Small-scale disturbance in old spruce-dominated forests of central British Columbia

Literature and Knowledge Gap Analysis

1.0 Introduction

Natural disturbance ecology encapsulates the interrelationships between the biotic and abiotic components of an ecosystem, attempting to characterize the patterns and processes influencing the rates of mortality and regeneration. Within all forest ecosystems, disturbance is a key driver of ecosystem function, affecting landscape pattern (Delong 1998, Hawkes *et al*. 1997, Delong and Tanner 1996), stand structure (Lewis and Lindgren 1999, Kneeshaw and Burton 1997, Oliver and Larson 1996) and biodiversity (Bunnell 1995).

White and Pickett (1985) proposed the most widely used definition of disturbance: "Any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment." Although disturbances may be distinct events in time, it is their persistence that maintains ecosystem structure and function, directly supporting the variety of life and processes called biodiversity (Keane *et al*. 2002, Morgan *et al*. 1994). At the stand- and landscape-level, disturbance can be characterized by the spatial and temporal pattern of mortality for the dominant individuals. This is referred to as the community's "disturbance regime" (Runkle 1985a). White and Pickett (1985) outlined the common descriptors used in quantifying disturbance regimes, these are: (1) distribution in time and space, (2) frequency or return interval, (3) predictability, (4) area or size, (5) intensity or severity, and (5) synergism between multiple agents of disturbance.

The list of forest communities that are directly influenced by disturbance is extensive, as many reviews have demonstrated (White 1979, Rogers 1996, Lewis and Lindgren 2000, Castello *et al*. 1995). Disturbance regimes, historically, have been defined in terms of the major catastrophic events, originating via the physical environment, and regarded as exogenous agents of vegetation change (White 1979). This paradigm has lead to a strong research focus on catastrophic wildfire, as the dominant agent of disturbance within the sub-boreal ecosystems of central British Columbia. An explanation for this is that sub-boreal ecosystems are comparable to boreal ecosystems, with short fire return intervals that maintain the landscape with low diversity in age-class structure, simply because fire return intervals are shorter than tree life spans (Veblen 1986; Frelich and Reich 1995). Though this focus has been informative, our understanding of what occurs in the natural absence of fire is limited. White (1979) highlighted two major problems with this simplistic view: (1) there is a gradient from major to minor disturbance events rather than a uniquely definable set of major catastrophes, and (2) some disturbances are initiated or promoted by the biotic component of the ecosystem. This gradient between minor and major disturbance regimes promotes incredibly complex and dynamic ecosystems, leading to an extensive range in natural variability.

It has been suggested that successful conservation and the maintenance of overall forest health require an understanding of disturbance patterns and processes (Pickett and Thompson 1978, White 1979, White and Pickett 1985, Bergeron *et al*. 1999, Lewis and Lindgren 2000).   It has

also been suggested that values inherent in forest ecosystems can best be maintained by using forest practices that mimic natural disturbance regimes (Bergeron *et al*. 1999, Hawkes *et al*. 1997, Bunnell 1995). However, in many ecosystems, we either do not fully understand the agents of disturbance, or have made assumptions about the agents that are frequently wrong.

In response to these limitations, the "range of natural variability" concept is gradually being accepted for its value in understanding and illustrating the complex nature of forested ecosystems as a result of disturbance (Morgan *et al*. 1994, *Landres et al*. 1999, Millar and Woolfenden 1999, Swetnam *et al*. 1999). The major aim of characterizing natural variability is to understand how driving processes vary from one site to another, how these processes influenced ecological systems in the past, and how these processes might influence ecological systems today and in the future (Landres *et al*. 1999). The essential role for the description of a range in natural variability is to define the bounds of ecosystem behaviour that have remained relatively constant over time. The use of historical information for identifying desired future conditions, however, does not imply managing for static conditions. The importance of temporal change is reflected within the phrase "range of natural variability". The focus is not on a single condition, but on a range of conditions and the variability under which ecosystems were sustained in the past (Swetnam *et al*. 1999). Natural resource managers increasingly rely on an understanding of the range in natural variability to develop plans that guide management within the bounds of ecological and evolutionary conditions appropriate for a defined area. The use of natural variability in management relies on two intertwined concepts: (1) that past conditions and processes provide context and guidance for managing ecological systems today, and (2) that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems (Landres *et al*. 1999).

If natural disturbances are fundamental to the development of forest ecosystems, then management of these areas should be based on an understanding of disturbance regimes (Lewis and Lindgren 2000, Bergeron *et al*. 1999, Angelstam 1998, Bergeron and Harvey 1997, Attiwill 1994, White and Pickett 1985, White 1979). In British Columbia forest practices are by law based on sustainable forest management (BC Forest Practices Code Act 1995). The assumption is that managing forests with silviculture systems similar to natural disturbance processes will maintain a diversity of ecosystems and habitat types. In the recent past, forest managers within British Columbia have attempted to use a natural disturbance type model (NDT, Biodiversity Guidebook 1995). As mentioned previously, however, forest practitioners do not have the information required to prescribe and apply silviculture systems that more closely approach natural disturbance processes. Further, they do not have the indicators of natural disturbance processes needed to monitor success.

One of the reasons for developing the research outlined in the study plan is to assist in revising the Natural Disturbance Type (NDT) model (Biodiversity Guidebook 1995) to reflect a greater range in natural variability in disturbance regimes that exists within the central interior of British Columbia. Over the eight years, since the introduction of this NDT model, a modest volume of research has been completed that highlights the need for this revision. One attempt has been made thus far by Craig Delong (2002)[1]. Within this document, Craig Delong has developed a

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Natural Disturbance Unit (NDU) model for the entire Prince George Region. In comparison to British Columbia's 5 natural disturbance types (4 forested), for the Prince George region alone there are 9 NDUs. It has been suggested that the NDU model be used as a framework for developing research questions within the Prince George Region (Delong pers. comm. 2003).

In the broadest sense, the objective of this research will be to quantify the natural variability in small- an intermediate-scale disturbance in old spruce dominated forest patches within three distinct biogeoclimatic variants of central British Columbia. More specifically the research will attempt to characterize two things: (1) present stand structures as a result of small- and intermediate-scale disturbance regimes in old, spruce dominated forest patches, and (2) the etiology of small- and intermediate-scale disturbance agents that influence, and are influenced by, present stand structure.

2.0 Disturbance Ecology of Sub-Boreal Spruce and Engelmann Spruce-Subalpine Biogeoclimatic Zones

The terrestrial ecosystems of British Columbia have been hierarchically classified using the biogeoclimatic ecosystem classification. The system incorporates primarily climate, soil, and vegetation data, and provides a universal framework for resource management and scientific research (Meidinger and Pojar 1991). The biogeoclimatic subzone is the basic unit of classification resulting from zonal (climatic) classification and they represent groups of ecosystems under the influence of the same regional climate (Delong et al. 1993). Subzones can be grouped to form biogeoclimatic zones and divided to define biogeoclimatic variants. Variants reflect further differentiation in regional climate and are generally recognized for areas that are slightly drier, wetter, snowier, warmer, or colder than other areas in the subzone (Meidinger and Pojar 1991).   Similar climax vegetation can occur over a range of subzones and variants, and in extreme cases between biogeoclimatic zones. In consequence, even a climax plant association may represent ecosystems from different regional climates and with different soils (Meidinger and Pojar 1991).

Two of the dominant biogeoclimatic zones located in central and east-central British Columbia are the Sub-Boreal Spruce (SBS) and Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zones. Both the SBS and the ESSF are recognized as part of the Canadian Boreal Forest Region. However, in contrast to the boreal, the sub-boreal and sub-alpine climates are slightly less continental, thus slightly warmer in January and cooler in July (Meidinger and Pojar 1991).

2.1 General description of the Sub-Boreal Spruce Zone

The Sub-Boreal Spruce (SBS) biogeoclimatic zone is located within central British Columbia. It is bordered by the Interior Cedar Hemlock (ICH), Sub-Boreal Pine-Spruce (SBPS), Interior Douglas-Fir (IDF) and Engelmann Spruce-Subalpine Fir (ESSF) zones. It occurs from valley bottoms up to 1100-1300m elevation and between the 52° and 57° N latitude and 122° and 128° W longitude (Meidinger and Pojar 1991).

Due to its moderate boreal climate the SBS is affected by seasonal extremes in temperature and by relatively moderate levels of precipitation. The region is broadly continental with long, cold, snowy winters and short, warm, moist summers (Delong et al. 1993). Mean annual temperature of the SBS ranges from 1.7 to 5 C and average temperatures are below 0 C for 4-5 months of the year, and above 10 C for 2-5 months (Meidinger and Pojar 1991).   Mean annual precipitation data from long-term stations ranges from 440-900 mm, of which perhaps 25-50% is snow (Meidinger and Pojar 1991). Short-term data indicate that mean annual precipitation can range from 415 to 1650 mm in the SBS (Meidinger and Pojar 1991).

Upland soils are primarily from the Luvisolic, Podzolic, and Brunisolic soil orders (see Agric. and Agric-Food Can. Publ. 1998).   Brunisolic and Orthic Gray Luvisols, and Podzols are the most common soils found on abundant morainal deposits (Meidinger and Pojar 1991). Imperfectly to poorly drained sites typically will display gleyed soil horizons.

The SBS is dominated by upland coniferous forest. Hybrid white spruce (*Picea engelmannii x glauca*) and subalpine fir (*Abies lasiocarpa*) are the dominant climax tree species. Lodgepole pine (*Pinus contorta var. latifolia*), a seral species in the SBS, is common in mature forests in the drier parts of the zone and both lodgepole pine and trembling aspen (*Populus tremuloides*) pioneer the extensive seral stands (Meidinger and Pojar 1991). Paper birch (*Betula papyrifara*), another pioneer species, will establish on moist, rich sites. Douglas-fir (*Pseudotsuga menziesii*), a long lived species, will occur abundantly on dry, warm, rich sites as a consistent, although small, component of mesic forest types. Ten subzones are recognized in the SBS, largely due to the variability in climate especially precipitation. Within this study, two biogeoclimatic variants will be considered for research: the Stuart Dry Warm Sub-boreal Spruce (SBSdw3) and the Willow Wet Cool Sub-boreal Spruce (SBSwk1).

2.2 General description of the ESSF

The Engelmann Spruce-Subalpine Fir (ESSF) zone is one of the most extensive forest zones in British Columbia, covering 13.3 million hectares or 14% of BC's land area (Jull et al. 1996). It is the uppermost-forested zone in the southern three-quarters of British Columbia. The ESSF is the widest ranging biogeoclimatic zone in British Columbia and can be found outside of the province in Alberta, as well as in the Pacific Northwest and Rocky Mountain states. In British Columbia, it occurs at elevations of 1200-2100 m in the Southwest, from 1500-2300 m in the south-east and from 900 to 1700 m in the northern part of the zone (Meidinger and Pojar 1991). In east-central British Columbia it is found on the McGregor Plateau below the Alpine Tundra (AT) and above the SBS and ICH. The McGregor Plateau is at the eastern edge of the interior plateau, between the offset ends of the northern and southern portions of the rocky mountain trench (Delong et al. 1994).

At this elevation (> 1000 m), the climate is cold and precipitation is variable with windward slopes being wetter than the lee slopes (Delong et al. 1994). The ESSF is characterized as having a cold, moist, snowy continental climate. According to available data, mostly from south-eastern British Columbia, mean annual temperatures range from -2 to 2 C (Meidinger and Pojar 1991). Mean monthly temperatures are below 0 C for 5-7 months and above 10 C for 0-2 months (Meidinger and Pojar 1991). Although precipitation is highly variable, windward slopes

can receive up to 2200 mm annual precipitation. Most of the precipitation (50-70 %) falls as snow and maximum snow pack ranges from 1-4 m (Meidinger and Pojar 1991). Due to the short and cool growing seasons, and long and cold winters, the ESSF is one of the most severe climates for forest growth and regeneration (Jull et al., Farnden 1994).

Within east-central British Columbia, at the lower elevation range, soils are predominantly Brunisols, Luvisols and Podzols (see Agric. and Agric-Food Can. Publ. 1998). Humo-Ferric Podzols have formed on parent materials consisting predominantly of medium textured morainal and colluvial deposits (Delong et al. 1994).

The ESSF includes continuous forest at its lower and middle elevations and subalpine parkland at its upper elevations (Meidinger and Pojar 1991). At lower elevations the ESSF has climax forests dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Spruce, which is the longer-lived species, usually dominates the canopy of mature stands despite its relatively limited recruitment in the understory (Meidinger and Pojar 1991, Kneeshaw and Burton 1997, Veblen 1986, Veblen et al. 1991, Veblen et al. 1994, Lewis and Lindgren 1999, Lewis and Lindgren 2002). Fifteen forested subzones are currently recognized in the ESSF, largely due to the broad latitudinal and elevational range, and to the variability in climate, especially precipitation. Within this study, one biogeoclimatic variant will be considered: the Misinchinka Wet Cool Engelmann Spruce – Subalpine Fir (ESSFwk2).

2.3 SBS and ESSF Stand Dynamics

Contemporary models of stand dynamics are fundamental in understanding stand genesis, maintenance, and renewal over long periods of time. The seemingly equivalent patterns and processes that appear after major stand replacing disturbances have long been recognized by ecologists. This progressive change in vegetation has lead to the development of two competing models of forest succession. The first, where one species invades after another, until one species or a group of species invades, predominates and replaces itself rather than being replaced, is known as *relay floristics* (Oliver and Larson 1996). This process of replacement creates a stable endpoint to succession known as the "steady state", "equilibrium" or "climax" vegetation association. The second is the "initial floristics" concept where species that predominate later have been present since or almost immediately after the stand replacing disturbance event (Drury and Nisbet 1973).

Due to the stochastic nature of a single disturbance event, an enormous range in variability exists. The elements of both *initial* and *relay floristics*, thus, are characteristic of forest development. However, the invasion patterns after disturbance predominantly follows the initial floristics pattern (Oliver and Larson 1996). As a direct outcome of the latter model, Oliver and Larson (1996) proposed four distinct successional phases to characterize the progression of forest succession. These phases are (1) stand initiation, (2) stem exclusion, (3) stem reinitiation and (4) old growth. The stand dynamics model has been reasonably applied to spruce-dominated SBS, ESSF and comparable forest types (Antos and Parish 2002a, Antos and Parish 2002b, Newbery 2001, Lewis and Lindgren 1999, Kneeshaw and Burton 1997, Aplet et al. 1988). Stand dynamics and disturbance ecology studies within the SBS and ESSF, however, have unveiled a huge range of natural variability, which suggests that the phases are not ecologically strict.

The dominant controversy today, intimately linked to the range in natural variability concept, is based on the roles of wildfire and gap-phase processes and their relative influence of stand structure. Stands initiated by catastrophic wildfire are invariably affected by various subsequent partial disturbances (Agee 1993, Antos and Parish 2002a). Under certain circumstances however, an argument can be made that initial stand replacing event will continue to control stand dynamics, even if long periods occurred between stand initiating events (Antos and Parish 2002a). On the other hand, some SBS, ESSF and equivalent forest types are strongly influenced by single- and multiple-tree gap-phase processes (Newbery 2001, Lewis and Lindgren 2000, Kneeshaw and Burton 1997, Lertzman 1992, Lertzman and Krebs 1991, Veblen 1986). This dichotomy closely parallels White's (1979) theory that: (1) there is a gradient from major to minor disturbance events rather than a uniquely definable set of major catastrophes, and (2) some disturbances are initiated or promoted by the biotic component of the ecosystem.

2.4 Fire Driven Ecosystems of the SBS and ESSF

The role of fire as a natural process vital to the health and renewal of boreal, sub-boreal and sub-alpine forests of western Canada has long been acknowledged (Johnson and Rowe 1977, Heinselman 1981, Romme 1980, Hawkes 1980, Pyne, 1984). More recently, the SBS and ESSF of central and east-central British Columbia are currently receiving greater attention in respect fire as a catastrophic disturbance agent (Andison 1996, Delong 2000, Delong and Tanner 1996, Hawkes *et al*. 1997, Newbery 2001, Sanborn *et al*. 2001). Catastrophic fires have historically been thought of as the most important natural disturbance agent (Johnson 1992, Andison 1996, Oliver and Larson 1996, Hawkes *et al*. 1997, Newbury 2001). Although the SBS and ESSF, in most cases, do originate by fire, recent studies have shown that the times since these catastrophic stand originating events are enormously varied (Hawkes *et al*. 1997, Sanborn *et al*. 2001). In the wet SBS spruce-fir dominated ecosystems fire may be so infrequent that the development of true old-growth forests may be possible. Hawkes *et al*. (1997) report that fire return intervals in very wet and cool SBS forests near the Rocky Mountains likely range from 1200 to 6250 years. Delong and Tanner (1996) reported return intervals ranging from 227 to 345 years in slightly drier SBS forests in the foothills of the Rocky Mountains.

The most recent wildfire studies have been based in areas that have limited human impact (Hawkes *et al*. 1997, Delong and Kessler 1999, Hawkes *et al*. 1997, Delong 1996, Delong and Tanner 1996). Study areas have relatively intact forest patches and/or few modifications by harvesting that would confuse the delineation of historic events. These areas also have witnessed less fire suppression due to their remote settings.

The studies have emphasized the quantification of pattern (e.g. example size and shape of fire patches, island remnants and complexity) and have had little success with the quantification of processes such as snag recruitment and soil formation (Hawkes et al. 1997, Delong and Kessler 1999, Hawkes et al. 1997, Delong 1996, Delong and Tanner 1996).

There has been a review, albeit limited, detailing the current anthropogenic landscape patterns compared to the hypothesized "natural" landscape patterns that would have resulted from wildfire (Delong 2002, NDU refinement). A number of studies have attempted to understand the

quantity and quality of coarse woody debris (CWD, above and below ground) and snags that are left behind by wildfire (Wei et al. 1997, McRae et al. 2001, Delong and Tanner, 1996, Delong and Kessler 1999, Delong 1996). There have been a limited number of studies that quantify the major differences in CWD and snags left behind by wildfire compared with traditional harvesting methods (Wei et al. 1997, McRae et al. 2001, Delong and Tanner, 1996, Delong and Kessler 1999, Delong 1996).

2.4.2 Gaps in knowledge

Although there has been some work done on landscape heterogeneity caused by "between" patch variation, there is little or no information on "within" patch variation. Variation in wildfire severity/behaviour should result in variation in disturbance patterns within a patch. This would produce stand level heterogeneity that could feasibly be significantly important to landscape or ecosystem function (see Delong and Kessler 1999).

Very few studies have focused on the interaction between fire and other disturbance agents. For example, the effect of fire on populations of other forest health agents, particularly those currently viewed as pests. For example, the relationship between mountain pine beetle and fire has been examined to a limited extent with respect to fuel loads from beetle-killed wood, and in terms of the effect of natural fire on reducing susceptibility of stands to beetle outbreaks (Safranyik et al. 2001, Hawkes pers. comm. 2003). The interactions between fire and most other pest organisms have not been studied. For example, the role of decay fungi and windthrow in the development in specific fuel types is unknown.

Pattern and process comparisons between wildfire and harvesting pattern has seen some attention; however, there is still a gap in this knowledge (Delong pers. comm. 2003). Some non-regional studies can be extrapolated to this area (McRae et al. 2001); however, the Prince George Timber Supply Area (PGTSA) is unique, and its fire regime is incredibly varied. Therefore, local studies are required to provide finer resolution. The latest NDU refinements by Delong (2002) can be used as a backdrop to formulate specific PGTSA fire regime questions.

Even though there is a tremendous emphasis on resource protection, which has lead to a very successful system for wildfire suppression, we do not know what the impacts of suppression will be on biodiversity and forest productivity. Craig Delong (pers. comm.) suggests that we may be omitting rare early-seral, and wildfire dependent plant communities, thereby putting these communities at risk. However, we lack monitoring, documentation and the habitat modelling capacity to answer such questions. We may not realize the importance of young seral forests.

Similarly, we have no local information about relationships between the structures left behind after fire, such as charred snags and logs, and wildlife communities, although strong relationships have been documented elsewhere (Huuto 1995).

2.5 Ecology of Biotic Patch Disturbance Agents

At 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. The most common patch initiating agents in central interior BC, spruce beetle and mountain pine beetle, are discussed below as they appear to have the greatest impact on landscape pattern.

The spruce beetle has caused severe mortality in the Prince George Forest Region at regular intervals since the 1960s (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 change of stand age structure (Schmid and Frye 1977). Such effects are most pronounced in stands with a homogeneous, spruce-dominated canopy. In heterogenous stands, only the larger spruce trees are successfully attacked, resulting in a less patch-like mortality event. 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, 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 negative linear relationship between mortality and the availability of susceptible trees, relative spruce mortality would decrease rapidly at some point due to changes in infestation dynamics. In heterogenous stands, the effect is a release of suppressed trees not dissimilar to that observed following selective harvesting of overstorey spruce (Veblen et al. 1991, Lindgren and Lewis 1997). Thus, from an ecological point of view, the long-term impacts on a stand may be fairly moderate. From a forest management point of view, however, even moderate spruce beetle-caused mortality may constitute a considerable loss in timber volume, given that a relatively small proportion of large diameter spruce would contribute a large portion of the harvestable volume in the stand.

Clearly the spruce beetle can be a major disturbance agent in mature spruce forests. In the Prince George TSA, 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 research using dendrochronological methods (Lindgren and Lewis 1997), and supported by observations by McLean (1849), that a major outbreak occurred in this area in the early half of the 19th century. Zhang et al. (1999) found that outbreaks in the east-central interior had occurred in the late 1720's, 1810-1820's, and the 1960's – early 1980's. These recent epidemics further indicate that this insect can affect stand and landscape level processes in the PGTSA 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, decay fungi maintain heterogeneity. In stands where root disease or other mortality agents act selectively on sub-alpine fir, spruce dominance may increase over time. This leads to significant impact when spruce beetle populations build up (Veblen 1986, Lewis and Lindgren 1999, Lindgren and Lewis 1997) which may have a patch initiation-like effect on the stand.

The mountain pine beetle (*Dendroctonus ponderosae*) is the most aggressive of all bark beetle species, and is responsible for devastating outbreaks in lodgepole pine forests (Safranyik 1995). In the PGTSA it is of concern primarily within the warmer, drier ecosystems, 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, resulting in patch creation. In the absence of subsequent fire, which would re-establish lodgepole pine dominance, the result may be a change in species composition, favouring spruce, subalpine fir, and sometimes Douglas-fir.

2.6 Gap-Phase Disturbances in the SBS and ESSF

Small-scale disturbance agents influence forest dynamics by killing trees, although the pattern and frequency of mortality differs from physical disturbances such as fire and wind throw (Schowalter et al. 1997). With increasingly greater time periods between stand replacing events, small to intermediate scale disturbance events can become more important in forest dynamics. These disturbances, caused by biotic and abiotic agents, maintain and renew the forest structure in stands with long fire return intervals (Newbery 2001, Lewis and Lindgren 1999).

An extensive body of literature exists describing gap-phase disturbance patterns and processes in tropical (Denslow 1987, Lawton and Putz 1988), temperate North-American forests (Frelich and Graumlich 1984, Runkle 1984, Lorimer et al. 1988, Lorimer and Frelich 1989, Payette et al. 1990, Abrams et al. 1995), eastern sub-boreal forests (Frelich and Reich 1995), western coastal forests (Canham 1988, Lertzman et al. 1996, Brett and Klinka 1998) and western subalpine forests (Lertzman and Krebs 1990, Lertzman 1992, Lundquist and Beatty 2002). Although there is an emerging body of literature that suggests small-scale disturbances are an important element of boreal/sub-boreal forest structure (McCarthy 2001), little is know about small-scale disturbance regimes in the SBS and ESSF forests found in central and east-central British Columbia.

Much of this work has been dedicated to describing gap structure and tree regeneration dynamics (White and Mackenzie 1985, Yamamoto 1995, Kneeshaw and Bergeron 1998) not the agents of gap formation. Individual tree, or small group mortality, can be caused by a variety of abiotic and biotic agents, however there is increasing evidence that insects and fungi play a significant role in gap formation (Dickman and Cook 1989, Hennon 1995, Lewis and Lindgren 1999).

2.6.1 Stem Decays and decay fungi

In the context of matrix disturbance processes (also called gap dynamics), the most important decay fungi are those that directly or indirectly cause mortality of living trees. Normally these decay fungi weaken the roots and/or the bole, eventually to such an extent that breakage occurs. Root and butt rots are one of the most important gap-making agents in sub-boreal and related forest types (Hennon 1995, Holah et al. 1993, Lewis and Lindgren 1999, Veblen 1986, Worrall and Harrington 1988), and therefore are major contributors to processes that maintain the forest matrix.

Sapwood of living trees is very resistant to decay. 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), both of which tend to increase with stand age. It also takes years from the time of infection for extensive decay to develop. Therefore, the prevalence of decay fungi usually increases with stand age, becoming evident only in older, climax forests.

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).

Decay fungi generally cause breakage of individual trees, although broken trees may knock over or substantially damage other trees, such that a several-tree gap is created over time (Hennon 1995). These gaps contribute to structural and species heterogeneity typical of old growth forests in the Prince George TSA.

Stem decays have an important role in the creation of habitat for wildlife. This habitat includes living or dead trees with internal decay or cavities, trees that have snapped due to bole weakness, and logs on the forest floor. The northern long-eared myotis and the fisher are two examples of the many wildlife species that depend on trees with stem decay for habitat.

2.6.2 Tomentosus root disease

Inonotus tomentosus is the dominant root rot pathogen in boreal and sub-boreal ecosystems of B.C. This fungus attacks a broad range of conifer hosts but is most frequently found on spruce and pine species. Hardwood species are thought to be immune to *I. tomentosus* (Whitney 1962, Whitney and Bohaychuck 1976).

Inonotus tomentosus causes gradual dysfunction of the root system; eventually the tree dies standing or is windthrown. The disease occurs in small clumps (2-3 trees) that gradually coalesce into larger areas of infected trees. Therefore the effect on stand structure depends on the incidence of root disease. At low levels it causes occasional gaps, but at higher levels (e.g., >20% spruce infected), *I. tomentosus* can result in a species shift to sub-alpine fir or other resistant species or a more open, brushy stand structure.

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) has termed this condition a root disease climax.

In a study that compared stand dynamics in unmanaged and partially cut forests (harvested between 1940 and 1950), with and without *I. tomentosus*, spruce mortality was 50% lower in partial cut forests than in old-growth forests regardless of infection status. The functional gap

size caused by a single tree averaged 16.76 m^2. Summed gap-size measures for all trees dying in a decade indicated that between 6.9 and 8.1% of stand area was made available to understory trees per decade. Due to high mortality rates and low recruitment rates to the canopy for spruce old-growth forests are shifting to a canopy dominated by *A. lasiocarpa*. In the partial cut plots, higher relative spruce populations may rise relative to present densities.

In old-growth forests, the spatio-temporal patterns of canopy disturbance and canopy patch structure were quantified from 0.49ha (n=6) stem-mapped plots using Moran's I and Standard Normal Deviates. Canopy disturbance and canopy composition were similar for *I. tomentosus* infected and uninfected stands at low levels of incidence. For stand types pooled, average decadal canopy disturbance ranged from 5.09%-6.0%. Gap size averaged <7m in diameter and were irregularly distributed across the forests. Species patch structure analysis indicated that spruce is found in small patches which are probably remnants of a once nearly homogenous spruce canopy. These results show that small-scale disturbances are important successional mechanisms in old-growth Sub-Boreal Spruce forest because of their effects on stand structure and dynamics (Newbery 2001)

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 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 has indicated that at endemic population levels, spruce beetles are more successful when diseased trees are attacked. At outbreak levels, there was no difference in attack success between healthy and infected trees (Lewis and Lindgren 2002). Therefore, tomentosus root disease is an important matrix modifier and at times may modify patches as well. It also influences population dynamics of spruce beetle, another late successional matrix modifier that has varying effects on the forest depending on population size. This demonstrates that we cannot view individual organisms in isolation from each other, regardless of their disturbance category.

2.6.3 Insects

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 climax stands, where a heterogenous stand structure and composition is generated by disease-driven gap dynamics (Lertzman et al. 1996). In young to mature homogenous stands, mortality rates are lower, so breeding resources are sparse and scattered, and tend to keep insect populations at low to moderate levels. Occasionally, however, increased availability of scattered windthrow will lead to a buildup in the populations of these insects and also of potential tree-killing bark beetles. While the populations of wood borers and secondary beetles will decline as soon as the abundance of dead host trees declines, primary bark beetle populations have the capability to switch to live trees. The fate of high populations of primary bark beetles (i.e., whether the populations decrease again or if they lead to epidemics) depends on whether or not environmental conditions are conducive to sustaining high insect 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-processes enough to constitute the initiation of a patch. The western balsam bark beetle, *Dryocoetes confusus*, is a good example of an insect that can cause either small scale (gap) disturbances, or larger scale (patch) disturbances depending on climatic factors and stand structure.
Western balsam bark beetle is widespread in British Columbia wherever subalpine fir grows (Garbutt 1992). Mortality caused by the western balsam bark beetle can be widespread and severe, but is generally scattered over large areas and outbreaks are sustained for many years (Stock 1991). Harder (1998) observed that attacked trees were disproportionately found in larger diameter classes. Bleiker (unpublished data) found that successfully attacked trees had reduced growth rates in the last 10 years relative to unattacked trees, indicating that this insect prefers declining trees.

Subalpine fir is subject to many mortality agents, and in TFL 30 species-specific mortality prevents this species from displacing spruce in many areas (Lewis and Lindgren 1999). The western balsam bark beetle appears to contribute significantly to the turnover rate, but rarely becomes the driving force, i.e., in the absence of declining trees mortality rates will decline also.

2.7 Research Objectives

British Columbia's central interior is ideal for the study of small-scale disturbance regimes because the SBS and ESSF biogeoclimatic zones span the dry plateau of the central interior and grade eastward into the progressively wetter, cooler, high-elevation ecosystems of the Rocky Mountain Foothills. The precipitation and temperature gradient offers a significant opportunity to study how climate can influence disturbance processes in spruce-dominated ecosystems.

The general objectives of this research will be to: (1) quantify the range of natural variability in small-scale disturbance regimes within three climatically distinct spruce-dominated ecosystems and; (2) compare and contrast these individual regimes as they result from the influence of a west to east climatic gradient. Specific objectives of the research are:

1. to characterize forest structure and small-scale disturbance (i.e. mean gap size, variance about the mean and distribution in gap size);
2. determine the spatial and temporal arrangement of small-scale disturbances within and between climatically distinct spruce dominated ecosystems and;
3. link the incidence of the various disturbance agents to present stand structure.

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