
Ecological Processes in the McGregor Model Forest: Interactions with Insects and Pathogens



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1. Introduction

The purpose of this synthesis paper is to provide a summary of the current knowledge or hypotheses regarding the interactions of insects and diseases with natural ecological processes, and to make some general interpretations with respect to ecosystem function.

The development of any model that attempts to describe natural processes is difficult because of the complexity of natural systems, the interrelationships that exist between various components, and the different perspectives that result when the system is viewed at different temporal and spatial scales. For example, beetle outbreak and resultant mortality on an area when viewed over a short time period is seen to have one effect on the system, but when the same area is viewed over a time span of 300 years, the effect is seen differently. Therefore we have to be careful to define spatial and temporal scales when discussing or modelling agents of ecosystem or landscape change.

A landscape is normally thought of as a somewhat arbitrary area encompassed by a view or scenery. In the discipline of landscape ecology, the term landscape has been formalized in order to make the term useful. Thus, a landscape is an area of land, which contains a repetition of a given set of attributes. When the set of attributes change, the landscape is also changed. In the McGregor Model Forest, we are concerned with the forested landscape. The attributes of this landscape, in a retrospective context, would be a mosaic of forested areas of various ages. Each unit of this mosaic consists of a number of similar stands, with a similar successional history. Therefore, we also discuss agents of change that occur at a stand level but that affect the overall landscape.

2. Spatial and Temporal Scales

There is a hierarchy of organization in biological systems which begins with the cell as the basic unit and moves upward in complexity through organism, population, community, ecosystem and biosphere. Each level is a system that has elements of structure and processes common to every other system, such as birth and death. However, this hierarchy depends on the spatial scale, so when we attempt to describe ecological processes we must carefully define the scale the process is operating on. For example, when describing the invasion of hardwoods, such as aspen, following a fire, and the changes that occur to the aspen stand as shade tolerant spruce develop in the understory, we are speaking of processes occurring in a community. At the same time, but on a different spatial scale, there are processes, such as decay and succession, occurring within a single

old aspen tree, which when viewed on a smaller scale is an entire ecosystem occurring within the aspen/spruce community.

In the McGregor Model Forest, we are primarily interested in landscape-level processes. These obviously include large-scale events, such as fires, that generally occur over a large area but a very short time frame. In addition there are processes such as decay, which also occur over a large scale when viewed by area affected, although the time frame is considerably longer. Decay occurs at a cellular level but the effects are seen over vast areas in terms of plant growth and wildlife habitat. These are generally not viewed as landscape-level processes or disturbances, although their impacts may be more influential on the landscape than the large-scale agents such as fire. Thus, processes occurring at vastly different spatial scales, when viewed over short periods, may have similarly significant effects at the landscape level when viewed over a longer time.

3. Definition of Disturbance

The processes of birth, growth and death are common to all levels of biological organization and result in constant change of the system at that level of organization. Individual growth and death are the foundation for more complex processes that occur at higher levels of organization where interactions among organisms, and between organisms and their environment occur. Within ecosystems there are events involving the death of many organisms, followed by a somewhat orderly progression of birth and growth of other organisms. These processes are typically called disturbance and succession, respectively. Disturbances occur on a wide variety of spatial and

temporal scales (White and Pickett, 1985). The spatial and temporal scale, as well as the severity of the disturbance (magnitude of change effected), have a resultant effect on succession.

Disturbances involve the often selective death of organisms. The causes of death may be normal, frequent events within any given ecosystem, or events that are extremely rare in that ecosystem. Forman and Godron (1986, p. 266) would call only the latter event a disturbance, because in the former case, plants and animals within the system are adapted to the changes brought on by the agent. However, White and Pickett (1985) narrowly define a disturbance that is new to a spatially and temporally defined system as a perturbation, whereas the term disturbance broadly includes environmental fluctuations and destructive events that disrupt system structure and change resources or the physical environment at any given spatial or temporal scale. It is this latter definition of disturbance that we will use to discuss the role of insects and pathogens in ecosystem processes. However, we further define two types of disturbance: a patch disturbance and a matrix disturbance.

According to Forman and Godron (1986), a landscape is composed of several different elements. The matrix is the most extensive and most connected element and plays the dominant role in how the landscape functions, for example energy flow. The patch is embedded in the matrix, varies widely in shape, size, texture, heterogeneity, turnover rate, and boundary characteristics.

In our model of disturbance ecology with respect to pathogens and insects, we group disturbances into those that operate over a long time period and serve to modify the matrix and eventually

modify patches. These are called matrix disturbances. The second type of disturbance is called a patch disturbance and is caused by agents that operate over a relatively short time frame and initiate major, sudden changes on the landscape. A third type of disturbance is caused by organisms that modify patches, eventually resulting in their blending into the matrix.

Although they are defined as discrete entities, patches and the surrounding matrices are best viewed as a continuum because some disturbance agents operating within a matrix can actually form patches. Many disturbance agents can have varying effects on the landscape depending on other factors, such as stand composition, soil moisture, weather etc. Figure 1 illustrates this continuum of characteristics from matrix to patch. The type of effect that any one disturbance agent has, and whether or not the effect occurs within a matrix or changes/creates a patch depends on many inter-related biotic and abiotic factors.

4. Conceptual Model of Disturbance Ecology in the McGregor Model Forest

(i) Model Assumptions

We have had to make several generalizations and assumptions about successional processes in order to continue with this analysis.

a) Historic Species Composition

TFL 30 is dominated by climax spruce/subalpine fir forests, with some remnant Douglas-fir in the drier areas. Lodgepole pine is common in the warmer and drier SBS mk subzone in the western

part of the TFL, but is otherwise relatively rare. The presence of lodgepole pine is often interpreted as a sign of historical fires (Veblen et al. 1990), since this species is highly fire-adapted. Western hemlock and western red cedar are restricted to the ICH in the eastern part of the TFL. Trembling aspen, birch and cottonwood are locally common, but are minor components on the landscape. The presence of hardwoods appears to be a result of human intervention at least in part, rather than a dominant feature of the historical landscape. Thus, stand replacing fires would not normally have resulted in shifts to early successional or seral species, but returned the sites to the more shade tolerant climax species, spruce and subalpine fir (C. DeLong¹, pers. comm.). Douglas-fir does well on well drained ridges in the warmer areas, but has probably played a minor role in the recent history of the landscape.

b) Fire

Based on our best current knowledge, spruce-subalpine fir dominated climax stands are largely replaced by spruce dominated stands in TFL 30, even after stand replacing fires (C. DeLong¹, pers. comm.). Spruce invades disturbed sites rather quickly, depending on seed source location and availability. A study in eastern Canada estimated that white spruce invaded openings at a rate of 2 km in 20 years (S. Gauthier², pers. comm.). Furthermore, the establishment is uneven, giving rise to structurally diverse (multi-storeyed) stands at an early age. This would also be expected to have a significant impact on forest health (see below). Thus, the early hardwood-dominated, and

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the seral, fire-adapted lodgepole pine successional stages, are missing or rare over most of the TFL. Due to the mobility and number of its seeds, birch may have invaded disturbed sites under some circumstances, e.g. very severe fires which destroyed much of the organic layer.

(ii) Spatial and Temporal Model

As discussed above, it is critical to set spatial and temporal boundaries on a system in order to discuss the agents of change on that system. For this model we use a hypothetical system that when viewed at a defined point in time (time 0) consists of a relatively homogenous forest - in other words it is composed entirely of matrix. The spatial scale is at the forest level, which normally consists of a collection of stands. Within this system operate processes (matrix disturbances) that have characteristics consistent with the left side of Figure 1. These processes modify the matrix, cause individual and small group mortality, alter species mixes and affect other changes to the system. Matrix processes result in continual creation, and filling in, of gaps in the forest canopy. Gap creation can occur rapidly (e.g. windthrow), or slowly (e.g. root disease) with varying effects on forest structure (Lertzman et al. 1996).

At some point in time, a patch will be created by the occurrence of a disturbance external to our spatially defined system. This is a rapid change to a relatively large area where there is significant tree mortality. The patch disturbance is short lived and once the patch is created, a new set of processes begin. These processes are partly driven by succession, and partly by disturbance agents that once again effect small amounts of change over longer time periods. These patch disturbance agents are at first significantly different from those operating in the matrix because of younger tree

ages and different species. Mortality processes result in thinning rather than gap formation. As time progresses however, the agents and processes become more and more similar to those operating in the matrix. Figure 2 illustrates this progression of processes from matrix, to patch, and back to matrix.

(iii) Matrix and Patch Disturbance Agents and Successional Processes

Forest Insects and Diseases have developed relationships with trees that are often species or age specific, or specific to certain forest stand structures. These specific relationships enable interpretations of insect or disease roles at various stages in forest development.

In order for disease or insect attack to occur, three factors have to be satisfied at the same time. These are illustrated in Figure 3. There must be a pathogenic or insect agent present that is virulent and at an infectious stage in its life history. There must be a susceptible host present that is also at a susceptible stage in its phenology. Thirdly, the appropriate environmental conditions for infection and disease development, or attack by an insect agent, must occur. For example, rust infections by *Endocronartium harknessii* (western gall rust) require rust spores produced at the same time as pine candles are extending and there is high relative humidity. Rust infections typically occur in “wave years” with up to ten years between years of infection due to these requirements. Another example is the white pine weevil (*Pissodes strobi*) which thrives in unshaded, vigorous spruce leaders. Such leaders are generally prevalent in young stands of trees between 10 and 30 years old. Young trees in the understorey are not attacked for a number of

reasons (see below). This triad of requirements explains the variation in incidence of disease organisms and insects at different successional stages.

Figure 4 summarizes the changes in abundance of various groups of insects and diseases as a stand progresses from an early successional stage to a later one. The succession model is based on matrix, patch and patch modifying processes illustrated in Figure 1. Some forest pathogens and insects are primarily found in late succession stands, where they play a role in gap creation. Others, such as black army cutworm, are specific to early stage stands. The relative frequencies of many of these organisms have been altered by forest management practices, but Figure 4 is meant to indicate the frequencies in natural systems. For example, in the sub-boreal ecosystems, trees most susceptible to *Pissodes strobi* were probably only available in relatively small gaps within mature forest canopies. Larger patches of immature spruce would have been relatively rare in time and space. However, when fire did occur, and young spruce became available, the incidence of weevil would be high relative to neighboring mature forests. Therefore, the wide bar at the late succession end indicates increased incidence over a large spatial scale, whereas the wide bar at the early stage indicates increased incidence over a long temporal scale.

5. Matrix and Patch Disturbance Agents in the McGregor Model Forest

Most of the organisms discussed below have a preferred host, or range of hosts. Therefore, their incidence, and resultant influence on the landscape, is closely related to species composition at the stand level.

The distribution of biogeoclimatic subzones across TFL 30 runs from SBSmk1 in the southwestern corner, into a wide northwest-southeast band of SBS wk1, with SBSvk and ESSF mv2 in the northern-most part of the TFL. A small area of ICHmc1 is found in the eastern-most section. Species distributions follow a similar pattern. Pine and Douglas-fir occur primarily in the southwest and southeast portions of the TFL, spruce dominated stands occupy the majority of the central portion of the TFL, and hemlock and cedar occur only in the easternmost section. Subalpine fir is found throughout the TFL, especially in the ESSF and SBSvk, as well as a strip along the Fraser River. This strip is most likely due to partial cutting in the 1940-60s where spruce was selectively removed.

In the following discussion of insect and pathogen disturbance agents, we do not attempt to indicate where in the TFL particular agents are active. Some, such as spruce beetle, move frequently, so such information is only useful over a short time period. Others, such as tomentosus root disease, are ubiquitous and hence can be expected at any site where the stand characteristics are appropriate. We have provided host ranges for each of the organisms discussed below, which enables their association with particular stand types across the TFL.

(i) Introduction

a) Pathogens

Organisms that cause disease usually operate over long time scales. Although some root rot fungi can cause large openings in forests that appear as “patches” on the landscape, the time period

over which they do so is measured in centuries (Shaw and Roth 1976, Smith et al. 1992). Since we define a patch as a landscape feature that occurs over a short period of time, most disease organisms do not fit the “patch initiating” description. Epidemic fungal defoliators may be one exception if significant mortality occurs.

Abiotic causes of mortality can produce patches upon the landscape. These include avalanches, wind storms, winter drying (e.g. red belt phenomenon), floods and others as well as fire. These are beyond the scope of this paper.

b) Regulation of Insect Populations

Insect populations vary spatially and temporally as a result of variations in regulating mechanisms that alter the carrying capacity of the environment (Coulson and Witter, 1984). The populations of different insects are regulated by one of two main factors: 1) environmental factors, including climate, host quality, predation, parasitism and disease, and 2) host availability. Under endemic conditions, the populations of defoliating insects, such as the western hemlock looper, *Lambdina fiscellaria lugubrosa*, and the 2-year cycle budworm, *Choristoneura biennis*, are regulated by environmental factors. Their host resource is generally not a limiting factor, except when epidemic populations totally exhaust the foliage of host trees. Populations of bark beetles, wood borers, and the white pine weevil, *Pissodes strobi*, on the other hand, are largely limited by the availability of susceptible hosts, at least in natural forests.

As illustrated by the forest health triangle (Figure 3), these regulating influences are intimately linked, so that the availability of a resource to a species that is resource limited may be influenced by environmental processes, e.g., blowdown of live spruce will increase host availability for the spruce beetle. Similarly, tree mortality or stress caused by other forest health agents, such as root disease or defoliating insects, may increase the pool of available resources for bark beetles and wood borers. Because of these linkages, the processes described below for individual organisms categorized by ecosystem process type (matrix, patch initiating, and patch modifying) cannot be viewed in isolation from each other or from the impacts of abiotic disturbance agents.

(ii) Matrix Disturbance Agents

Collectively, matrix disturbance agents operate in climax, or near climax forests. They cause individual or small group mortality which can occur slowly over several decades, or within one growing season. Fungi, insects and abiotic factors can be matrix disturbance agents. The most common of these agents operating in the boreal forest include the following:

a) Decay Fungi

In the context of matrix disturbance processes, the most important decay fungi are those that directly or indirectly cause mortality of living trees. Normally these decay fungi weaken the bole, eventually to such an extent that breakage occurs.

Sapwood of living trees is very resistant to decay, due in part to mobilization of phenolic and other inhibitory compounds. Decay fungi in living trees are therefore limited to the dead heartwood, or areas of the sapwood killed by other agents or actions. Access to the heartwood by decay fungi occurs through natural openings (true heart rots), and through wounds (wound-entry heart rots). True heart rots enter trees through natural openings such as twig and branch scars, which are more prevalent in mature forests with relatively closed canopies. It takes years from the time of infection for extensive decay to develop. Therefore, these decay fungi are usually evident only in older, climax forests. True heart rot fungi common to TFL 30 include the following:

Phellinus pini - Red Ring Rot.

This fungus causes a white rot in spruce primarily, but is also common in other conifers such as lodgepole pine and Douglas-fir. In TFL 30 it is most prevalent in subzones of the SBS and ESSF, and less so in the ICH.

Echinodontium tinctorium - Indian Paint Fungus.

This is a true heart rot that is thought to enter trees through twig scars, and can take several decades to become established in the trunk heart rot (Etheridge and Craig 1976). It causes a yellowish, stringy rot and is extremely common in hemlock and true firs, particularly in the ICH.

Phellinus tremulae and *P. ignarius* - Aspen and Birch Heart Rot.

These two fungi attack aspen and birch trees respectively. They are able to enter through natural openings and can establish extensive decay columns in these hardwoods. *P. tremulae* is the most

important fungus with respect to volume loss in aspen (Hiratsuka et al. 1990). It is thought to be responsible for much of the aspen stand breakdown that occurs between ages of 80 and 100 years. These fungi are also important for cavity nesting animals who utilize the soft interior for nests that are well protected by the sound outer sapwood.

Wound-entry heart rot fungi are numerous and usually have broad host ranges that include many members of particular tree families (e.g. Pinaceae). Many of these fungi are saprotrophs with a limited ability to decay wood in living trees. For example, *Fomitopsis pinicola* is one of the most important decay fungi of dead coniferous wood, but in boreal ecosystems, it is also known as a wound-entry heart rot (Etheridge 1973). Development of decay in wounded trees is a function of host resistance to decay and species of decay fungus. Resinous species, such as pine, are particularly resistant to decay (Etheridge 1973). In the McGregor Model Forest area, pines are most resistant to decay, followed by Douglas-fir, spruce, true fir, hemlock and cedar in order of decreasing resistance to decay fungi (pers. obs.). Cedars are typically resistant to most decay fungi, but in the ICH there are fungi particularly adapted to attacking cedar trees (Buckland 1946).

b) Root rots

Inonotus tomentosus - Tomentosus Root Disease

In boreal and sub-boreal ecosystems of BC, the dominant root rot pathogen is *Inonotus tomentosus*. This fungus attacks a broad range of conifer hosts but is most frequently found on spruce and pine species. Douglas-fir, larch, and true firs are infrequent hosts and other conifer

species such as hemlock and western red cedar are rare hosts. Hardwood species are thought to be immune to *I. tomentosus* (Whitney 1962, Whitney and Bohaychuck 1976). Worldwide, the fungus is found in boreal forests throughout the Northern Hemisphere. In the central interior, it is most frequently found in lower elevation, spruce dominated ecosystems. These include the SBS wk1, mk and some of the vk, and several subzones of the BWBS and the ESSF.

A study that examined site and soil features associated with root disease found that very wet or very dry sites do not normally have root disease present. Furthermore, *I. tomentosus* may be a very important factor in development of certain ecosystems that are disturbance-dependent (Box 1).

Inonotus tomentosus causes dysfunction of the root system which occurs slowly over time.

Eventually the tree dies standing or is windthrown. Windthrown trees have short, stubby roots in which the pits caused by *I. tomentosus* are obvious, particularly when viewed end-on. The disease occurs in small

clumps of trees (often only 2-3 trees per clump) with the clumps gradually coalescing into larger areas of infected trees. Therefore the effect on stand structure depends on the incidence of root

Box 1

Bernier, D. and Lewis, K. J. 1997. Site and Soil Characteristics Related to the Incidence and Spread of *Inonotus tomentosus*

Inonotus tomentosus causes tomentosus root disease in spruce trees throughout the boreal forests of central and northern British Columbia. Several ecosystem variables were related to the incidence and spread of this fungus in the Sub-Boreal Spruce, wet-cool subzone (wk1) located near Prince George, BC. Plots were examined to determine the incidence of *I. tomentosus*, and several ecosystem variables were measured. These included site series, soil moisture regime, soil nutrient regime, mesoslope position, soil texture, soil coarseness, humus form, spruce density, tree species composition and soil pH. The incidence of *I. tomentosus* infection ranged from none to 31% of spruce trees per plot. Significant differences ($P < 0.05$) in percent infection were found between site series, soil moisture regimes, edatopic grid cell and mesoslope positions. Trends were also observed between infection incidence, and soil nutrient regimes and humus form. The soil pH did not influence the incidence of infection. The interactions between ecosystem variables are discussed as they relate to the incidence and spread of tomentosus root disease. The most important variables influencing the distribution of *I. tomentosus* are suggested to be: 1) the availability of oxygen in the soils as regulated by the moisture regime and mesoslope position; 2) the rooting depth of spruce trees, which are related to soil nutrient regimes and humus forms; 3) the number of root contacts that occur between susceptible roots.

disease. At low levels it causes occasional gaps, but a higher levels (e.g. >20% spruce infected) stands are much more “broken up” with patches of brush and lower stem densities.

Little is known about the infection process of tomentosus root disease. The fungus can spread from infected roots to roots of uninfected trees across root contacts, and it is thought that the fungus is able to directly penetrate the bark of small roots (less than 5cm diam.). Ectotrophic mycelium has been observed in roots of various sizes, and appears on or just below the outer bark (Lewis et al. 1992). This mycelium may play a role in spread of the fungus. Spread by root contacts suggests that several stand structure and composition factors are important in determining incidence and severity of disease. These include stem density, species composition (higher spruce component provides a greater opportunity for spread from tree to tree), and size distribution. Larger trees have larger root systems and are more likely to become infected than smaller trees, particularly on sites where there is a lower incidence of root rot, or a lower spruce component (Lewis, 1997). There is also evidence to indicate that the disease is spread by basidiospores (Lewis and Hansen, 1991a).

This disease causes four main types of losses: mortality, windthrow, growth reduction and cull. The magnitude of loss varies with the level of infection within any one stand. One study found that severely infected trees (more than 75% of the root system infected) suffered a 20% reduction in growth. Losses to butt cull were measured at up to 25% of the total log volume. (Lewis, 1997). Spruce regeneration established on sites with root disease have been shown to become infected by root contact with infected stumps and on severely infected sites the losses to

tomentosus root disease can be substantial and result in insufficient stocking (Lewis and Hansen 1991b). As a result, the presence of tomentosus root disease on a site can limit the selection of species for regeneration.

In natural ecosystems this fungus is very important in causing small openings, thereby creating more structural and compositional diversity in the forest. Root diseases are often considered to be diseases of the site. Once established in an area, they persist from one generation to the next and result in different processes occurring on infected sites than would occur without root disease (VanderKamp 1991).

It is thought that *Inonotus tomentosus* is able to infect vigorous trees as easily as stressed trees. However, once the fungus is in the tree, mortality may occur earlier in trees that are stressed by other factors as well. Tomentosus root disease itself is thought to predispose trees to attack by root collar weevils (Cerezke 1994) and other agents that are more successful on stressed trees. Recent work (see box 2) has indicated that spruce beetles do not preferentially attack diseased trees, nor are they more successful on such trees. Attack incidence and success appears to be lower on infected spruce trees than on healthy trees.

Other Root Rots

(Excerpted and modified from Hansen and Lewis (1997))

Phaeolus schweinitzii causes brown cubical root and butt rot in many coniferous species.

Infection by this fungus occurs in scattered mature trees. Unless basidiocarps are present, evidence of infection is often not revealed until felling, or when trees collapse due to the extensive decay caused by the fungus.

Basidiocarps are velvety in texture and are a dark rusty brown, with a yellow rim when active. Bracket forms grow from damaged

wood in above ground parts of the tree and at its base. More circular structures with short stalks may arise from decaying roots around the tree base.

In areas where basidiocarps exist, there is normally a persistent infestation of the fungus in the soil in the form of basidiospores (Barrett 1985). Infection caused by spores in soil contrasts with infection processes for most root rots that involve root to root contact resulting in disease pockets of several trees to several hectares in size.

Box 2

Lewis, K.J. and Lindgren, B.S. 1997 .Relationship between spruce beetle and *Inonotus tomentosus* in sub-boreal forests of British Columbia.

Spruce beetle (*Dendroctonus rufipennis*) and tomentosus root disease (*Inonotus tomentosus*) are both important agents of mortality and volume loss in spruce forests of central and northern British Columbia. Both organisms occur in similar stand types with respect to species composition and tree age. Two studies have examined the relationship between these organisms. The first was an intensive survey of 19 spruce stands, where trees were sampled for both beetle and root disease. Tree condition (dead standing, live, windthrown) was also recorded. No significant relationships were found between incidence of spruce beetle and incidence of root disease, regardless of tree condition. Preliminary analyses indicate that beetles actually avoided severely infected trees. The second study, to be carried out early summer of 1997, involves pheromone baiting of paired healthy and infected trees. Phloem thickness, and the success of attack in healthy trees will be compared to infected trees. It is suspected that as root disease progresses in infected trees, the phloem thickness is reduced, resulting in sub-optimal beetle habitat. The relatively slow progression of tomentosus root disease, and resultant slow deterioration of tree vigour may explain the lack of association with spruce beetle compared to other root disease/bark beetle systems where bark beetles are more successful in root diseased trees.

Despite the near ubiquitous presence of *P. schweinitzii* in many forest soils, successful invasion of trees is not common, and suggests some predisposing agent. These may include mechanical or storm damage, or previous infections by other organisms (Barrett and Greig 1984).

There are several other root diseases that may be found in TFL 30. These are summarized in Table 1.

Table 1. Other commonly or occasionally occurring root diseases in TFL 30.

Scientific Name	Common Name	Type of rot	Hosts
<i>Perenniporia subacida</i>	Feather rot	white, stringy	dead conifers, living hemlock and true fir
<i>Oligoporus sericeomolis</i>		brown rot	cedar and others, particularly dead
<i>Ceriporiopsis rivulosa</i>		white, laminated	living cedar, other dead conifers

c) Dwarf Mistletoe

Dwarf mistletoe is the name given to a group of plants that are parasitic on conifers. These plants

are obligate parasites; they must have a living host. Therefore they have evolved a mechanism by which nutrients are derived from the host without killing the host cells. Organisms that have such close associations with their host are normally host specific and dwarf mistletoes are no exception. Across BC there are four species, each with a different preferred host. In the McGregor Model Forest area, there is only one species, *Arceuthobium americanum*, or lodgepole pine dwarf mistletoe (PLDM).

This parasitic plant is native to BC and although it can have significant impacts on timber volume in managed forests, in natural ecosystems it only causes patchy mortality. However, it can increase the incidence and intensity of fires. PLDM is most prevalent in uneven-aged, pure lodgepole pine stands. It is a dioecious plant and the seeds are forcibly ejected from the fruit when ripe. Seeds can travel horizontally 20m or more, and are most effective at causing new infections when the mistletoe plants are in the canopy above a susceptible understory. Infections can move upward in the crown although the rate of spread is quite slow and is usually less than vertical tree growth. Once the mistletoe plant is shaded out by an overstory canopy, the plant ceases to reproduce. Therefore, pine stands can “outgrow” mistletoe infections, particularly if the stand is even-aged (Baranyay and Smith 1972).

The mistletoe plant does not have a true root system, although root-like structures invade the pine tree’s phloem and divert nutrients from the tree to the mistletoe. As the infected branch or trunk grows, the tree’s xylem envelopes “sinkers” of the mistletoe plant which become embedded in the wood. The impact of infection on the tree is growth loss due to the mistletoe acting as a nutrient

sink, and wood deformity. Multiple, large infections on trees can result in tree mortality, particularly as the tree loses dominance in the canopy.

PLDM also causes the tree to branch excessively around the area of infection resulting in a broom. These can be quite pendulous and act as “fire ladders”, drawing ground fires into the canopy. Trees killed by mistletoe provide high fuel loads, and the dead brooms are particularly flammable fuels (Hawksworth and Wiens 1996, p. 70-71).

Dwarf mistletoe brooms are known to be important habitat for some animals such as fisher, marten, squirrels and many species of birds (Mamone 1996).

d) Insects

Insects play an important role in nutrient recycling in forest ecosystems (Furniss and Carolin 1977). Woodboring insects contribute to the mechanical and chemical breakdown of woody tissues by tunnelling and feeding on wood, and by vectoring or providing infection courts for fungi, primarily stain and yeasts, and to a lesser extent, decay fungi (Schowalter et al. 1992). More “aggressive” species also contribute to a speeding up of the turnover rate as mortality agents of old, suppressed, and diseased trees.

The populations of many wood borers and secondary bark beetles (bark beetles normally unable to cause mortality) vary directly with the availability of recently dead trees. Thus, their populations tend to be a function of the mortality rate of host trees in stands. Mortality rates are

generally highest in immature stands after crown closure, and in old growth stands where a heterogenous stand structure and composition is generated by disease-driven gap dynamics (Lertzman et al. 1996), than in younger, more homogenous stands. Under normal circumstances breeding resources are sparse and scattered, keeping populations at relatively low levels. Occasionally, however, increased availability of scattered windthrow will lead to a buildup in the populations of potential tree-killing bark beetles. The fate of such population buildups, i.e., whether the populations decrease again, or if they lead to epidemics, depends on whether or not environmental conditions are conducive to sustaining populations in live trees (Safranyik 1985). Climatic factors are generally responsible for predisposing trees to insect attack, and together with stand structure will determine to what extent such mortality will deviate from matrix gap dynamic processes enough to constitute the initiation of a patch (see below). The species of particular interest in the McGregor Model Forest are the spruce beetle, *Dendroctonus rufipennis*, the Douglas-fir beetle, *D. pseudotsugae*, and the western balsam bark beetle, *Dryocoetes confusus*.

Dendroctonus rufipennis - Spruce Beetle

The spruce beetle preferentially acts as a secondary bark beetle, i.e., it will always attack dead trees if these are available rather than living trees (Furniss and Carolin 1977, Safranyik 1995). Climax spruce stands always have more or less healthy populations of spruce beetles, so one can expect rapid population buildup as a result of increased availability of resources. In particular, scattered windthrow can lead to rapid increases in populations, while sheet blowdown tends to produce relatively less brood per available surface area of bark (Safranyik 1985). This is due to the fact that spruce beetles prefer shaded locations, and will only utilize the bottom of exposed

logs. Tomentosus root disease causes patches of windthrown trees that could potentially contribute to beetle population maintenance. (However, see Box 2).

Scattered mortality may occur in stands as a result of fluctuations in beetle populations. Such mortality may lead to appreciable volume losses over a long time, but essentially contributes to the normal matrix processes. In old-growth stands even relatively severe beetle outbreaks would have limited impacts in terms of number of trees killed due to stand structure heterogeneity (see Figure 5). However, since the trees that are killed are the largest diameter ones, volume losses can be appreciable.

Dendroctonus pseudotsugae - Douglas-fir beetle

The Douglas-fir beetle also prefers dead and dying trees (Furniss and Carolin 1977, McMullen 1984), and in British Columbia, this insect rarely causes appreciable mortality at the landscape level (McMullen 1984). However, it is a very common insect wherever Douglas-fir is found, and periodically kills large numbers of trees. Relatively high beetle populations can be generated in dead Douglas-fir as small as 15-20 cm in diameter, e.g. branches left after logging (McMullen 1984). Douglas-fir is close to the northern limit of its range in the McGregor Model Forest, and so called veterans grow in pockets or scattered on slopes and ridges in many parts of the TFL. These old trees are often affected by heart rots, and often fall victim to the beetle when further stressed by unfavourable climatic conditions such as drought. Typically, mortality by the Douglas-fir beetle is patchy and infestations usually die out very quickly, i.e. within 3-4 years. In

spite of the relative rarity of Douglas-fir in the TFL, the Douglas-fir beetle has the ability to act as a patch initiating disturbance agent (see below).

Dryocoetes confusus - Western Balsam Bark Beetle

This bark beetle is widespread in British Columbia wherever subalpine fir grows (Garbutt 1992).

In the McGregor Model Forest, this bark beetle appears to be almost exclusively a secondary

species, infesting mature subalpine firs dying from other causes, primarily heart rots. In the

SBSwk and SBSvk heart rot caused primarily by *Echinodontium tinctorium* is usually advanced in

subalpine fir at or before age 150 years (Lindgren and Lewis 1997). Thus, the ecological role of

the western balsam bark beetle in these forests appears to be largely as a scavenger of dead trees.

In forests where subalpine fir dominates, the western balsam bark beetle is often responsible for

annual mortality of scattered trees over large areas (Garbutt 1992). Thus, this species may

accelerate matrix processes.

In the context of matrix processes, then, most insect populations are normally regulated by the

processes under most conditions, rather than driving them. The heterogeneity of the climax

spruce-subalpine fir forests of TFL 30 ensure some level of resilience to insect disturbance.

(iii) Patch Initiating Disturbance Agents

At more or less sporadic intervals a limited number of insect species have the capability of acting

as patch initiating disturbance agents. These are the primary bark beetles and a number of

defoliating insects. In addition to the bark beetle species discussed above, the mountain pine beetle, *Dendroctonus ponderosae*, and the defoliators western hemlock looper and, to a lesser extent, the 2-year cycle budworm can cause appreciable damage when populations reach outbreak levels.

Dendroctonus rufipennis - Spruce Beetle

The spruce beetle has caused severe mortality in the Prince George Forest Region at regular intervals since the 1960's (Humphreys and Safranyik 1993). Outbreaks have often, but not always, followed severe windthrow events (Safranyik 1985). During such outbreaks this insect has the capability to cause sustained mortality over a number of years, sometimes leading to drastic species conversion and stand age structure (Schmid and Frye 1977). Such effects are most pronounced in stands with a homogeneous, spruce-dominated canopy. Due to the influence of aggregation pheromones, which are species specific chemicals produced by the bark beetles to concentrate attacks on trees (Borden 1982), attacks on single trees often spill over to adjacent trees. In heterogeneous stands, such as the majority of stands in the McGregor Model Forest, the likelihood of such spillover attacks is lower since the large susceptible spruce trees are generally spaced further apart, and the impact of outbreaks is generally much less severe. Thus, one can deduce a hypothetical relationship between stand structure/species composition and impact (mortality). In addition to a linear decrease in mortality due to a decrease in the availability of susceptible trees, relative spruce mortality would decrease rapidly at some point due to changes in infestation dynamics (Fig. 5). From an ecological point of view, the effect of this is not dissimilar from that resulting from a “high grading” cut of overstorey spruce, leading to a release of

suppressed trees (Veblen et al. 1991, Lindgren and Lewis 1997). Thus, the long term ecological effects may be fairly moderate. From a forest management point of view, however, even moderate mortality may constitute a considerable loss in terms of volume, since a relatively small proportion of large diameter spruce would contribute a large portion of the harvestable volume in the stand.

Since the life cycle of the spruce beetle is quite flexible, ranging from a 1-year cycle in exposed, warm locations, to a 3-year cycle in wet cool areas at high elevations and latitudes (Safranyik 1995), climatic influences affect the rate at which populations change, but not necessarily the probability of the occurrence of outbreaks. It is known that epidemics occur when population buildup is followed by dry, warm conditions, which allow high populations to sustain themselves in living trees (Safranyik 1985). While spruce beetle outbreaks can be sustained over many years in a region, they are normally of relatively short duration (3-5 years) (Safranyik 1995). This is due in part to lower reproduction in standing trees killed by the beetle than in down trees. The beetles usually occupy less than the lower half of the bole on standing trees, whereas down trees are utilized along almost the entire length. Energy devoted to overcoming tree defenses probably also lead to lower reproductive rates, at least of the so called pioneer beetles. Furthermore, woodpeckers have significant impact on spruce beetle larvae above the snow in standing trees, directly by feeding, and indirectly by promoting the drying out of the phloem (Safranyik 1995).

In order to overcome tree resistance, higher attack densities may be necessary, which could lead to reduced productivity by **intraspecific** competition. On the other hand, live trees constitute an

essentially enemy free space, so **interspecific** competition in these trees may be lower than in down trees.

It is clear that the spruce beetle can be a major disturbance agent in mature spruce forests. In TFL 30 the annual impact of the spruce beetle varies from highly significant to slight, depending on the year and level of stand heterogeneity. Major outbreaks, with mortality of up to 90 % of the standing mature spruce, have been recorded from Alaska in the north to Colorado in the south (Schmid and Frye 1977, Holsten 1990). There is some evidence from our research (See Box 3, Lindgren and Lewis

Box 3

Lindgren, B.S. and Lewis, K.J. 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study

The spruce beetle, *Dendroctonus rufipennis* (Kirby), is the most significant insect pest of spruce forests in North America. This bark beetle is responsible for intermittent, large scale outbreaks in mature stands, sometimes causing up to 90 % mortality. For that reason, spruce beetle outbreaks, along with stand replacing fires, have been considered driving forces in landscape level dynamics of these forests. In sub-boreal spruce stands in central British Columbia, we found that these stand replacement events are infrequent, and stand change generally gradual, largely due to root diseases and stem decays. Spruce beetle outbreaks act as species specific “high-grading” agents, removing mostly large, over-mature stems. Affected stands remain dominated by spruce, apparently due to this species’ lower susceptibility or higher tolerance to stem and root decay than subalpine fir, *Abies lasiocarpa*.

1997), and supported by observations by McLean (1849), that a major outbreak occurred in this area in the early half of the 19th century. More recent epidemics further indicate that this insect can affect stand and landscape level processes in TFL 30 in a dramatic fashion.

The effect of spruce beetle on stand structure is such that heterogeneity increases following outbreaks (Veblen et al. 1991). Thus, susceptibility of the stand decreases. In the absence of stand replacing fire, this heterogeneity is then maintained by root disease. In stands where root disease or other mortality agents act selectively on subalpine fir, spruce dominance may increase over

time, again leading to significant impact when spruce beetle populations build up (See Box 3, Veblen 1986, Lindgren and Lewis 1997).

Dendroctonus ponderosae - Mountain Pine Beetle

This is the most aggressive of all bark beetle species, and it is responsible for devastating outbreaks in lodgepole pine forests (Safranyik 1995). In TFL 30 it is of concern primarily within the SBSmk, where lodgepole pine is relatively common. Since lodgepole pine is dominant only as a result of fire, stands tend to be homogeneous, resulting in extreme mortality when beetle epidemics occur. Thus, the majority of the mature pine may be killed during the course of an outbreak. In the absence of subsequent fire, which would re-establish lodgepole pine dominance, the result is a change in species composition, favouring spruce, subalpine fir, and sometimes Douglas-fir.

Dendroctonus pseudotsugae - Douglas-fir Beetle

The Douglas-fir beetle is a less aggressive bark beetle than the spruce beetle. Its main impact is as a mortality agent of overmature, diseased, or otherwise stressed trees (McMullen 1984). In very dry regions, such as the Intermountain region of Idaho, the Douglas-fir beetle can kill significant numbers of trees (Furniss and Carolin 1977). In the cooler conditions existing in TFL 30 its impact tends to be relatively limited in the absence of other stress factors. Nevertheless, large Douglas-fir trees have been killed in several areas within the TFL. The trees killed are generally the remnants of populations growing in the area during a more favourable climate, which was

present before the Little Ice Age, a period of colder average temperatures which lasted from around 1500 to 1850 A.D.

Most of the large Douglas-fir trees in the TFL are more than 300 years old, i.e., they were established in the 17th Century. A lack of fires and a cooler climate has favoured spruce and subalpine fir regeneration, and these species now dominate the younger age classes even where Douglas-fir “veterans” are fairly numerous. The mature Douglas-fir trees are slowly being eliminated by advancing heart rot and the Douglas-fir beetle. In areas where Douglas-fir is relatively common, which is mostly in the western parts of the SBSwk1, the Douglas-fir beetle may act as a patch initiating disturbance agent since large diameter Douglas-fir may be locally abundant. The result would be a more or less permanent stand conversion to spruce and subalpine fir, since very little natural Douglas-fir regeneration takes place. Thus, the created patch would quickly merge into the surrounding matrix in terms of its characteristics and processes.

Dryocoetes confusus - Western Balsam Bark Beetle

D. confusus does not normally act as a patch disturbance agent, because it tends to attack single or small groups of trees over fairly extensive areas (Garbutt 1992). In the McGregor Model Forest this insect is mostly found in association with stressed trees, i.e., as a secondary bark beetle. In the ESSF it may have a more prominent role, as is often the case in other areas, e.g., in the Bulkley Forest District.

Lambdina fiscellaria lugubrosa - Western Hemlock Looper

This defoliator can cause extremely devastating outbreaks, killing the majority of trees in a short time (Harris et al. 1982) as evidenced by the recent outbreak near McBride, B.C.. It is normally associated with wet and cool cedar-hemlock old growth forests, and occurs periodically in the ICH. This insect is characterized by sporadic outbreaks which usually last only a few years. Outbreaks in BC have been separated by 50 years or more (Harris et al. 1982). Consequently, landscape level impacts may be considerable, but the long term effects may be small.

Choristoneura biennis - 2-year Cycle Budworm

A relative of the notorious spruce budworms, the 2-year cycle budworm attacks primarily spruce, and can cause severe defoliation (Unger 1986). Because of its life cycle, severe defoliation occurs only every other year in a given stand. Nevertheless, severe damage is possible following complete defoliation, and as a result of bark beetle-caused mortality of the trees.

(iv) Patch Modifying Agents

As illustrated in Figure 1, a patch is created by some large scale mortality event that happens over a short period of time. Once the patch is created, the increase in light and nutrient availability as well as other changes initiate successional processes that begin with colonization by early seral species. Insects and pathogens are an integral part of these processes and influence, or are influenced by, changes in species composition and density over time. Shortly after the patch is created and trees begin to establish, tree mortality is very low. As trees continue to establish and

grow, and density increases, mortality rates also increase as young stands undergo natural thinning. Young stands may develop as a homogenous population of even-aged cohorts (e.g. lodgepole pine following a fire disturbance) or as a heterogenous collection of species and ages. In either system, there are organisms that play an important role in natural thinning. In addition to a small collection of generalists (e.g. *Armillaria ostoyae* and *Hylobius warreni*) there are insects and pathogens specifically adapted to these early successional stages and are usually either species specific, or limited by tree size or age, or stand structure.

a) Root Disease

Most root diseases are considered generalists in that any age of host trees are susceptible. Older trees with large root systems are more likely to form root contacts with inoculum sources (Bloomberg and Morrison 1989; Lewis, 1997). The dominant root disease fungus in TFL 30, *I. tomentosus*, moves from inoculum in stumps to young planted or naturally-regenerated trees (Lewis and Hansen 1991b). In natural forests, *I. tomentosus* may cause patches of low spruce density in regeneration stands following fire or other patch disturbances. However it is rare in stands that are subject to frequent patch-initiating events, where pine is the dominant tree species.

b) Dwarf Mistletoe

Dwarf mistletoes are generalists in that they will attack any age of host tree, but are specific to species of trees. In TFL 30, lodgepole pine is the only species attacked by dwarf mistletoe. In stands that have developed following a fire or other patch disturbance, dwarf mistletoe may act as a patch modifying agent provided that an overhead source of infection remained following the

patch disturbance event (e.g. residual, living, infected pine trees). Seeds produced from mistletoe plants in the residual trees will rain down on young trees within an area of approximately 15m radius around infected residuals (Baranyay and Smith 1972). As the stand develops, the infected trees will produce seeds that will infect surrounding trees, and eventually individuals will die, thereby creating gaps in the developing patch. In severely infected stands, stand structure is altered from a relatively homogenous one, to an uneven-aged structure that may be more species diverse.

c) Stem Rusts

Rusts are parasitic fungi that require two living, unrelated hosts in their life cycles. Within TFL 30, the most important of these are *Cronartium coleosporioides* and *C. comandrae* (stalactiform and comandra rust respectively). Both of these attack lodgepole pine and their alternate hosts are indian paint brush (*C. coleosporioides*) and bastard toad flax (*C. comandrae*). Western gall rust (*Endocronartium harknessii*) is also common on lodgepole pine, but does not frequently cause mortality.

Infections are caused by wind-borne spores that must attack elongating branch or cone tissue at a time when moisture is high (e.g. after rain). The infection spreads to the phloem, and for the *Cronartium* rusts, will grow into the phloem of the main stem. The tree is eventually girdled and dies. Young trees are more easily killed because their circumference is smaller and it therefore takes less time for the fungus to girdle the tree.

Individual trees vary in their resistance and/or tolerance to infection, and wind currents and microsite are important factor in infection rates. Therefore it is most common for patches of scattered individuals to be infected rather than entire patches or stands.

d) *Atropellis piniphila* - Atropellis Canker

Atropellis piniphila is a fungus that attacks the living bark of lodgepole pine trees. It is specific to pine and will only attack trees older than 15 years. Furthermore, very few infections occur in tissues that are less than 10 years old or greater than 29 years old (Hopkins and Callan 1992). Therefore in pole-sized and larger trees, infections tend to be in the lower to middle stem, with upper crowns remaining healthy. Similar to the rusts, it girdles pine stems and is more frequently found killing young trees rather than older ones. It also has a higher incidence in dense stands and serves as a natural thinning agent. Vigorous, well-spaced trees are unlikely to be killed by the fungus, and fewer trees exist to produce spores or become infected. It is suspected that microclimate changes in thinned stands may also contribute to the lower incidence of infection (Hopkins and Callan 1992).

e) Insects

Most of the organisms that modify the processes within patches are pests of regenerating and young stands. In a forestry context these pests are often extremely important. In a natural context, these organisms largely affect succession by causing mortality or growth reduction of individual trees, thereby affecting stand density and species composition at stand maturity.

Pissodes strobi - White Pine Weevil

The white pine weevil, or spruce weevil as it is mostly called in British Columbia, is the prime example of such an insect in the TFL. This insect causes significant damage in regenerating spruce by killing the leader and the previous year's growth (Alfaro 1994). As spruce planted on large tracts of land in the last 15 years reach susceptible age, the white pine weevil will be of paramount importance in this area. However, in an ecological context, the importance of the weevil is likely a function of patch size and distribution, both in time and space. In a mature stand weevil populations will be moderate at best, since suitable host trees have a patchy distribution, and most provide only a moderately favourable brood environment (Alfaro 1994).

It is unlikely that host volatiles play a significant role in host location unless young spruce are significantly different from the surrounding mature trees. Thus, one may hypothesize that the weevil is photopositive within a forest environment. Orientation to a suitable patch can only occur if the patch is of some critical minimum size (Fig. 6). Patches smaller than this would suffer negative population growth because of low brood production and emigration losses exceeding immigration gains. In large patches, however, populations would relatively quickly increase due to a positive immigration gain/emigration loss ratio combined with high brood production in the vigorous spruce leaders. Figure 7 is a diagrammatic representation of parameters which may affect weevil behaviour. Thus, a weevil emerging from overwintering in a small patch may be more likely to disperse than one emerging in a large patch due to the light intensity within the patch. Dispersal will continue until a large patch is encountered, at which time visual host location

will occur (VanderSar and Borden 1977). The time required for finding a suitable patch is a direct function of the size, as well as the spatial and temporal distribution of patches.

Since the creation of large patches prior to human harvesting in the TFL appears to have been a relatively rare event, we surmise that at the landscape level, the white pine weevil has had little impact on successional processes. In fact, it appears to be a rare insect in natural old growth Sitka spruce stands (Alfaro 1994). Nevertheless, it is clear that after stand replacing fires the open-grown, regenerating spruce may have suffered weevil damage similar to what regenerating stands experience today (Kimoto 1997). However, the current situation is considerably more severe for several reasons. Firstly, if the population dynamics of the weevil are driven by the size and spatial and temporal distribution of patches, then high populations would be temporally and spatially limited in the natural landscape, whereas today high weevil populations are present continuously throughout the area. Secondly, because of regeneration delays, i.e., stand establishment occurring over a long time in fire-generated patches (C. DeLong¹, pers. comm.), spruce stands in a natural system would have been heterogeneous in terms of individual tree age and species composition. This in turn would be less favourable for the weevil than the current situation, where large areas are planted with even-aged spruce.

Pissodes terminalis - Lodgepole Terminal Weevil

This weevil is similar in appearance and biology to *P. strobi* (Maclauchlan and Borden 1994). However, there are some important differences. It is specific to pines, being most commonly associated with lodgepole pine. Larvae kill the current leader by mining up the shoot, so the

previous year's growth is unharmed. In comparison to *P. strobi*, it is relatively uncommon in the Prince George Forest Region. In fact, leader mortality in lodgepole pine is often caused by *P. strobi* rather than *P. terminalis* in this region. At the stand or landscape level, the ecological effect by the lodgepole terminal weevil on naturally regenerating lodgepole pine would be relatively minor. Since lodgepole pine naturally regenerates as relatively even-aged, homogenous stands over large areas created after fire, current forest management practices create rather similar conditions. Therefore, the lodgepole terminal weevil is unlikely to become more prominent due to harvesting and planting.

Hylobius warreni - Warren Root Collar Weevil

H. warreni is a widespread pest of regenerating and mature spruce and pine (Cerezke 1994). Mature stands commonly harbour high populations, with more than 50 % of trees attacked. Regenerating stands, particularly lodgepole pine, are invaded from surrounding stands or attacked by insects completing their development in stumps after harvesting (Cerezke 1994), and it is in these young stands that this long-lived, flightless insect may have some impact on successional processes. Adult weevils feed on the bark of branches, shoots, and root collar, causing minimum damage. Eggs are laid on or near a root or the root collar of trees, and the larvae mine the phloem, often scoring the sapwood as they get bigger. Small trees are most susceptible to damage, because the insect attacks the root collar, whereas major roots are attacked on larger trees (Cerezke 1994). In extreme cases, trees will be girdled and killed, but more commonly trees outgrow the damage. Severe damage may weaken the root system of trees. Since lodgepole pine

is frequently established at very high densities, the main effect of this insect may be as a thinning agent.

6. References

- Alfaro, R.I. 1994. The white pine weevil in British Columbia: Biology and damage. Pp. 7-22 in Alfaro, R.I., Kiss, G. and Fraser, R.G. (eds.), The White Pine Weevil: Biology, Damage and Management, Symp. Proc., FRDA Report No. 226, 311 pp.
- Baranyay, J.A. and R.B. Smith. 1972. Dwarf mistletoes in BC and recommendations for their control. Can. For. Serv. BC-X-72. 18pp.
- Barrett, D.K. 1985 Basidiospores of *Phaeolus schweinitzii*; a source of soil infestation. European J. For. Pathol. 15:417-425.
- Barrett, D.K., Greig, B.J.W. 1984. Investigations into the infection biology of *Phaeolus schweinitzii*. Proceedings of the 6th International Conference on Root and Butt Rots of Forest Trees (IUFRO Working Party S2-06-01), Melbourne, 93-1-3.
- Bernier, D. and Lewis, K.J. 1996. Site and soil characteristics related to the incidence and spread of *Inonotus tomentosus*. Western International Forest Disease Work Conference, Proceedings, Sept. 16-20, 1996, Hood River, OR, pp. 49-54.
- Buckland, D.C. 1946. Investigations of decay in western red cedar in BC. Can. J. Res. 24:158-181.
- Bloomberg, W.J. and Morrison, D.J. 1989. Relationship of growth reduction in Douglas-fir to infection by *Armillaria* root disease in southeastern BC. Phytopath. 79:482-487.
- Cerezke, H. F. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae), in Canada: Ecology, behaviour, damage relationships, and management. Can. Entomol. 126: 1383-1446.

- Etheridge, D.E. 1973. Wound parasites causing tree decay in BC. Canadian Forest Service. Pac. For. Res. Centre, Victoria, BC. FPL No. 62. 15p.
- Etheridge, D.E. and Craig, H.M. 1976. Factors influencing infection and initiation of decay by the Indian Paint fungus (*Echinodontium tinctorium*) in western hemlock. Can. J. For. Res. 6:299-318.
- Forman, R.T. and Godron, M. 1986. Landscape Ecology. Wiley and Sons. 619pp.
- Furniss, R.L. and Carolin, V.M. 1977. Western Forest Insects. U.S. Dept. Agric., For. Serv., Misc. Publ. No. 1339, Washington, D.C., 654 pp.
- Garbutt, R. 1992. Western balsam bark beetle. Can. For. Serv., Pac. For. Cent., Forest pest Leaflet No. 64, 4 pp.
- Hansen, E.M. and Lewis, K.J. 1997. A Compendium of Worldwide Conifer Diseases. APS Press, in press.
- Harris, J.W.E., Dawson, A.F. and Brown, R.G. 1982. The western hemlock looper in British Columbia 1911-1980. Can. For. Serv., Pac. For. Cent., Report BC-X-234, 18 pp.
- Hawksworth, F.G. and Wiens, D. 1996. Dwarf mistletoe: Biology, Pathology and Systematics. Ag. Handbook 709. 410pp.
- Hiratsuka, Y., Gibbard, D.A., Bakowsky, O., and Maier, G.B. 1990. Classification and measurement of aspen decay and stain in Alberta. Forestry Canada, Info report NOR-X-314. 29pp.
- Holsten, E.H. 1990. Spruce beetle activity in Alaska: 1920-1989. U.S. Dept. Agric., For. Serv., Tech. Rep. R10-90-18, 28 pp.

- Hopkins, J.C. and Callan, B. 1992. Atropellis Canker. Forest Pest Leaflet No. 25. Forestry Canada. 4pp.
- Humphreys, N., and Safranyik, L. 1993. Spruce beetle. Nat. Res. Canada, Pac. For. Cent., Forest Pest Leaflet No. 13, 7 pp.
- Kimoto, T.T.M. 1997. Past infestations of the white pine weevil, *Pissodes strobi* Peck (Coleoptera: Curculionidae) within naturally regenerated spruce stands of the McGregor Model Forest, Prince George, B.C. M.P.M. Thesis, Simon Fraser University, Burnaby, B.C., 48 pp.
- Lertzman, K.P., Sutherland, G.D., Inselberg, A. and Sunders, S.C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. *Ecol.* 77: 1254-1270.
- Lewis, K.J. 1997. Growth reduction in spruce infected by *Inonotus tomentosus* in central B.C. *Can. J. For. Res.* (Accepted July 2, 1997).
- Lewis, K.J. and Hansen, E.M. 1991a. Vegetative compatibility groups and protein electrophoresis indicate a role for basidiospores in spread of *Inonotus tomentosus* in spruce forests of British Columbia. *Can. J. Bot.* 69:1756-1763.
- Lewis, K.J. and Hansen, E.M. 1991b. Survival of *Inonotus tomentosus* in stumps and subsequent infection of young stands in north central British Columbia. *Can. J. For. Res.* 21: 1049-1057.
- Lewis, K.J. and Lindgren, B.S. 1997. Relationship between spruce beetle and *Inonotus tomentosus* in sub-boreal forests of British Columbia. Proceedings, IUFRO Root and Butt Rot Working Party Meeting, Sept. 1-7, 1997 (submitted)

- Lewis, K.J., Morrison, D.J. and Hansen, E.M. 1992. Spread of *Inonotus tomentosus* from infection centres in spruce forests in British Columbia. *Can. J. For. Res.* 22: 68-72.
- Lindgren, B.S. and Lewis, K.J. 1997. The natural role of spruce beetle and root pathogens in a sub-boreal spruce forest in central British Columbia: A retrospective study. pp. 122-130 in Gregoire, J.-C., Liebhold, A.M., Stephen, F.M., Day, K.R. and Salom, S.A (eds.), *Proceedings: Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests*. U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. NE-236.
- Maclauchlan, L.E. and Borden, J.H. 1994. Spatial attack dynamics and impact of *Pissodes terminalis* in three biogeoclimatic zones in southern B.C. Pp. 76-89 in Alfaro, R.I., Kiss, G. and Fraser, R.G. (eds.), *The White Pine Weevil: Biology, Damage and Management*, Symp. Proc., FRDA Report No. 226, 311 pp.
- Mamone, M.S. 1996. Wildlife use of Douglas-fir dwarf mistletoe. *Proceedings, 44th Western and International Forest Disease Work Conference, Hood River, Oregon. Sept. 16-20th.*
- McLean, J. 1849. Notes of a Twenty-five Years' Service in the Hudson's Bay Territory. p. 286, Vol. I, R. Bentley, London.
- McMullen, L.H. 1984. Douglas-fir beetle in British Columbia. *Can. For. Serv., Pac. For. Cent. Forest Pest Leaflet No. 14*, 6 pp.
- Safranyik, L. 1985. Infestation incidence and mortality in white spruce stands by *Dendroctonus rufipennis* Kirby (Coleoptera, Scolytidae) in central British Columbia. *Z. ang. Entomol.* 99: 86-93.
- Safranyik, L. 1995. Bark beetles. Pp 155-163 in Armstrong, J.A. and Ives, W.G.H. (eds.), *Forest Insect Pests in Canada*, Nat. Res. Canada, Ottawa.

- Schmid, J.M., and Frye, R.H. 1977. Spruce beetle in the Rockies. U.S. Dept. of Agric., For. Serv., Rocky Mtn. For. Range Exp. Stn., Gen. Tech. Rep. RM-49, Fort Collins, CO., 38 pp.
- Schowalter, T.D., Caldwell, B.A., Carpenter, S.E., Griffiths, R.P., Harmon, M.E., Ingham, E.R., Kelsey, R.G., Lattin, J.D and Moldenke, A.R. 1992. Pp 373-383 in Singh, K.P. and Singh, J.S. (eds.), Tropical Ecosystems: Ecology and Management, Wiley Eastern Ltd., New Delhi.
- Shaw, C.G. III and Roth, L.F. 1976. Persistence and distribution of a clone of *Armillaria mellea* in a ponderosa pine forest. *Phytopathol.* 66:1210-1213.
- Smith, M.L., Bruhn, J.N., Anderson, J.B. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. *Nature* 356:428-431.
- Unger, L.S. 1986. Spruce budworms in British Columbia. Can. For. Serv., Pac. For. Cent., Forest Pest Leaflet No. 31, 4 pp.
- VanderKamp, B.J. 1991. Pathogens as agents of diversity in forested landscapes. *For. Chron.* 67:353-354.
- VanderSar, T.J.D., and Borden, J.H. 1977. Aspects of host selection behaviour of *Pissodes strobi* Peck. (Coleoptera: Curculionidae) as revealed in laboratory feeding bioassays. *Can. J. Zool.* 55: 405-414.
- Veblen, T.T. 1986. Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology* 67: 644-649.
- Veblen, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1990. Methods of detecting spruce beetle outbreaks in Rocky Mountain subalpine forests. *Can. J. For. Res.* 21: 242-254.

- Veblen, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72: 213-231.
- White, P.S. and Pickett, S.T.A. 1985. The ecology of natural disturbance and patch dynamics. Academic Press. 472pp.
- Whitney, R.D. 1962. Studies in Forest Pathology XXIV: *Polyporus tomentosus* Fr. as a major factor in stand-opening disease of white spruce. *Can. J. Bot.* 40:1631-1658.
- Whitney, R.D. and Bohaychuck, W.P. 1976. Pathogenicity of *Polyporus tomentosus* and *P. tomentosus* var. *circinatus* on seedlings of 11 conifer species. *Can. J. For. Res.* 6:129-131.

7. Figures

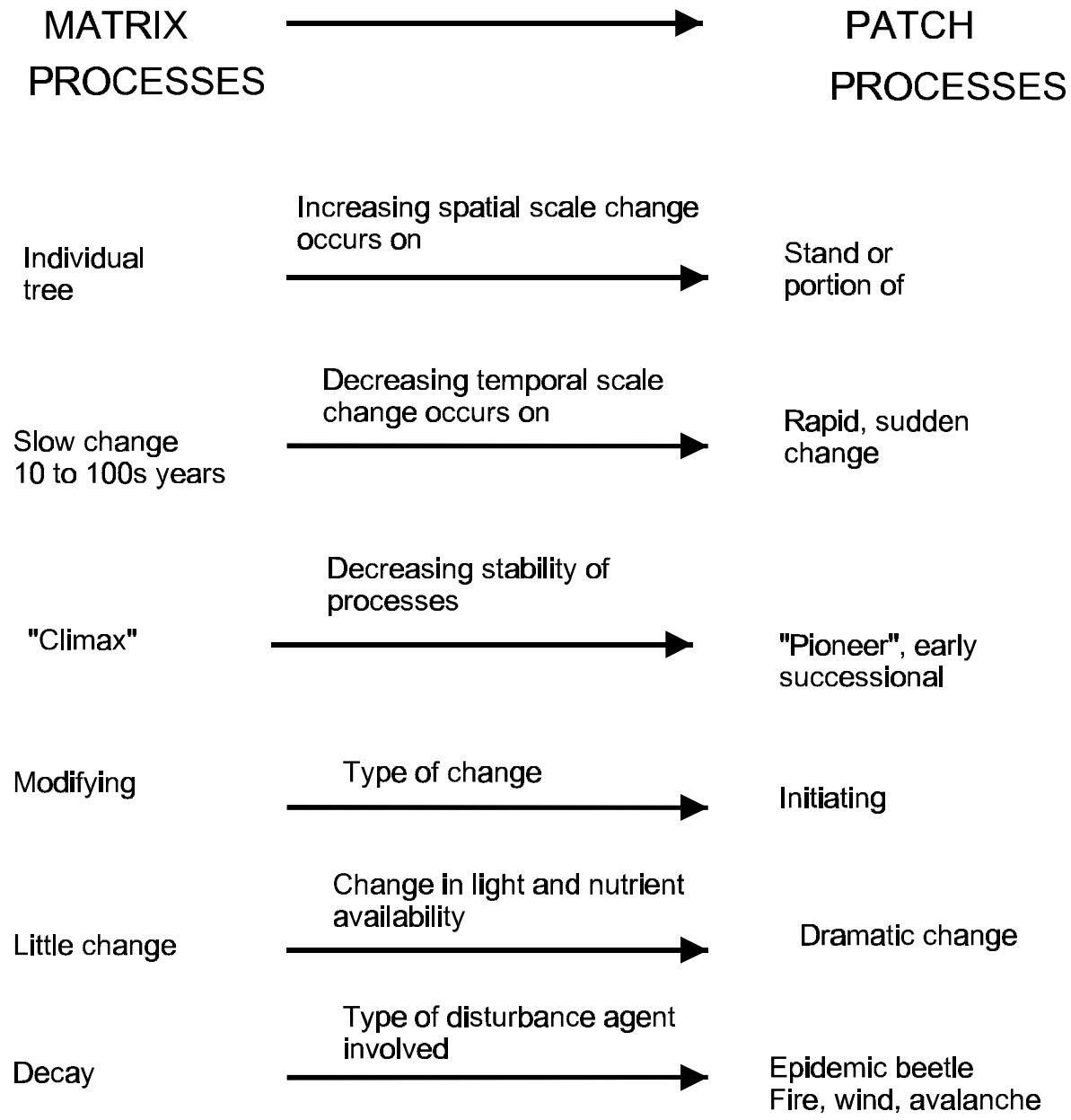


Figure 1. Matrix and Patch Processes

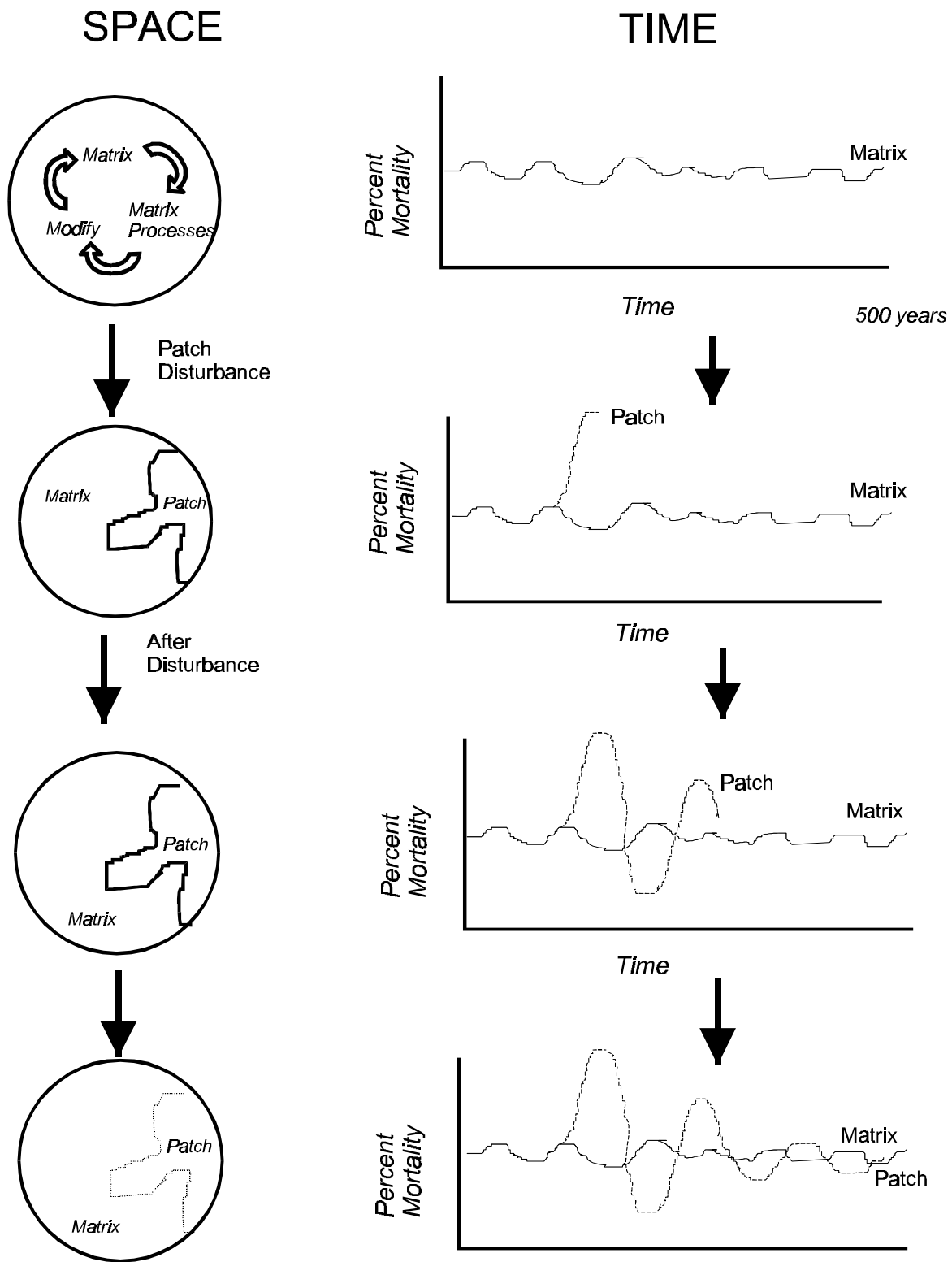


Figure 2. Disturbance Ecology Model

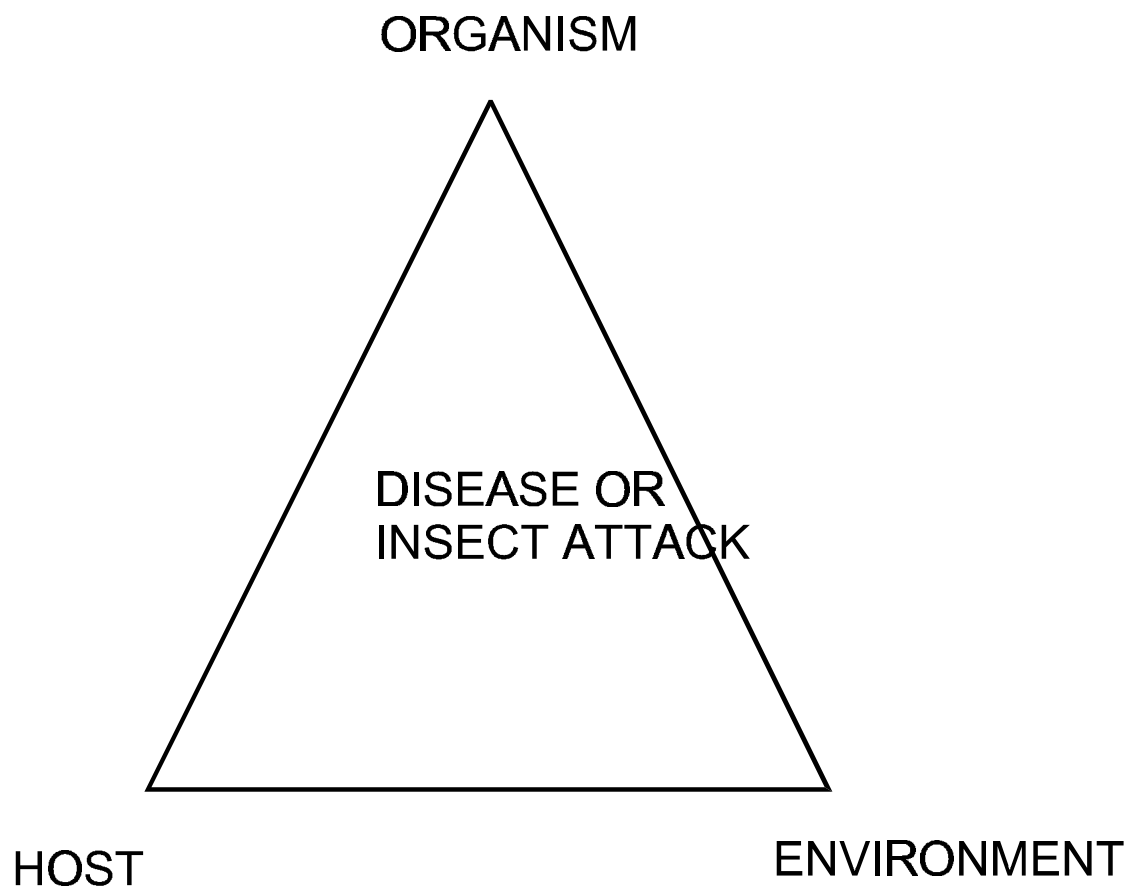


Figure 3. Forest Health Triangle

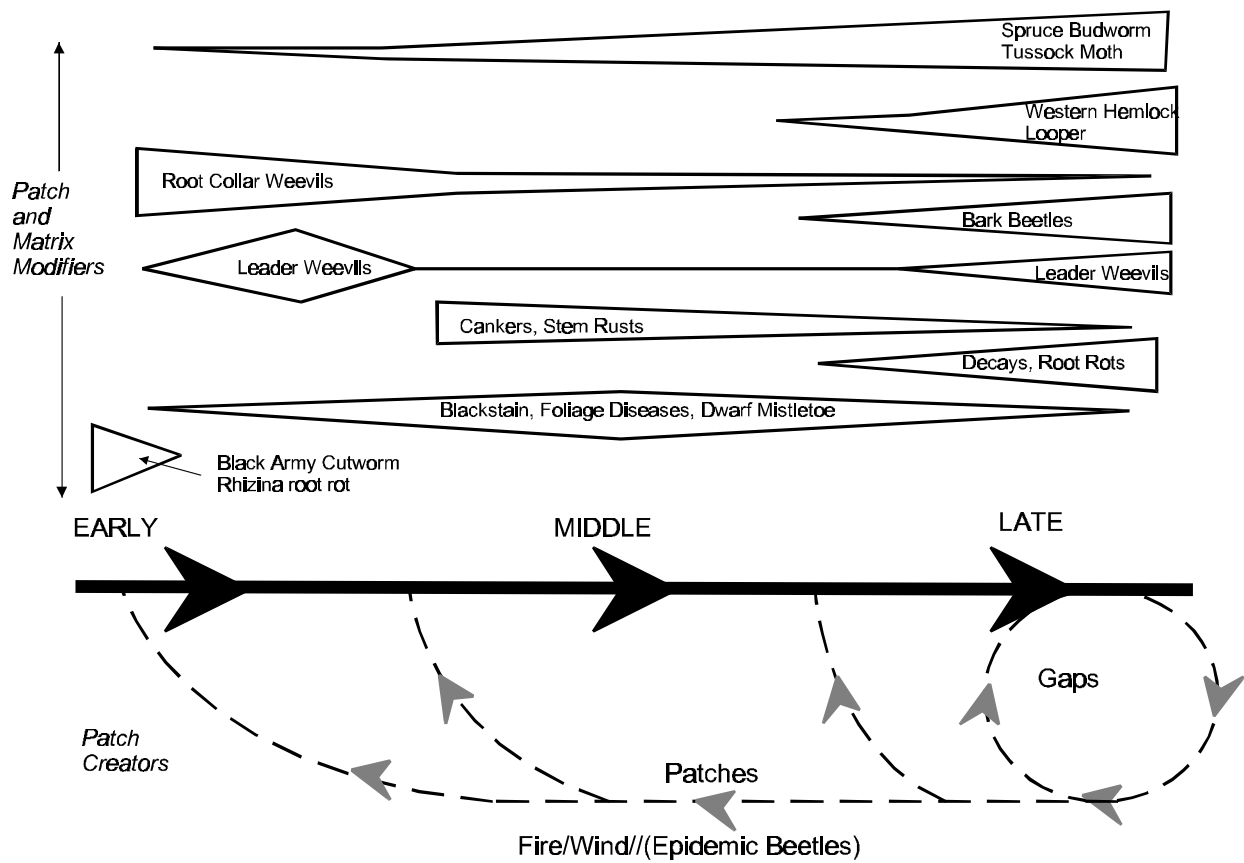


Figure 4. Conceptual model of forest health agents and succession at the stand level. Width of bars indicate relative abundance

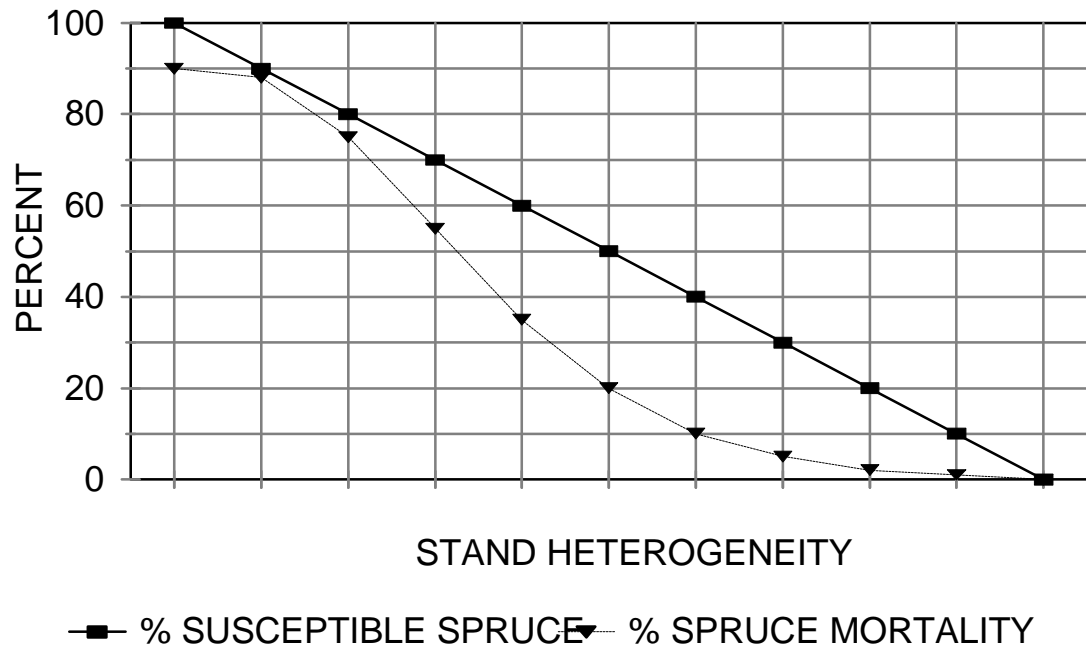


Figure 5. Hypothetical relationship between percent spruce trees in a stand and percent spruce mortality.

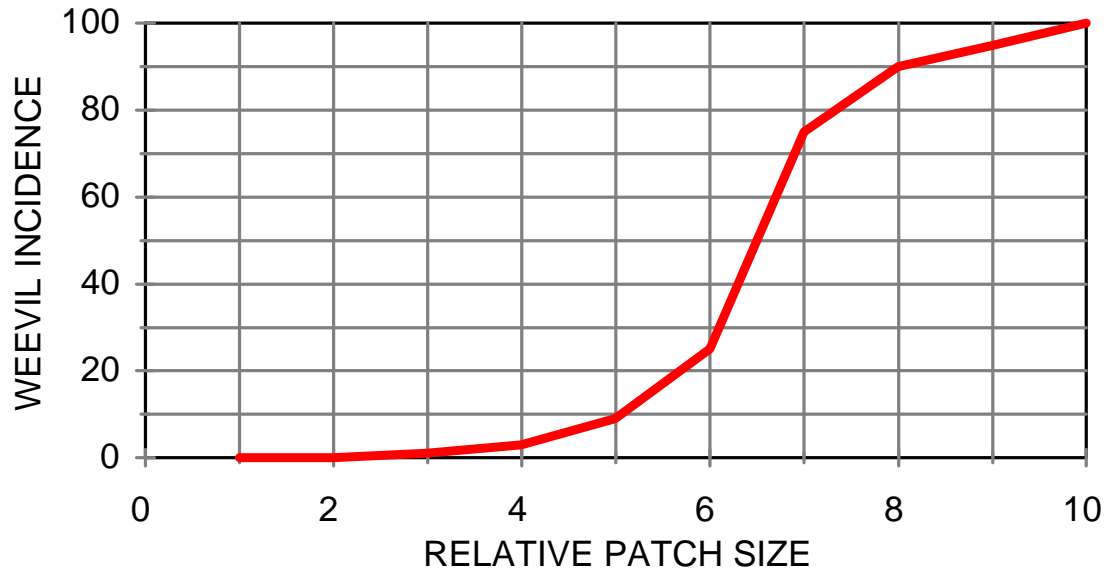


Figure 6. Hypothetical relationship between relative patch size and the probability of weevil damage to regenerating spruce.

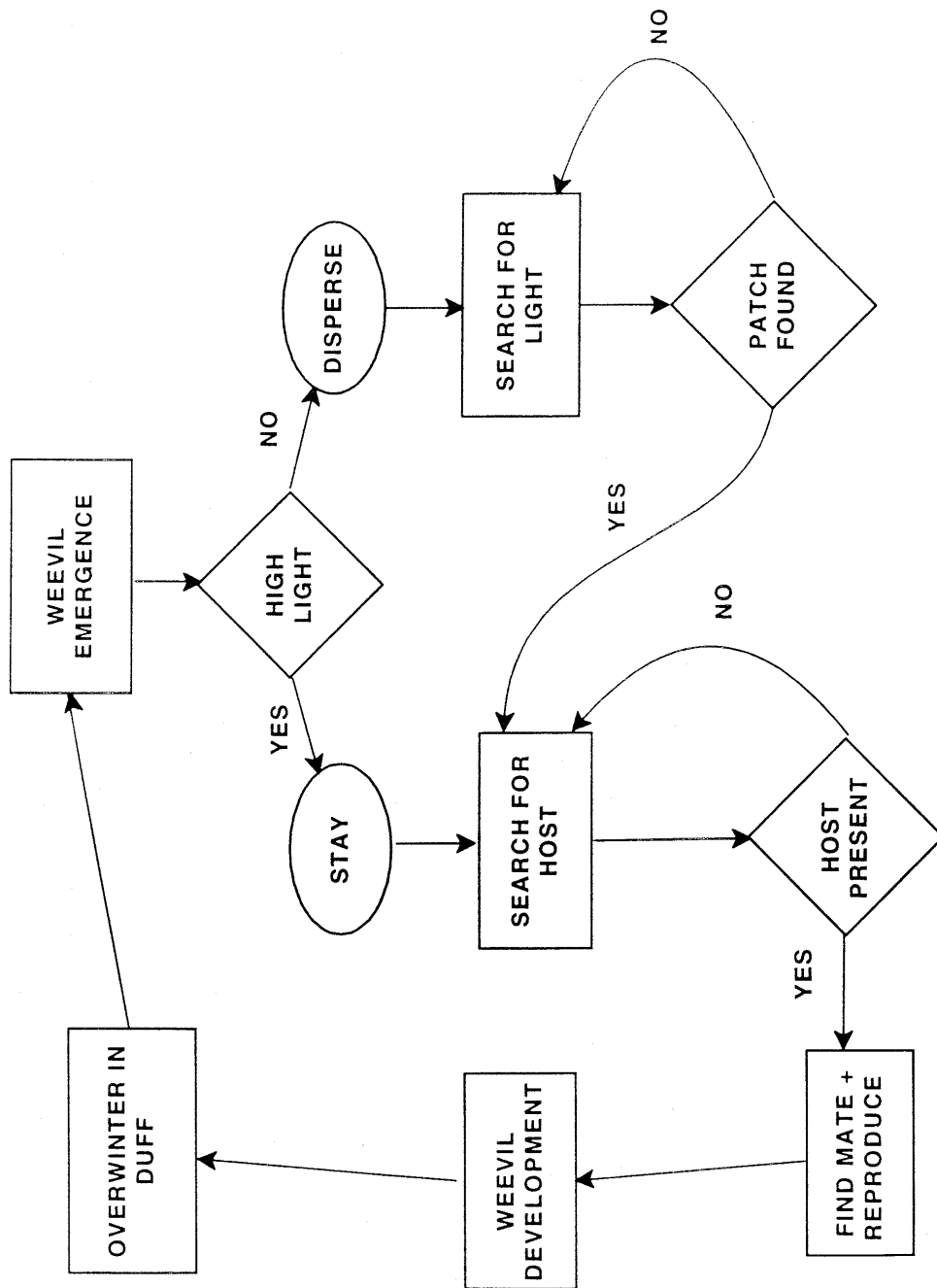


Figure 7. Hypothetical diagram describing behaviour of spruce weevil in response to patch size.