Forests with animals eating their trees

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

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Woodlands and forests stand anchored to the ground, each tree robustly resisting storms and hungry animals that would eat them. The forest persists decade after decade over wide areas despite severe damage inflicted randomly by fire and storm. More discretely and less randomly the 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 canopy and nutrients are recycled as ash or the end products of fungal decay.

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

Gaps in tree cover provide 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.

The number and variety of microbes, fungi and animals that feed on trees is so great that I need to focus on just two contrasting examples of herbivores that live in two areas of forest lands. These must suffice to show mechanisms by which some animals live by eating trees and how the trees continue to thrive by defending themselves from attack. 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 losses they cause to commercial forestry.

Adult moth of genus *Choristoneura*. Credit: Jeffrey J. Witcosky, USDA, Wikimedia.

In the same forests lives the largest species of deer: moose, *Alces alces*. This splendid 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, as with some other species of deer such as caribou/reindeer, are distributed in boreal forests all around the north polar region. They are well studied in north

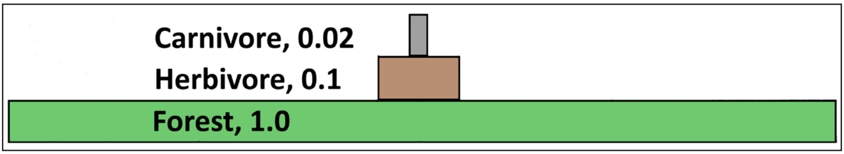
America and north Eurasia in relation to their direct effects on forests and as examples of the relationships between deer, large predator mammals, and the dynamics of the forests they all live in.

Adult male moose (or elk) *Alces alces*. 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, the chemical compounds that make up the substance of plants and as stored 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 termed respiration. All the reactions that will combine nutrients from the soil with carbohydrate from photosynthesis to grow as grass, or trees, and the rest of plant life.

For each individual tree life is temporary whilst the forest lives on. All organisms wear out as our 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. Even ancient trees are not everlasting and whilst standing there are eaten alive. 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 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 by eating plants.



Trophic levels (feeding levels) drawn as access to **energy**. Width of the bars represents levels 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 and seasonal levels of light. Shade from clouds and other plants also limit access to this energy from the Sun. A tree seedling may only grow to maturity if its parent trees and others nearby are windthrown by storm or consumed by fire leaving a gap into which sunlight pours. Nevertheless, ample energy is available to maintain something as big as a forest. But for a plant to use that energy to grow and reproduce itself there is a loss of this photon energy, from when a leaf gains it to when the plant has constructed more mass of growth. 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 is: 9.5 megajoules/square-metre/day of sunlight energy onto the canopy diminishing down to 0.05MJ/m^2/day of energy embodied in leaves and stems. See 'Photosynthesis' chapter for details.

The simple but seemingly weird laws of energy, of thermodynamics, operate here. Specifically the second law of thermodynamics: this states that 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. (This more disordered state of energy is termed *entropy*, the greater the disorder the higher the entropy.) During that transformation, work can be done, molecules can be put in place as plant tissues are formed or the plant moves.

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 viruses (if you agree that they are not truly alive) 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, in terms of energy available to the levels of plant to herbivore to predator is termed a trophic pyramid. There is much written in textbooks of ecology about which way these feeding relationships work. Do top predators rule an ecosystem as influences of fear and death 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?

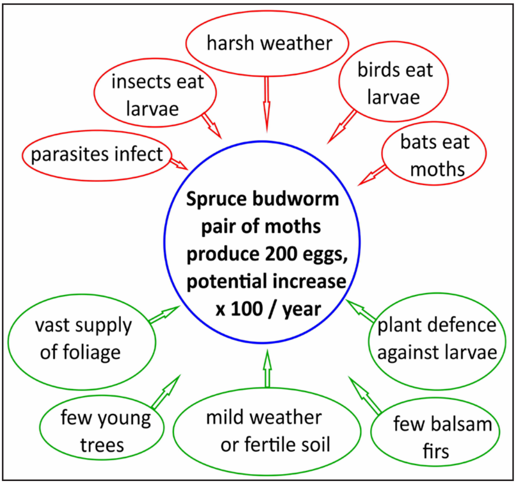
Relative to large carnivores, deer are common and widespread. They are ruminant animals, as are the closely related sheep, goats and cattle. Their digestive system has four chambers followed by a very long intestine. The first two in line of these chambers are termed the rumen. These allow fermentation 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, red deer, white-tailed deer, roe deer – all have populations known to be increasing in density or expanding their range.

> Vernacular names in English of these mammals are confusingly variable between countries. Moose (*Alces alces*) are also known as elk in the Fennoscandian countries (Norway, Sweden, Finland) whilst in North America elk or wapiti refers to *Cervas canadensis* and this species also inhabits central Asia and Siberia. Red deer of Europe and elk of North America are closely similar but red deer are *Cervas elaphus*. Caribou is the North American name, and reindeer is the Eurasian name, for *Rangifer tarandus*.

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 can 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?

This type of ecological influence is termed *top-down*. The effect flows down through the food chain of the forest, it cascades through the trophic levels. Also there is another direction of ecological influence that goes in the opposite direction: *bottom-up*. The growth and general condition of the 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.

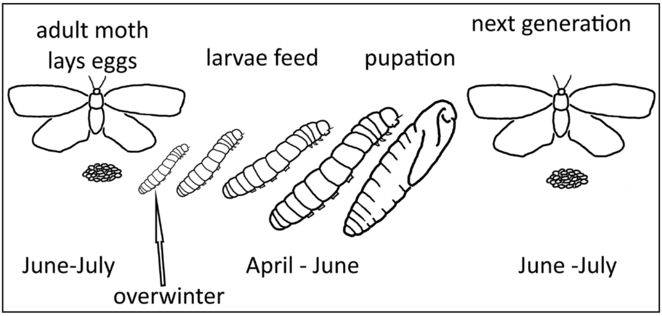
At a conference of ecologists there are often earnest debates between those who identify themselves as top-downers, or as bottom-uppers. Also there will be a few top-down-bottom-uppers, feeling little need to defend their flexible stance.



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

Further non-living influences can have massive effects on forests that initially and suddenly are devastating but in the long slow life of a forest are of great benefit to health of the forest as a whole. 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.

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.



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.)

The immature stages, the ones that do the damage by feeding, are ordinary caterpillars. These are familiar to us as insects that will develop into butterflies and there is little difference between moths and butterflies. This immature stage of the insect is called larva, and as they grow rapidly they 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. Then this transforms into the adult stage, a female or male moth: a fundamental change – 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 and reproduce. Adults are small, cannot feed on vegetation, 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 fertilization is done have no further place in the life stages.

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 such as bark of branches and stems. Here they spin silken threads as a collective shelter in which to over-winter in a dormant state. Reactivated larvae in spring seek feeding sites where they group together on needle-leaves and feed voraciously. Larvae spin a covering of silk over their feeding sites to protect against predators such as insects, spiders and birds. Warbler species of birds are important: the bay breasted, Cape May, and Tennessee for example. 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.

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.

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 next page. A life-table like this portrays 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.)

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

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 obvious outbreaks of huge populations of larvae on trees and moths on the wing. 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.

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%)

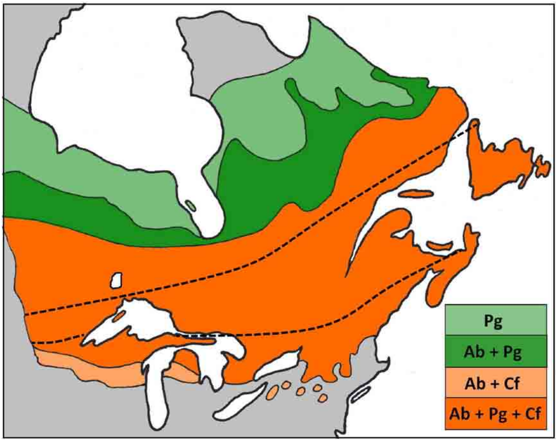
If, instead of only 2 of a batch of 200 eggs surviving to adults (as in this life-table) 150 out of 200 do survive. Several years of favourable climate and foliage might be sufficient to start a trend. That survival rate gives a population growth rate of 1.75 per yearly generation of moths instead of 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 a particular 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 of budworm 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. Currently, three or four hypotheses about this are available, but none proven or widely accepted for practical use. 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.

These are 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 of 100 metres, or 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 natural 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.

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

Tree defences against herbivores.

We people take leaves as food for granted: raw lettuce, lightly cooked spinach, well boiled cabbage. Not providing much energy, leaves being mostly cellulose indigestible by us, but useful for minerals, vitamins, roughage and taste. We would need a different type of teeth and digestion to survive on leaves. Herbivores eating grass need teeth that can withstand the abrasion of granules of silica in the leaves of grass, and digestive systems with ability to cope with 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.

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. In the same forests are insects adapted for feeding on mammalian blood. Moose are plagued by swarms of blood-suckers in summer feeding on this rich and easily digested food. Making a living by eating needle-leaves is difficult, but at least they are there by the tree-full: static, all-season, with few other herbivores competing for them.

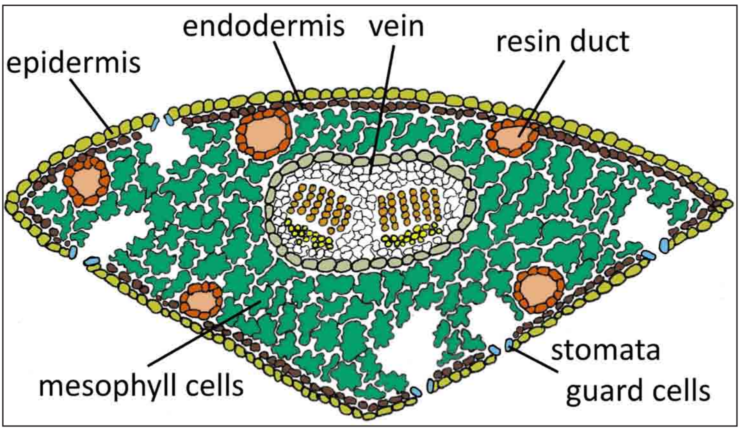
Many plants produce chemical compounds that are poisonous, as toxins of potent effect toward insects. Tasty spices we use in cooking are, for the plant, usually repellents against herbivores. Some of the most potent of these toxins are alkaloid chemicals, such as nicotine with its strongly insecticidal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

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 can be described as preformed, or technically known as constitutive. Also there various rapid responses directed against herbivores: responses induced directly by the feeding attempts of herbivores. Furthermore, 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. There is evidence that the conspicuous white bark of birch species, *Betula*, is an adaptation of this genus that warns deer of the presence in the bark of a chemical called betulin. This is repellent to deer and reduces the risk to the tree of bark-stripping.

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. 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. Lignin, the massive molecule that forms the bulk of wood, may be incorporated with cellulose in non-woody cells to toughen leaves against various insects (see 'Leaf-fall, + 'Buildings'.) The shine of needle-leaves comes from a thick waxy cuticle that keeps moisture inside and invaders outside. Within this layer are molecules of tannin. Tannins of various kinds are the same substances as found in the bark of trees that are, or used to be, used for curing animal hides to make leather. Tannins are phenolic compounds, polyphenols, that will rapidly coagulate any proteins they come in contact with. The astringent taste of tea as a drink is from a tannin acting on our taste-buds. The tea-bushes produced the tannin as constitutive defence against many leaf-eating insects of tropical countries.

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 poly-phenol 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. Latex is a similar type of defensive material produced by several families of flowering plants. 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, 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 length-wise along each leaf: into them resin rich in terpenes is secreted and stored. These preformed stores are typical constitutive defences. Also the ducts can rapidly produce more resin in direct response to herbivore attack.



Diagrammatic cross section of a typical needle-leaf showing five resin ducts.

Limonene is a terpene component of both resin and exuded from conifer trees and the oil-glands in the skins of oranges and lemons. Another member of that group, the limonoids, is called azidirachtin which occurs in the seeds of the neem tree, *Azidirachta indica*, a common species in tropical regions. We extract this plant compound for use as a powerful botanical insecticide for domestic and commercial use. For the neem tree this and similar secondary metabolites act as constitutive defences against insects by making the tree smell repellent to insects seeking a potential food. If insects do feed despite the repellent action, then azidiractin will interfere with the complex hormone systems of the attacker.

Not only insects but leaf-eating mammals are also deterred by these types of plant defences. Even moose placidly munching on large bunches of leaf and twig of a conifer as their main source of food during winter nevertheless will feed on herbaceous vegetation when available. Unlike budworm moths, deer don't fly nor are they adept at rising up on their hind legs to reach higher foliage. In the history of a tree species this mammalian herbivory has been a strong evolutionary imperative to grow from seed rapidly to outreach hungry deer. This is specially important for conifers. They have a pattern of growth highly dependent on the activity of the core growing tissue that can keep growing throughout the long life of the tree. This is the tissue at the tips of roots, of branches, and particularly at the tip of the stem. Here is the apical *meristem* of conifers, the growing point that dominates the tree and produces the typical shape of a steep cone. The branches may point downward or upward, but 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, and of which moose have the biggest jaws and appetites.

Soils poor in mineral nutrients, typically phosphorus and nitrogen containing compounds, inhibit the growth rate of seedlings. Availability of phosphorus in soils directly affects the ability of conifers to mount a rapid response of resin flow to deter herbivores by repellent terpenes. Also, deficiency of phosphorus reduces the constitutive accumulation of phenolic compounds in leaves. Soils within the various areas of a forest can vary greatly in their fertility for plant growth. The intensity of herbivory by budworm larvae and by moose and other deer in the same area can be as much affected by soil condition as by weather and history of storm and fire that have created gaps where most regeneration occurs.

A factor that may or may not be important in defences of the conifer trees of this chapter is the influence of substances that vaporize easily (*volatile organic compounds*, VOCs) and are produced into the air by trees and other plants. For example, these can act as signals to attract flying insects that are predatory on herbivorous insects such as caterpillars. This fascinating and controversial topic is beyond the scope of this chapter but two papers here introduce the topic: Heil & Karban, 2010; Mumm & Hilker, 2006, see References and notes.

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

Control of budworm at the scale of forest.

The 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 and other pests and pathogens. Similarly, the action of the polyphenol known as piceol in white spruce trees in defence against spruce budworm is being actively studied, using methods of molecular genetics, for the potential of breeding a variety of this tree with enhanced resistance to budworm attack. 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.

When foresters detect the start of an outbreak of budworm they have often used the control method of applying insecticide onto the affected trees. The bulk sort, made in a factory by chemical synthesis, of the type used for protecting arable crops against insects. The insecticide 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 massive 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?

Insecticide treatment remains available to act against budworm: modern insecticides with high specificity for larvae of moths include tebufenozide. This synthetic chemical acts as if it is a moulting hormone of the insects. When applied to budworm it disrupts their ability to moult between life stages, so larvae cannot grow to become adult moths. Another insecticide of potent effect against larvae of moths that is used for aerial spraying is derived from a bacterium. This type of bacteria was first found as a devastating parasite of the larvae of moths, silk-worm moths to be specific. 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 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.

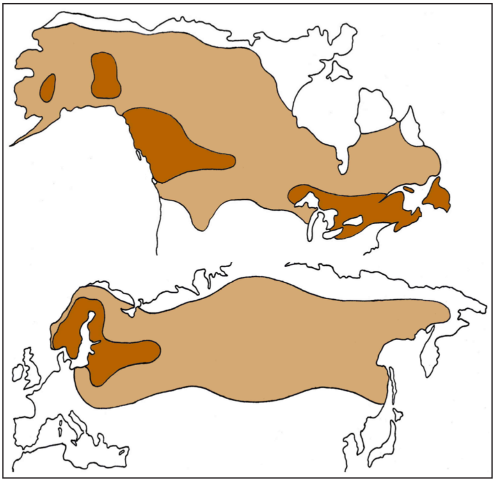
Against the background of problems of attempting to suppress outbreaks of budworm, researchers continue to experiment with varied methods of managing the structure and dynamics of forests to reduce risk of infestations and disease. Their aim is to combine commercial forestry operations with knowledge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

One starting point is the fact of ecology that a population of spruce budworm in a forest of spruce and firs is living in its natural place, in its ecological *habitat*. The way it survives here through its life cycle is its evolved set of adaptations to that habitat. These adaptations are its *niche*, as ecologists call it, how the budworm works as part of its habitat.

When forests are managed for long term sustainable harvest of timber the foresters come into direct competition with wild species of animals: these insects and deer, also in their natural habitat. People compete with budworm and moose for the resource of conifer trees, as food or as timber. None of them are going to move out of the forest. However, one strategy for the people is to compromise, since wild animals don't negotiate. The better the influence of the natural dynamics of the forest is understood the more likely it is that the management of the forest can mimic the ecological influences that produce a stable state of low population density of budworm. Thus, the probability of outbreaks of budworm will be reduced. The overall susceptibility of the forest needs to be reduced, long term and at large scale. Not easy or cheap, but potentially cheaper than spraying insecticide or losing large areas of living forest. Balsam fir is more susceptible to attack by budworm than are spruce trees. These firs are less valuable as timber than spruces, so felling management to change the proportion of these species will reduce forest susceptibility to budworm over large scales. 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 coups 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 some robust entomological survey method, with the intention to spot-treat these areas when a threshold of infestation is reached.

Moose and other deer eating trees.
During winter, an adult moose needs to eat about six kilograms of twigs with their needle-leaves 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 but moose are so well studied that they supply the example needed here. However, the forests of Eurasia are without spruce budworms and the problems they cause.

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 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 coups that are reached by constructed access tracks. After felling a coup 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 coups are of many shapes and sizes, a typical one covers 150 hectares. Amongst the wider areas of these forests are protected areas as nature reserves and national park where the original character – old-growth of natural vegetation – of these lands is retained. These silvicultural patterns are clearly visible in images from satellites when viewed close-up, usually sufficient to distinguish individual mature trees.



Distribution of moose / 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.

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.

Forestry methods in these areas with moose use harvester and forwarder machines and gravel access roads for the logging trucks. These methods have created over large scales (many hundreds of kilometres) conditions that are favourable to the moose and other deer.

Forest landscape in south-central Sweden: forestry track; recently clear-felled coup; 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.

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 and insect infestations that create natural gaps. In the managed forests there are now many more, smaller and fairly regularly spaced gaps.

Landscape of forestry area of south-central Sweden, a forestry road leads to a felling coup in the distance. Photograph from area close to the satellite image of Swedish site on page 24. Credit: Göte Lindholm, 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 in the forest. 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. This potential conflict 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. More wolves may lead to fewer deer, until the deer population crashes and then the wolves as well.

Adult moose surrounded by a wolf pack on Isle Royale, from aerial survey in 1966. Credit: Wikimedia

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. 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 are 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.

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. It has seemed to some ecologists who study these relationships that, so far at least, it is 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 decades long pace of change, have often bewildered ecologists who study this community.

The landscapes where the problems of insect infestations damaging trees, and mammalian herbivores reducing the regeneration rate of trees are man-made. This is an obvious statement 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 and niches. 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 the forests of this chapter the way they are: they are man-made, 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 amongst 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. Despite the busyness of these forests, some of them (in central Norway and Sweden and in south-east Finland) have wide and permanent populations of wolves, in addition to widely distributed moose and other deer species. 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.

Both the high population densities of the deer and the permanent and spreading populations of wolves are generally considered by the people who live and work in these forested areas as routine problems they need to manage, or simply live with. It may be that deer and wolves and people have become adapted to each other through changes in their behaviour. Structure of the forests seem to have become more favourable to both people and these wild animals because of the way they are managed for timber production. How sustainable are these technological ways of managing these forests and the animals that live on what they produce is a question that needs to be constantly asked and tested. Are the forests over-exploited? How well can the forests adapt to changing environments of rainfall and temperature?

We have converted forest from natural things living as they are adapted by evolution, into technological means of production for our benefit. If the way we use these forests makes them more favourable for high population densities of damaging herbivores such as budworms and deer, how can we keep a balance between the cost to us of these herbivores and benefit to us of the technologically managed forests? It is up to us also to adapt to the forests because in the long run the forests are fully able to live on and flourish in their slow way through time with huge mass and inertia. They work the same as when they adapted, migrated and spread as they colonized the lands left bare as the ice-sheets retreated.

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