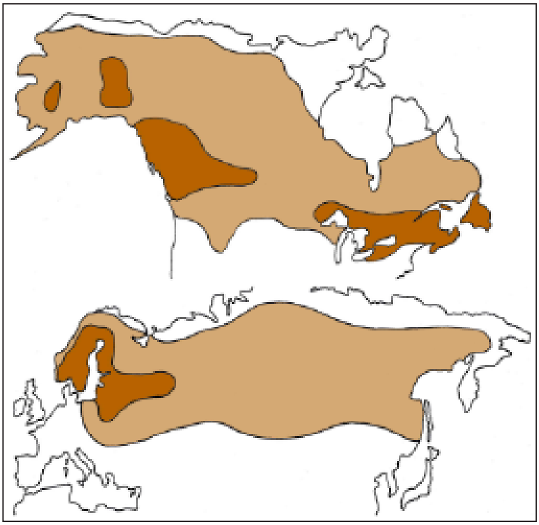


Curving line in black then grey represents an oscillating density of budworms in the forest. This oscillation is driven by varying rates of population growth, starting from endemic to epidemic and going back and forth under the influence of an ecological trigger. Black square is insecticide treatment. This reduces budworm population to level of the star, with smaller reduction thereafter because of lower reproduction rate of the diminished population.
Redrawn from: Johns, R.C., *et al.*, 2019.

This control method is being promoted, with attention to the wider context of who owns the forest and are private owners willing to allow access for monitoring budworm and have that area sprayed. Traditional rights of forest access and use, and attitudes of the wider public need to be respected. The benefits and problems associated with aerial spraying of chemical pesticides needs good public relations to be maintained. The cost to benefit ratio of this control strategy is estimated to be between 1: 3.8 and 1: 6.4.

Moose and other deer eating trees.

During winter, an adult moose needs to eat about six kilograms of needle-leaves, with their twigs, each day, for about 150 days. During summer moose can rely on easier, lusher vegetation of broad-leaf trees such as birch, alder, rowan, and herbs growing prolifically in any wet or swampy and fertile areas of the forest. Other species of deer live in these boreal forests stretching from Alaska to Labrador and Norway to far eastern Russia, but moose are amply studied to provide the example needed. However, the forests of Eurasia are without spruce budworms and the problems they cause.



Distribution of moose or elk in North America and Eurasia. Light brown shading represents population densities of 0.001 to 0.15 per square kilometre; dark brown 0.15 to 4.34 per square kilometre. Redrawn from Jensen *et al.*, 2020.

The two main geographical examples of this chapter centre on north east USA and Canada, bounded westwards by the Great Lakes and north eastwards toward Hudson Bay and Newfoundland. Here dominant conifers are balsam fir and white spruce. In Fennoscandian forests dominant conifers are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Silvicultural methods used in both these large areas are similar, see the satellite images below. These are forests originally of indigenous species of trees, in contrast to plantations of introduced species such as Sitka spruce. Now in both these areas the forests are managed for timber production predominantly by clear felling of isolated coupes that are reached by constructed access tracks. After felling the trees in a defined area, a coupe is left for natural or aided regeneration from the same stock as trees that are already growing nearby. Over wide areas a patchwork of varying stages of regeneration develop and here also are larger areas of mature trees. These felling coupes are of many shapes and sizes, a typical one covers 150 hectares. These silvicultural patterns are clearly visible in images from satellites when viewed close-up, usually sufficient to distinguish individual mature trees.

Landscape of a natural habitat for moose on Isle Royal. Vegetation comprises stands of balsam fir and other conifers, patches of deciduous trees such as birch, poplar, aspen. Rocky areas with scrub vegetation and many lakes and swampy patches form a natural patchiness. Credit: Google Earth.

Moose and other deer are becoming an increasing problem for the productivity of managed forests. Numerous reports from North America and many countries of northern Europe stress an increasing population density and range of most species of deer within their borders. Many well studied explanations are available to explain this trend but none apply in any general or simple way. And deer in most of these forests cannot be understood without taking into account the animals that prey on them. This is specially the case where one predator, wolf, is also increasing by the area of its known range and possibly of population density.

Moose cause loss of production in managed forests through winter-time feeding, when they browse for forage of needle-leaves round on conifer saplings, up to the height where adult moose can reach. This browsing includes the apical meristem the tree, and if only the bark is partly stripped by moose or red deer the tree is less likely to thrive. Lost production in timber forests has been quantified variously: 10% of harvest volume of Scots pine and Norway spruce in Norwegian forests; 65% of balsam fir and white birch in Canada; and others.

Forestry methods in these areas also with moose use harvester and forwarder machines and gravel access roads for the logging trucks. These methods have created, over scales of many hundreds of kilometres, conditions that are favourable to moose and other deer. Natural regeneration within the felled areas, as part of the forestry cycle, provide accessible herbage and the younger trees that the moose use mostly during winter. Clear cuts have a similar overall effect on the structure of the forest as the natural effects of storm and fire, insect infestations, rocky ground, that create natural gaps. In the managed forests there are now many more, smaller and fairly regularly spaced gaps than naturally.

Scots pine saplings as a source of winter browse for deer species on needle-leaves and to gnaw at bark for nutrients. This can lead to loss of apical meristem and stunted growth in timber forests.

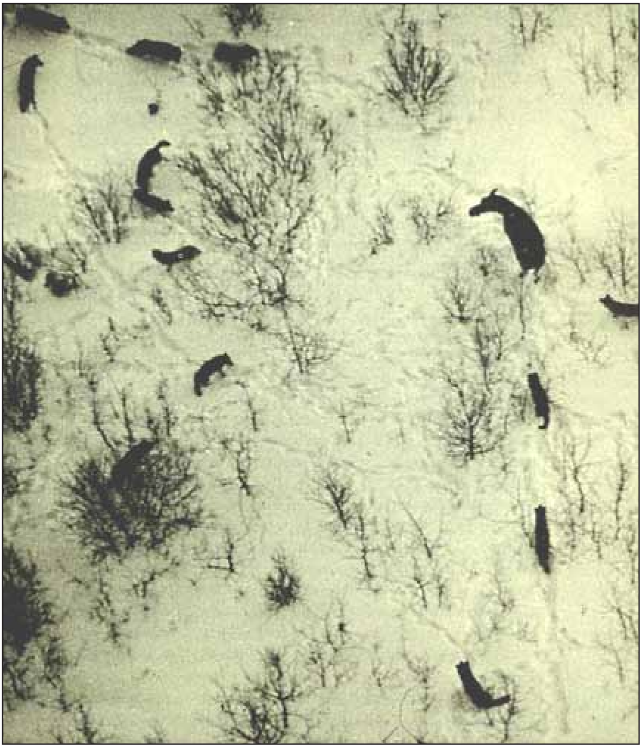
Forest landscape in south-central Sweden: forestry track; recently clear-felled coupe; patches of regenerating forest; cabins. Credit: Google Earth.

Forest landscape of an area in Quebec prone to severe outbreaks of spruce budworm infestation. Features as above for Swedish forest. Credit: Google Earth.

Another factor influencing the number of moose in such forests is hunting of them by people and by wolves. The people have different objectives than cold and hungry wolves. One consideration for people is that the more moose there are in a forest the easier it will be to have a successful day of hunting. If hunting is organized on a commercial, fee-paying, basis then there is more profit to be had from a high population density of moose. Harvest of venison for human consumption adds to the commercial incentives. These conflicts between the interests of foresters and human hunters can be partly resolved by paying professional hunters to cull moose and other deer in a wide area of forest. But who will permit this on their private land and who will pay? The relationship between large mammal herbivores and wild predators is also complex and difficult to formulate as simple and predictable mechanisms.

Landscape of forestry area of south-central Sweden, a forestry road leads to a felling coupe in the distance. Photograph from area close to the satellite image of Swedish site on page 25. Credit: Göte Lindholm, Google Earth.

Long term studies have been made about moose, forest and wolves in a protected reserve of 1200 square kilometres. This is Isle Royale, near the north west shore of Lake Superior, Michigan, USA. One of these studies examined the effects of the patchy distribution of balsam fir, as an important source of food for moose during the severe winters here. This patchiness is created by natural fires and rocky ground. Also studied was the use by moose of the patchily distributed areas of lush waterside vegetation that the moose grow fat on during summer. Researchers studied the effect of transfer of nitrogen as a plant nutrient, from these watery sites onto drier land, in the form of moose carcasses (3616 of them plotted between 1958 to 2005). Researchers also plotted distribution of wolves on the island, and here moose were the main prey of wolves. Variation in population numbers, distribution of live and dead moose, and concentration of nitrogen over the island was highly variable and heterogenous over space.



Adult moose surrounded by a wolf pack on Isle Royale, from aerial survey in 1966. Credit: Wikimedia. (NOTE: soon after this photograph the wolves retreated and the moose lived on. See: Colinvaux, P., 1993, page 279.)

The researchers found no single or simple ecological mechanism that regulates the population of moose here, other than the fundamental transfer of energy between vegetation to herbivore to predator, as predicted by theory of trophic levels. Some ecologists who study these relationships have found it a forlorn endeavour to seek predictable balances between top-down and bottom-up drivers of ecological process (wolves eat moose – moose redistribute nutrients) in environments like this. The complexity of potential interactions between many living and non-living factors, operating at a decades long pace of change is bewildering.

These landscapes, where insect infestations damage trees, and mammalian herbivores reduce regeneration of trees, are man-made. This is obvious in the sense that in some vast remote wilderness there can be no such thing as too many pests of this sort. “Pest” is a concept we use in relation to our industries and health. The insects and deer and trees in such a natural place are well adapted to their habits. Thus the defoliated and heavily browsed trees are fully natural. From our human perspectives, living in cities, towns, and houses, depending so highly on technological ways of living, from diesel powered transport to hydroelectric power connections, it is easy to be blind to the realities of the wider and more distant landscapes we live in or visit. This is particularly true of forests in comparison with agricultural food crops, almost as if we fail to see the forest for the trees.

People made these forests the way they are: they are anthropogenic in character. In some countries, often in Europe for example, many forests are fully man-made as plantations of conifer species that are not native and are grown in nurseries before being hand-planted. More commonly the original native forests have been domesticated for production of timber. The forestry access roads form a complex overall network of gravel roads that lead onto general purpose hard-top roads, lines of electricity pylons traverse the forest, quarries are torn out from rocky ground, there are small villages and towns and cabins among the trees for people to visit and go fishing. The land on which the trees grow is owned and legally demarcated by people as individuals, as collectives, as commercial businesses, or as the state in the form of national nature reserves. Not only are the trees managed by people, both the deer and their natural predators are managed by culling. This is done in the context of legal protections for wild animals and cultural norms and legal restrictions on the methods of culling, and of hunting for sport. These North American and Eurasian boreal forests seem to go on forever and in their remoter parts at first glance resemble some kind of wilderness. Look more closely and our human uses of this vastness of trees are widely evident. Such vastness could fool us into thinking the forests can be used as a natural resource that will survive forever. As the Chapter on Deforestation in this series describes, these trees and forests need our attention that we do not carelessly lose most of them.

References and notes.

(Many articles are accessible as abstract or text using search engines such as Google Scholar, an institutional login, or a pay-wall.)

Energetics and trophic levels.

Bouchard, M., Régnière, J. & Therrien, P., 2018. Bottom-up factors contribute to large-scale synchrony in spruce budworm populations. Canadian Journal of Forest Research, 48: 277-284.

Colinvaux, P., 1993. *Ecology 2*. John Wiley & Sons Inc., New York, ISBN: 0471558605. [Clear explanations of trophic levels, energy flow, second law of thermodynamics; page 279 for history of photograph of a moose surrounded by wolf pack.]

Myers, J.H. & Sarfraz, R.M., 2017. Impacts of insect herbivores on plant populations. Annual Review of Entomology, 62: 207-230. [Supports the bottom-up proposition that nutrients, climate, light, etc. limit populations of plants, not herbivores.]

Biology of eastern spruce budworm and damage done to trees.

Anonymous, 2022. Spruce budworm. Canadian Forest Service. [Biology and epidemiology of budworm outbreaks; also explains control methods known as Early Intervention Strategy.]

Anonymous, 2022. *Choristoneura fumiferana*. Wikipedia. [Detailed article includes: impact on host trees, reproduction, migration, predators.]

Baskerville, G.L., 1975. Spruce budworm: super siliviculturist. The Forestry Chronicle, 51: 138-140. [Timing of outbreaks in relation to forest structure.]

Bergeron, Y. & Leduc, A., 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. Journal of Vegetation Science, 9: 492-500. [Budworm outbreak dynamics in relation to forest fires.]

Bouchard, M., Kneeshaw, D. & Bergeron,Y., 2006. Forest dynamics after successive spruce budworm outbreaks in mixed wood forests. Ecology, 87: 2319-2329. [Long term population dynamics of budworms in relation to forest structure.]

Gray, D.R. & MacKinnon,W.E., 2006. Outbreak patterns of the spruce budworm and their impacts in Canada. The Forestry Chronicle, 82: 550-561. [Analysis of long term records on defoliation by spruce budworm and how this alters structure of forests.]

Johns, R.C., *et al*., 2019. A conceptual framework for the spruce budworm early intervention strategy: can outbreaks be stopped? Forests, 10: online. [Discussion of population dynamics and control in relation to Early Intervention Strategy.]

Lawrence, R.K., Mattson W.J. & Haack, R.A., 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. The Canadian Entomologist Vol. 129 Pages 291-318.

Leroux, S.J., 2021. Cumulative effects of spruce budworm and moose herbivory on boreal forest ecosystems. Functional Ecology, 35: 1448-1459. [Long term experimental study in a natural forest subject to budworm and moose herbivory.]

Liu, E.Y., *et al*., 2019. Economics of early intervention to suppress a potential spruce budworm outbreak on Crown land in New Brunswick, Canada. Forests, 10: online. [Economic analysis of a successful control scheme against spruce budworm.]

Miller, C.A., 1975. Spruce budworm: how it lives and what it does. The Forestry Chronicle, August: 136-138. ["Starting from a pre-outbreak density of less than five feeding larvae per tree, the population grows in about 4 years to reach 2000 larvae per tree and to cause noticeable defoliation (30%) of the new shoots. Population growth continues in the fifth and sixth years peaking at about 20,000 larvae per tree. In the sixth and seventh years the 20,000 budworms strip all the current needles and some of the old needles from the tree."]

Morris, R.F., 1957. The interpretation of mortality data in studies on population dynamics. The Canadian Entomologist, 89: 49-69. [Life-table of eastern spruce-budworm using field data from New Brunswick province, Canada.]

Nealis, V.G., 2015. Comparative ecology of conifer-feeding spruce budworms. Canadian Entomologist, 148: 33-57. [Detailed biology and population dynamics of spruce budworm species.]

Régnière, J. & Nealis,V.G., 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. Ecological Entomology, 32: 461-477. [Life stages and life-table data of spruce budworm.]

Régnière, J. 2019. Dynamics and management of rising outbreak spruce budworm populations Forests, 10: online. [Description of Early Intervention Strategy against spruce budworm.]

continued

St.George, Z., 2020. *The Journeys of Trees: a story about forests, people and the future.* W. W. Norton & Co., New York. ISBN: 9781324020233. [Chapter 6 for material about spruce budworm control in Quebec; also much interesting material here about how trees and forests work and are managed.]

Constitutive and induced defences of conifers against defoliating insects.

Howe, G.E. & Jander, G., 2008. Plant immunity to insect herbivores. Annual Review of Plant Biology, 59: 41-66. ["Rather than acting as passive victims in these interactions, plants respond to herbivory with the production of toxins and defensive proteins that target physiological processes in the insect."]

Lopez-Goldar, X., *et al*., 2020. Resin acids as inducible chemical defences of pine seedlings against chewing insects. PloS, online ["Our study reveals that inducibility of resin acids against insect herbivores is highly localized to the damaged tissue . . ."]

Mumm, R. & Hilker, M. 2006. Direct and indirect chemical defence of pine against folivorous insects. Trends in Plant Science, 11: 351-358. [Clear introduction to defences of trees against herbivores.]

Parent, G.J., 2017. Insect herbivory (*Choristoneura fumiferana*, Tortricidea) underlies tree population structure (*Picea glauca*, Pinaceae). Scientific Reports, 7. [Resistance of white spruce to budworm attack related to piceol and pungenol of foliage.]

Thomas, P.A., 2022. *Trees*. HarperCollinsPublishers, London. ISBN: 9780008304539 [Chapter 8 for general account of tree defences.]

Ullah, A., Klutsch, J.G. & Erbilgin, N., 2024. Complementary roles of two classes of defense chemicals in white spruce against spruce budworm. Planta, 259: online.

Wu, J. & Baldwin, I.T., 2010. New insights into plant responses to the attack from insect herbivores. Annual Review of Genetics. 44: 1-24. [Details of mechanisms of plant resistance to herbivores.]

Moose eating trees in boreal forests of North America and northern Europe.

Anonymous, 2023. Wolves and moose on Isle Royale. Wikipedia.

Beguin, J., *et al*., 2016. Management of forest regeneration in boreal and temperate deer–forest systems: challenges, guidelines, and research gaps. Ecosphere, 7: e01488.

continued

Botkin, D.B., 2012. *The Moon in the Nautilus Shell: discordant harmonies reconsidered.* Oxford University Press, UK. ISBN: 9780199913916. [Chapter 3 for discussion of relations between moose and wolves on Isle Royale, Michigan, USA.]

Bump, J.K., *et al.*, 2009. Large herbivores and aquatic–terrestrial links in southern boreal forests. Journal of Animal Ecology, 78: 338-345. [50 year field study of moose in relation to wolf predation on Isle Royale.]

Cassing, G., *et al.*, 2006. Moose (*Alces alces*) browsing in young forest stands in central Sweden: A multiscale perspective. Scandinavian Journal of Forest Research, 21: 221-230. [Use of landscape structure by moose in Sweden: home range and migration range.]

den Herder, M., Kouki, J. & Ruusila,V., 2009. The effects of timber harvest, forest fire, and herbivores on regeneration of deciduous trees in boreal pine-dominated forests. Canadian Journal of Forest Research, 39: 712-722.

Edenius, L., *et al.*, 2002. The role of moose as a disturbance factor in managed boreal forests. Silva Fennica, 36: 57–67.

Jedrzejewski, W. *et al.*, 2000. Prey selection and predation by wolves in Bialowieza primeval forest, Poland. Journal of Mammalogy, 81: 197–212. [Red deer were main prey but very few moose killed.]

Jensen, W.F., *et al.*, 2020. A review of circumpolar moose populations with emphasis on Eurasian moose distribution and densities. Alces, 56: 63-78.

Kalen, C., 2005. Deer browsing and impact on forest development. Journal of Sustainable Forestry, 21: 53-64. ["As a consequence of adopting modern silviculture practices during 1950s and 60s, larger forest areas were felled, creating an excellent habitat for these animals."]

Kolstad, A.L., *et al.*, 2018. Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. Ecosphere, 9: Article e02458.

McWilliams, W.H., *et al.*, 2018. Subcontinental-scale patterns of large-ungulate herbivory and synoptic review of restoration management implications for midwestern and northeastern forests. USDA Forest Service, Northern Research Station. Pages 1-22.

Nowak S. *et al.*, 2024. Wolves in the borderland – changes in population and wolf diet in Romincka Forest along the Polish–Russian–Lithuanian state borders. Wildlife Biology, online [Moose lowest frequency of predations; roe and red deer the staple diet.]

Speed, J.D.M., *et al.*, 2013. Regional-scale alteration of clear-cut forest regeneration caused by moose browsing. Forest Ecology and Management, 289: 289-299. [Field experimental study of two sites in Norway of effects of large herbivore browsing.]

van Beeck Calkoen, S.T.S., *et al.*, 2018. Does wolf presence reduce moose browsing intensity in young forest plantations? Ecography, 41: 1776-1787. ["In contrast to our predictions, wolf utilization was not the main driver of moose browsing patterns. Instead, moose browsing intensity declined with tree density and height."]