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VEGETATION DYNAMICS IN BOREAL FOREST ECOSYSTEMS

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Abstract: An overview of the literature on succession theory, patterns and processes in North American boreal forest ecosystems is presented, incorporating data that we have recently collected from the boreal forests of southeast and western Manitoba, northwest and east-central Ontario, and the montane region of southwest Alberta, Canada. Ecological theories and scientific concepts pertaining to boreal forest ecosystems are summarized and discussed. A spatio-temporal conceptual framework of boreal forest dynamics is also developed, emphasizing vegetation-environment relationships and the concept of ecosystem persistence.

1. Introduction

The boreal forest is one of the largest biomes in the world, occupying ca. 8% of the global continental land mass. Although some authors have described the North American boreal forest as a relatively simple ecosystem (e.g. Ritchie 1956; Larsen 1980), the dynamics of these forests remains poorly understood (Bonan & Shugart 1989). An important early contribution by Rowe (1961) noted that many concepts and assumptions of 'classical' succession theory are not easily applicable to the boreal forest. 'Classical' forest succession theory was developed primarily for the temperate deciduous forests of North America (Pickett et al. 1987), which are characterized by high species richness, variable species life-history strategies, and infrequent to rare large-scale catastrophic disturbances. By contrast, the boreal forest ecosystem is species-poor, and species have developed similar life-history strategies reflecting their adaptations to recurrent, large-scale, catastrophic forest fires (Heinselman 1973).

The underpinnings of classical succession theory were developed in the late 19th century (e.g. Cowles 1899). Further developments and elaboration occurred in the early 20th century, a period dominated by the works of Clements (1936). The Clementsian, 'community-unit' (Collins et al. 1993) or 'holistic' (Finegan 1984) model of succession viewed plant communities as natural organismic units, in which individual species are held together by the 'social bonds' of the dominants. Plant species were thought to modify their environment, paving the way for later-successional species while rendering the habitat unsuitable for themselves. A self-replacing 'climax' community was thought to develop once the full 'potential' of a particular climate-environment was realized. Johnson (1979) notes that "contemporary ecologists cannot read Clements and hope to understand him. He is a product of another age, he speaks a different language and expresses a different cognitive commitment, appropriate for a different world view". An alternative view of forest dynamics was offered by the 'reductionist' (Finegan 1984) or 'individualistic-based' model of Gleason (1926). Gleason's model views plant communities as fortuitous assemblages of species populations that evolve through species replacements. These replacements occur on a plant-by-plant basis, as determined by differences in species life-history characteristics. Over the past 50 years or so, the Clementsian view has been largely rejected in favour of Gleason's reductionist approach (Johnson 1979; Cook 1996).

More recent forest succession models recognize disturbance as an integral component of vegetation dynamics. Disturbance was "the nemesis of classical succession because it ... introduced heterogeneity and lack of compositional stability" (Johnson 1979). In ecosystems where disturbances are relatively frequent, the classic notion of a self-replacing 'climax' community becomes meaningless (Horn 1976; Pickett et al. 1987). Although Gleason (1926) acknowledged the role of disturbance, Watt (1947) was the first to explicitly incorporate disturbance into a model of vegetation dynamics. In his model, the community is viewed as a mosaic of patches, with each patch subject to cyclical rather than seral changes in composition and structure. Watt also recognized the stochastic nature of community dynamics, and the roles of life-histories strategies and competition in driving vegetation change. These ideas were expanded upon in Egler's (1954) 'initial floristic composition' model, which has been called "the cornerstone of a new succession theory" (Finegan 1984). This model views succession as proceeding from, and constrained by, the propagules available at a site following disturbance. Propagule availability is largely determined by site history and stochastic factors (McCune & Allen 1985). Two versions of Egler's model are distinguished (Wilson et al. 1992): the 'complete' model, in which succession reflects an 'unfolding' of the flora present from the beginning, as determined by differences in species life-history characteristics; and the 'preemptive' model, in which the dominant species that initially preempt a site have a long-term influence on the successional trajectory. Egler's model implies that succession is very heterogeneous, since vegetation development depends on 'who gets there first'.

Recent developments in forest succession theory reflect the integration, refinement and elaboration of the ideas developed by Watt, Egler and their contemporaries (Johnson 1979). Connell & Slatyer (1977) proposed three theoretical models: 'facilitation', in which succession is controlled by the vegetation itself, with one group of species making the environment more suitable for the next group; 'tolerance', in which succession results in the species assemblage that is most efficient at exploiting limiting resources, anticipating Tilman's (1985) 'resource-ratio' model; and 'inhibition', in which the species present at a site inhibit the establishment of potential competitors. Pickett et al. (1987) discuss some of the mechanisms underlying these three models, and note that they are not necessarily mutually exclusive. Other workers have stressed differences in species life-history strategies as the force driving succession. Grime (1977) recognized three basic plant life-history strategies: 'ruderals' are best adapted to disturbance environments, 'stress-tolerators' to extreme habitats, and 'competitors' to relatively undisturbed and productive habitats. Pickett (1976) viewed the landscape as a series of successional 'patches' that are continually changing in their size and relative position, in response to prevailing disturbance regimes. Variation in species life-history strategies results in different species being favoured at different successional stages. A climax community occurs when the level of species adaptations equals or exceeds that of potential competitors.

Explicit incorporation of life-history attributes into a Gleasonian model led to the concept of 'vital attributes' (Cattelino et al. 1979; Noble & Slatyer 1980). A species' vital attributes are determined by three factors: the method of arrival or persistence at the site during and following disturbance; the ability to establish and grow to maturity in the developing community; and the time taken to reach critical life-history stages such as reproduction. Depending on disturbance frequency, different vital attributes will be favoured. For example, attributes that are favoured when disturbances are rare will prove maladaptive in environments where disturbances are comparatively frequent. The 'life history' model (Huston & Smith 1987) incorporates these ideas into a comprehensive, disturbance-based vegetation dynamic model. This model is based on three premises: that competition for limiting resources occurs between all individuals in the community; that plants alter their environment such that the relative availability of resources changes though time, affecting relative competitive abilities; and that physiological and energetic constraints preclude any one species being a superior competitor under all circumstances. Using this model, the authors found that a steady-state dynamic equilibrium is only achieved if there is a balance between prevailing disturbance regimes and local successional dynamics.

Finegan (1984) states that the tolerance and life-history approaches cannot by themselves provide a complete model of forest dynamics, citing studies demonstrating the role of ecological facilitation. He suggests that the facilitation concept may have been abandoned by some researchers simply because of its neo-Clementsian connotations. He is critical of the neo-Gleasonian reductionist approach, stating that stochasticism is "a disorganizing power as elusive as the emergent properties of the holists". Despite such criticisms, a common consensus has emerged in the recent literature on forest succession (Finegan 1984; McCook 1994; Cook 1996). Most recently-developed models recognize that a Clementsian climax community is rarely achieved, that multiple successional pathways are possible, and that retrogression or the arresting of succession can occur. Spatially and temporally varying stochastic factors are generally recognized as being important in forest dynamics, the cumulative effects of which make prediction more difficult.

Modelling forest dynamics requires a pluralistic approach incorporating the life history characteristics of the dominant tree species found within an ecosystem (Pickett et al. 1987). Repeated observations over successional time are needed to unequivocally describe forest stand dynamics, but unfortunately such data are rarely available. An alternative approach is to infer successional trajectories by enumerating stands of various ages, an approach known as chronosequencing. This approach assumes minimal confounding of environmental factors, and the existence of a single underlying successional trajectory. If environmental variation occurs and/or multiple successional pathways are possible, chronosequencing may produce misleading and over-simplistic trajectories. Another limitation of chronosequencing is that late-successional stands are often poorly represented, particularly in disturbance-driven ecosystems. In the boreal forest, late-successional stands are restricted to small, fire-protected habitats such as islands, gullies, and the leeside of large lakes (Heinselman 1973). A second approach involves utilizing size-age class distributions of trees to infer successional trajectories, under the assumption that all species have similar mortality, natality and growth rates, and similar life-history strategies (Horn 1976). While these assumptions are clearly untenable, age-class distributions do offer a crude indication of potential stand dynamics. An approach combining chronosequencing and size-age class analysis has been widely used to infer successional trajectories in boreal forest ecosystems (e.g. Dix & Swan 1971; Grigal & Ohmann 1975; Carleton & Maycock 1978; Cogbill 1985; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990). However, our understanding of vegetation dynamics in boreal forest ecosystems is limited and subject to criticism (Bonan & Shugart 1989). In the absence of long-term permanent plot data, investigations of boreal forest dynamics require an underlying theory to provide guidelines for the collection and interpretation of data (Johnson 1979).

In this contribution, we provide an overview of boreal forest succession and provide guidelines for the development of a synoptic, conceptual model of boreal stand dynamics. Our approach is to synthesize the ecological theories and ideas that we feel pertain to boreal forest ecosystems. The discussion is based on the published literature, and on data collected by our laboratory as part of an ongoing program to develop predictive boreal forest succession models. These data were collected in south-eastern and western Manitoba, north-west and east-central Ontario, and the montane regions of south-west Alberta. Using this information, we develop a conceptual framework that incorporates the complex interrelationships between biological and environmental processes at various spatial and temporal scales.

2. Succession Theory and the Boreal Forest

Rowe (1961) was the first scientist to critically apply succession theory to boreal forest ecosystems. He characterized the boreal forest as a disturbance-driven system, in which catastrophic fires are so frequent that Clementsian successional concepts are probably not tenable (Bonan & Shugart 1989). He also noted that while boreal fires are catastrophic at the stand level, they promote heterogeneity at the landscape scale and maintain stand health and vigour. Rowe recognized the importance of stochasticism, site history, edaphic conditions, and species life-history characteristics in determining forest stand composition and dynamics, and speculated that multi-directional successional trajectories are likely in boreal forest ecosystems (Heinselman 1973, 1981).

Dynamics of Forest Structure and Composition

Cogbill (1985) used age-class distributions to establish patterns of stand development in east-central Québec. He found that ca. 70% of tree recruitment occurs in the first 30 years following a fire, from which he concluded that "apparent succession is simply an expression of differential longevity and conspicuousness of species". In other words, changes in boreal forest canopy composition over time are simply a reflection of differential growth rates of individuals that established contemporaneously. This conclusion is suggestive of the Eglerian 'complete initial floristics' model (Wilson et al. 1992). Similar results were obtained by Bergeron & Dubuc (1989) in west-central Québec. Although these authors found some evidence of successional convergence, they concluded the true self-replacement (i.e. the climax community concept) does not occur in boreal ecosystems. In their study, all tree species were present within the first 50 years following fire, and forest stand composition was similar to that before the burn. They concluded that both 'initial floristic composition' (Egler 1954) and 'tolerance' (Connell & Slatyer 1977) models of succession were applicable to boreal forest ecosystems (see also Bergeron & Dansereau 1993; Galipeau et al. 1997).

A number of studies have used chronosequencing and size-age class distribution analysis to infer boreal forest successional trajectories. Carleton & Maycock (1978) concluded that boreal forest stand trajectories were generally short, circular and somewhat divergent. Cogbill (1985) states that young stands of 'pioneer' species such jack pine, trembling aspen, and white birch are (in theory) transitional stages toward forests dominated by balsam fir and/or black spruce. However, he observed that older upland stands are invariably "decadent", displaying "rapid deterioration and degeneration" and limited regeneration. Zoladeski & Maycock (1990) found continuous recruitment of balsam fir into most stands. They hypothesized that stands of both trembling aspen and jack pine develop toward a mixed black spruce-balsam fir forest, but that fire will normally halt such a trend. Bergeron & Dubuc (1989) found that the lower canopy layers of established stands were dominated by balsam fir and white cedar, suggesting that these species have a 'later successional' status (see also Grigal & Ohmann 1975). In the absence of fire, the authors hypothesized that mesic and hygric upland sites will be dominated by balsam fir and white cedar, while white cedar and black spruce will predominate on xeric sites. However, they also recognized that patch dynamics (the result of windthrows, spruce budworm outbreaks, and so forth) may alter these 'ideal' successional pathways. Bergeron & Dansereau (1993) concluded that deciduous stands become increasingly dominated by conifers if fires are infrequent. However, this trend is periodically interrupted by outbreaks of spruce budworm, resulting in a patchwork mosaic of mixed coniferous-deciduous forest at the landscape scale. Heinselman (1973, 1981) noted that considerable variation exists in the stand dynamics of northern Minnesota forests. For example, some red and jack pine stands showed evidence of early invasion by balsam fir and white cedar, while others showed no such invasion after 350 years.

Factors Contributing to Differences in Successional Dynamics

A number of studies have demonstrated considerable variation in the successional dynamics of boreal forest stands (e.g. Heinselman 1973, 1981; Carleton & Maycock 1978; Cogbill 1985; Zoladeski & Maycock 1990). Potential factors contributing to this variation include seed availability, soil physical structure and nutrient status, ungulate herbivory, granivory, insect pests and fungal pathogens, light availability, rooting space, and seedbed quality (Heinselman 1973; DeGrandpré et al. 1993; Galipeau et al. 1997). Accumulations of surface organic litter and/or high bryophyte cover may limit recruitment by retarding germination and seedling establishment (Cogbill 1985). The development of a dense shrub layer may have a similar effect (Zoladeski & Maycock 1990).

Species Life-History Characteristics and Vital Attributes

Dix & Swan (1971) attempted to explain the composition and dynamics of Saskatchewan boreal forests in terms of the vital attributes and life-history characteristics of major tree species. They proposed that most boreal forest trees are 'pioneers', defined as species that do not normally regenerate beneath themselves. Included in this category are trembling aspen, jack pine, white birch, and balsam poplar (see also Bergeron & Dubuc 1989). Black and white spruce were deemed to be 'chiefly pioneer', since their presence in the subcanopy is often the result of suppression by canopy dominants rather than continuous establishment. They proposed that balsam fir is the only late-successional boreal tree species, although they noted that this species rarely dominates the upper canopy. However, Rowe (1961) suggests that no western Canadian boreal tree possesses all the attributes required of a self-perpetuating climax species, and that most species are adapted to recurrent catastrophic fires every 50-100 years. By contrast, in the boreal forests of Québec both balsam fir and white cedar appear to have the vital attributes (longevity, shade tolerance, ability to establish on organic substrates) characteristic of late-successional species (Bergeron & Dubuc 1989).

3. The Role of Climate Change

The boreal forest ecosystem is characterized by a continental climate of short, cool to moderately warm summers and long, cold-severe winters. The southern border of the boreal forest corresponds roughly to the mean January position of the Arctic Front separating dry, cold Arctic air from the comparatively warm, moist Pacific airmasses. In northern Ontario, the boundary between the Boreal and Great Lakes-St. Lawrence forests corresponds roughly to the 2°C mean annual isotherm (Liu 1990). The floristic composition of the boreal forest is strongly affected by climate; indeed, the dominance distribution of several boreal tree species can be accurately predicted using climatic variables such as air temperature and moisture availability (Lenihan 1993). Climatic variables also influence soil thermal regime and moisture content, which in turn determine rates of decomposition and nutrient cycling (van Cleve et al. 1983; Prescott et al. 1989). Climate also determines the frequency and intensity of forest fires, thereby affecting forest stand dynamics and the evolution of life-history strategies.

Vegetation Recolonization

Most of boreal North America was glaciated as recently as 11,000 years before present (BP). The early postglacial forest was dominated by white spruce, although oak, elm and poplar were also present. It is thought that the base-rich, unleached soils of newly deglaciated substrates favoured white spruce over black spruce (Liu 1990). Continued climate warming after 9000 BP resulted in the replacement of white spruce by jack pine, and the invasion of shade-intolerant shrubs and herbs. In eastern Canada, the much warmer and drier climate of the Hypsithermal (beginning 7400 BP) favoured the northward expansion of Great Lakes-St. Lawrence tree species such as white pine, eastern hemlock, beech and white cedar (Delcourt & Delcourt 1987). In western Canada, the drier conditions led to an expansion of grasslands at the expense of boreal forest. This northward expansion continued from 7000-3000 BP, moving the southern boreal ecotone to ca. 150 km north of its present position (Ritchie & Yarranton 1978; Liu 1990). By 3000 BP, neoglacial cooling resulted in much wetter, cooler conditions. This sudden change in climate eliminated most of the northern populations of white pine and white cedar while favouring the spruces, jack pine and balsam fir. As a result, the boreal ecotone retreated dramatically between 3000-2500 BP, and continued to do so until it reached its present position about 1000 BP (Liu 1990).

Vegetation recolonization of the post-glacial boreal landscape has been affected by a number of interacting factors. At the ecosystem scale, species recolonization was influenced by glacial refugia in the eastern and western North America. For example, jack pine recolonized from the southeast, whereas the refugium for lodgepole pine was in the south-western cordilleran region. Barriers to the movement of species were also critical. Potential barriers include surficial features such as mountain ranges and large glacial lakes, and variation in climate, substrate type, and fire frequency. For example, a number of species reach their western limit in the boreal forests of northwest Ontario and southeast Manitoba, including red and white pine, white cedar, black ash, bigtooth aspen and mountain ash, as well as a number of understory species. This western distributional limit corresponds roughly to the shore of glacial Lake Agassiz, to a change in surficial geology from granite to limestone, to increased fire frequency, and to a drier environment. It is possible that boreal vegetation has not yet reached an equilibrium with climate, implying that recolonization is still occurring from the south and that vegetation-environmental relationships are not full developed (Ritchie 1986; Prentice 1986).

4. Vegetation-environment Relationships

Landscape and Landform

The post-glacial landscape of boreal North America is highly variable. Much of the eastern boreal forest is characterized by shallow, sandy tills over early-Precambrian granitic bedrock (known colloquially as the 'Canadian Shield'). Granitic parent materials produce soils that are acidic and nutrient-deficient. Areas of coarse glacial outwash (material deposited by meltwaters along an icefront) are also common in the boreal forest. Lacustrine clay deposits occur in areas flooded by glacial lakes, including southern Manitoba, northwest Ontario, eastern Ontario and western Québec. The boreal forest west of central Manitoba occurs over basic parent materials such as shale, limestone and glacial till, resulting in less acidic conditions and higher nutrient availability. Subsequent modification of the post-glacial landscape has occurred from erosion processes, alluvial deposition, soil profile development, bog and dune formation, frost action, and the damming of watercourses by beaver.

Landform, which incorporates parent material and surficial topography, determines insolation and drainage patterns at the landscape level (Heinselman 1973; Foster & King 1986). These patterns in turn affect soil development, nutrient and moisture status, community composition, and prevailing disturbance regimes (Ritchie 1956; Viereck 1983). Landform is therefore an important determinant of the distribution, abundance and regeneration dynamics of boreal forest species (Heinselman 1973, 1981; Host et al. 1987; Bergeron & Brisson 1990; Frelich & Reich 1995). Many areas of the Canadian Shield are topographically variable, resulting in high levels of habitat diversity and ecosystem complexity (Clayden & Bouchard 1983; Foster & King 1986; Frelich & Reich 1995). By contrast, regions of low topographic relief are more frequently and evenly burned, resulting in extensive stands dominated by one or a few fire-tolerant tree species (Carleton & Maycock 1978). Fire-intolerant 'late-successional' species such as balsam fir, white spruce and white cedar are often rare or absent from such areas (Bergeron & Dubuc 1989). The absence of a seed source may severely limit successional trajectories (Heinselman 1973; Grigal & Ohmann 1975; Galipeau et al. 1997), allowing competively subordinate species to occupy habitats from which they might otherwise be excluded (Hurtt & Pacala 1995).

Edaphic Factors

Factors such as soil particle size, nutrient status, and organic matter accumulation are important determinants of species composition and regeneration dynamics in boreal ecosystems (Carleton & Maycock 1978; Cogbill 1985; Kenkel 1987; Zoladeski & Maycock 1990). Pine species and black spruce are commonly found on well-drained and nutrient-deficient sandy soils, whereas more fertile, fine-textured silts and clays generally support stands of white birch, trembling aspen, white spruce and/or balsam fir. Lowland areas may accumulate considerable amounts of poorly-decomposed organic peats, impeding drainage and tying up essential nutrients (Heilman 1966; Heinselman 1981). Peat substrates are often dominated by black spruce, although eastern larch may be favoured on more minerotrophic sites. Alluvial organic soils usually support stands of white cedar, black ash or balsam poplar. Because high acidity reduces soil nutrient availability, acidic substrates are generally dominated by pines, black spruce, ericaceous shrubs, feathermosses and other species tolerant of nutrient deficient conditions. In the far north, permafrost determines the northern distributional limits of deep-rooted species such as the pines, white birch and trembling aspen (Viereck 1983). Tree-line species (white and black spruce, balsam poplar) have relatively shallow root systems (van Cleve et al. 1993).

Low decomposition rates in boreal forest ecosystems are attributable to the combined effect of a short growing season and suboptimal substrate conditions (van Cleve et al. 1983; Prescott et al. 1989). Poor decomposition in peat bogs, for example, is attributable to a combination of cold temperatures and an anaerobic, acidic substrate (Heilman 1968). In dry uplands, the accumulation of acidic conifer detritus reduces nutrient availability over time (Par et al. 1993). Increased feathermoss cover further ties up nutrients, and creates a substrate less suitable to sapling establishment. Decomposition and nutrient cycling rates are higher in more mesic sites, particularly if deciduous litter predominates. A deciduous litter also limits development of a continuous feathermoss layer, resulting in more favourable seedbed conditions (Par et al. 1993).

The dynamics of boreal mixed-wood stands may be driven by changes in nutrient availability over time (Pastor et al. 1987). In addition, forest stand composition may directly affect soil development. In northern Hungary, the invasion of deciduous trees during postglacial climatic warming triggered a conversion from podzol to brown-earth soils (Willis et al. 1997). This synergistic feedback between vegetation and soil development is critical to understanding boreal forest composition and dynamics. Modification of soils by vegetation may favour some species while inhibiting others. For example, the accumulation of peat or feather moss favours black spruce over other species. The accumulation of dry, poorly-decomposed litter in jack pine stands promotes hot catastrophic fires, favouring pine regeneration while at the same time retarding soil development. Conversely, trembling aspen produces a readily decomposed litter, thus promoting nutrient recycling and soil development.

5. The Role of Disturbance

Fire

Many comprehensive reviews of the role of fire in boreal forest ecosystems are available (Rowe & Scotter 1973; Heinselman 1973, 1981; Wein & MacLean 1983; Bonan & Shugart 1989; Johnson 1992). At the landscape level, fire is undoubtedly the most important disturbance feature of boreal forests (Ritchie 1956; Dix & Swan 1971; Heinselman 1973; Carleton & Maycock 1978; Wein & MacLean 1983; Payette 1992). In the absence of human intervention, fire cycles in North American upland boreal forests range from < 50 years in many areas (Hirsch 1991) to >200 years in poorly-drained bogs, swamps and marshes (Payette 1992). While forest fires occur throughout the boreal forest, burn frequency and intensity vary widely (Heinselman 1973). The net result is a landscape of forest patches at different successional stages, where each patch has a unique fire history. The long-term cumulative effects of repeated fires exert a strong influence on vegetation composition and dynamics at a given site (Heinselman 1973; Cogbill 1985; Bergeron & Dubuc 1989).

Floristic composition (La Roi 1967; Dix & Swan 1971) and vegetation dynamics (Ritchie 1956; Wright & Heinselman 1973; Carleton & Maycock 1978; Bergeron & Dansereau 1993; DeGrandpré et al. 1993; Shafi & Yarranton 1973) are directly affected by the frequency and intensity of boreal forest fires. Boreal landscapes are a mosaic of communities adapted to fire cycles of varying duration. Under short fire cycles, 'pioneer' species that endure or evade fires tend to dominate, whereas 'seed-banking' fire-intolerant species are favoured in areas where fires are less frequent and/or severe (Zasada et al. 1992). Dix & Swan (1971) noted that the fire intervals in boreal Saskatchewan are normally well within the lifespan of the dominant tree species. They hypothesized that recurrent catastrophic fires 'stabilize' the floristic composition of a site, resulting in a post-fire vegetation that is floristically similar to that found before a fire. Carleton & Maycock (1978) note that upland sites in boreal Ontario are usually dominated by young monocultures of pioneer tree species adapted to recurrent fires. They conclude that a self-regenerating vegetation complex is meaningless in boreal ecosystems, that fire must be considered as an integral part of the ecosystem, and that boreal forest composition and dynamics reflect species adaptations to recurrent and unpredictable fire events (see also Zoladeski & Maycock 1990).

Payette (1992) describes the boreal flora as consisting of robust 'generalist' species capable of withstanding recurring, severe environmental change. A common life-history adaptation to recurrent fire (seen in jack, lodgepole and red pines, and black spruce) is the production of fully to semi-serotinous cones (Muir & Lotan 1985). White birch, balsam poplar, and trembling aspen, and most boreal shrubs and forbs, reproduce both vegetatively and from seed (Zasada et al. 1992). Trembling aspen suckers following a fire, and continues to do so until stands are overmature (Peterson & Peterson 1992). With the exceptions of balsam fir, larch and black spruce (Frelich & Reich 1995), boreal tree species require an exposed mineral substrate for successful germination and establishment. The burning of accumulated organic litter during a fire exposes the required mineral seedbed (Johnson 1992).

The general successional path of a boreal stand is dependent on fire cycle duration, with frequent fires favouring resprouting, shade-intolerant species and seed-banking ephemerals. Bergeron & Dubuc (1989) and DeGrandpré et al. (1993) proposed that convergent succession only occurs if seeds of shade-tolerant trees are available, noting that such a seed bank is often not present in stands subject to recurrent catastrophic fires. Shade-tolerant boreal trees such as balsam fir and white cedar, which are frequently encountered in the regenerating layers of established stands, are often assumed to form a "climax" community in the absence of fire (Ritchie 1956; LaRoi 1967; Dix & Swan 1971; Grigal & Ohmann 1975; Carleton & Maycock 1978; Cogbill 1985). This rarely occurs, however, since fire almost invariably interrupts such a successional process (Zoladeski & Maycock 1990).

Herbivory and Pathogens

Connell & Slatyer (1977) note that successional mechanisms are generally based on plant-plant interactions, while other biotic interactions such as herbivory have been ignored. Ungulate herbivores are selective in their choice of browse and can potentially alter understory composition and successional trajectories (Pickett et al. 1987; Hobbs 1996). Moose show a strong preference for balsam fir in winter (Belovsky 1981), whereas white-tailed deer prefer white cedar (Grigal & Ohmann 1975). In Riding Mountain National Park, balsam fir saplings and trembling aspen suckers are actively sought out by moose, elk and white-tailed deer, limiting the regeneration of these species in older stands. Elk have a similar effect on interior douglas-fir and trembling aspen in Banff National Park. Squirrel granivory also appears to be important in these Parks. Beaver activity plays an important role in boreal forest dynamics at more localized spatial scales. Damming activity kills trees in flooded low-lying forests and has adverse effects on downstream hydrology (Naiman 1988). Beaver activity also results in the removal of trembling aspen and willows from the catchment area, favouring conifer regeneration.

Insect herbivores may also alter boreal forest successional trajectories. Spruce budworm selects for balsam fir and white spruce, while the larch sawfly decimated eastern larch stands in the mid-1930's. Periodic infestations of spruce budworm kill mature balsam fir, releasing seedlings and favouring the regeneration of less shade-tolerant species such as white birch, black spruce and white spruce (Holling 1973; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Frelich & Reich 1995). It is hypothesized that spruce budworm and balsam fir form an interdependent, self-regulating system in which cyclical budworm outbreaks confer long-term ecological stability (Morin 1994; Bergeron et al. 1995; Su et al. 1996). A large number of fungal pathogens have been recorded on boreal forest trees (eg. Peterson & Peterson 1992). Parasitic dwarf mistletoes attack boreal tree species (particularly jack pine and white spruce) in western regions of the boreal forest.

Forest Gap Dynamics

Windthrow is relatively common in the boreal forest, affecting shallow-rooting species such as white spruce and white pine as well as trees growing on rock outcrops (particularly jack pine and black spruce). The exposure of mineral soil that results from a windthrow may be important in boreal forest regeneration dynamics, since many boreal trees require a mineral seedbed for their establishment (Jonsson & Dynesius 1993; Galipeau et al. 1997). Like windthrow, pathogens may open up gaps in the forest canopy by killing individual trees. While there are numerous studies of the role of gap dynamics in temperate and tropical forests, few such studies have been undertaken in the boreal forest. Frelich & Reich (1995) note that boreal stand dynamics is dependent on the timing and frequency of small-scale disturbances, as these create canopy gaps that allow late-successional species to invade. Forest gaps may be created by windthrow, snow and winter storm damage, insect pests, fungal pathogens or dwarf mistletoe.

Spatio-Temporal Scaling of Disturbances

Disturbances in boreal forest ecosystems occur at various spatial and temporal hierarchical scales. Furthermore, the intensity of these disturbances varies in both space and time (Ohmann & Grigal 1981). In boreal forests, the term 'site history' refers to the unique set of cumulative disturbance events that have occurred at a given site since glaciation. These disturbances are hierarchically layered across the landscape, resulting in a complex spatial mosaic of disturbance histories (Fig. 1). The disturbance history of a given

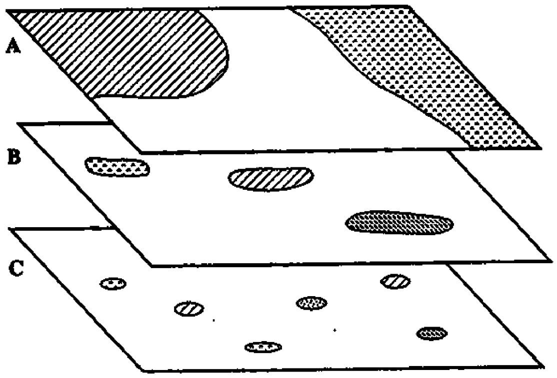

Figure 1. A simplified illustration of a spatio-temporal disturbance hierarchy in a boreal forest landscape. Three spatial disturbance hierarchies (A = fire, B = insect damage, and C = individual tree mortality) are shown; temporal variation is represented by different shadings. Note that each location on the landscape will develop a unique disturbance regime over time.

site is dependent upon a number of factors, including landform features, climate, and biotic interactions (e.g. herbivory, pest and pathogens). These cumulative disturbance events shape the 'evolution' of the community, and in doing so determine species composition and life-history characteristics. It follows that the suppression of natural disturbances such as fire may have important consequences on subsequent community development. Frelich & Reich (1995) hypothesize that, in the absence of natural fire, fine-scale (10-30 m) canopy disturbances caused by windthrow, insect pests, and pathogens will come to drive long-term boreal forest dynamics. Canopy openings are colonized by later-successional species, with the result that uniform, even-aged pine or trembling aspen canopies are gradually "chipped away" over time. This implies that boreal forest canopies become more spatially complex over time, a result that we recently confirmed for the boreal forests of Riding Mountain National Park. Frelich & Reich (1995) also note that stands deemed to be 'pure' at fine scales are part of a more complex mosaic at coarser spatial scales. Thus the nature and perception of successional dynamics is scale-dependent. A robust forest succession model should therefore incorporate both spatial scaling and changes in vegetation pattern at the landscape level.

6. Persistence and Forest Succession

The majority of boreal forest succession studies have focussed on the period between catastrophic fire events, under the assumption that fire is the end-point of succession. However, it is recognized that post-fire floristic composition often reflects that present before a fire (Rowe 1961; Dix & Swan 1971; Ohmann & Grigal 1981), suggesting strong carry-over effects in the dynamics of boreal forests. It follows that boreal forest succession models should consider the 'site history' or long-term 'evolution' of a stand. A ca. 10,000 year old post-glacial forest, for example, reflects the cumulative effects of ca. 1,000 catastrophic fires occurring every 100 years (on average). Following glacial retreat, the initial colonizers of a site contribute to the propagule base (seeds, vegetative parts) and determine and/or modify subsequent soil development. The initial colonizers are therefore expected to exert strong carry-over effects on subsequent stand development. Recurrent catastrophic fires may further 'stabilize' the floristic composition at a site (Dix & Swan 1971), resulting in strong temporal autocorrelation in boreal forest composition. Although the degree of temporal autocorrelation in boreal forest composition between fire events is poorly understood, fire severity and timing appear to be critical (e.g. Ohmann & Grigal 1981).

Measures of 'persistence' are used to quantify the temporal autocorrelation (sensu lato) of nonperiodic events (Hastings & Sugihara 1993). The concept of persistence is most easily illustrated by considering possible time-series traces (Schroeder 1991). White noise is defined when successive values in a temporal series are completely uncorrelated. The power spectrum of white noise is independent of frequency, implying that the system lacks memory or 'persistence'. The integral of white noise produces a trace known as 'brown noise', which is also known as a Brownian or 'random walk' trace since it represents the projection of Brownian motion onto a single dimension. Brown noise shows only short-term persistence, reflecting a weak information storage capacity. More generally, consider the expected change in V (vegetation composition) over a given time interval $\Delta t = t_2 - t_1$ (two fire events). Vegetation change $\Delta V = V(t_2) - V(t_1)$ as a function of time can be expressed using a scaling law:

$$\Delta V \propto \Delta t^H \qquad (1)$$

where H is the Hurst exponent. For white noise $H = -0.5$, while for brown noise $H = 0.5$. Natural geophysical time series generally have values of $H > 0.5$ and are termed 'black noise' (Schroeder 1991). Such temporal series exhibit nonrandom behaviour and 'infinite memory', with higher H values reflecting greater long-term memory or persistence in the system. We submit that boreal forest stands generally exhibit a high degree of temporal persistence between catastrophic fire events, attributable to the combined effect of evolved vegetation-environment relationships and available propagule sources. For example, jack pine stands on xeric, nutrient-poor sandy sites tend to be perpetuated as a result of evolved species life-history traits such as tolerance of xeric, nutrient deficient conditions and cone serotiny. The result is long-term persistence of this vegetation type, provided that catastrophic fires occur with sufficient frequency.

The term 'site-history' is also interpretable in terms of chaos theory (Godfray & Grenfell 1993). The recurrent themes of chaos theory are that seemingly random variation may in fact be deterministic, and that long-term trajectories

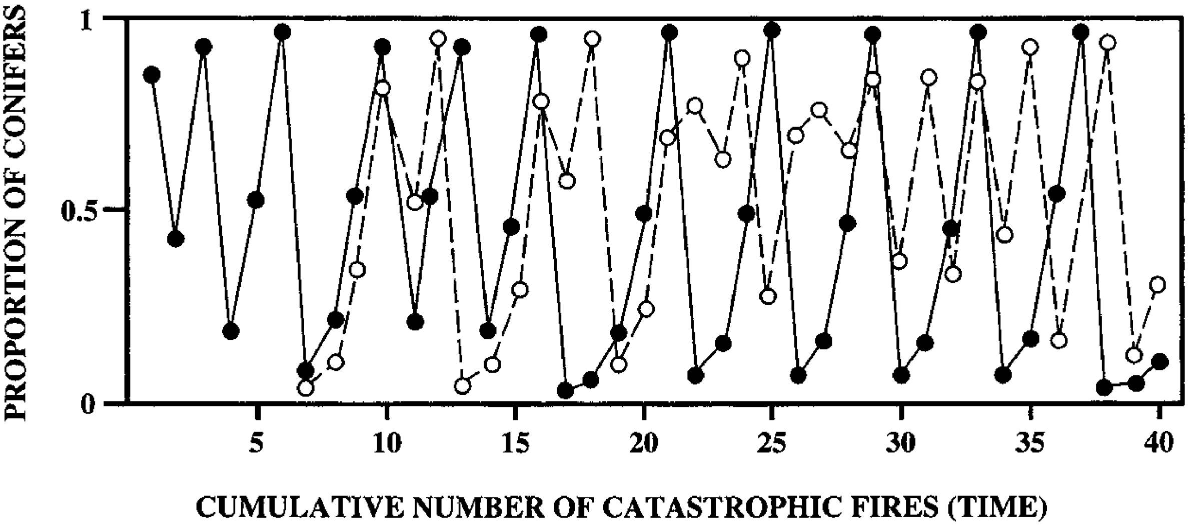

Figure 2. Illustration of chaotic behaviour in boreal forest dynamics. Two stands (closed and open circles) begin with virtually the same proportion of conifers in the canopy (ca. 80%). By the seventh generation the two stands have diverged, and trends thereafter quickly become independent. The example utilizes the first-order nonlinear difference 'logistic' equation [3] from May (1976).

are highly dependent on initial conditions (May 1976). Thus small initial differences in vegetation composition may be accentuated over time (Fig. 2), even if sites occur on similar substrates. When combined with high persistence, the result is a landscape of divergent vegetation types in what was initially a comparatively homogeneous post-glacial environment.

7. Changes in Disturbance Regime

Fire suppression is being practiced in many parts of the North American boreal forest, but little is known about the long-term consequences of suppressing this recurrent natural disturbance. Dramatic effects are expected, since most boreal species have life-history characteristics reflecting adaptation to catastrophic fires. Such characteristics will prove maladaptive under a fire suppression scenario. Fire suppression results in a paradigm shift in the disturbance regime of boreal forest stands (Fig. 3), from broad-scale, frequent and synchronous catastrophic disturbances (pyric ecosystems) to small-scale, asynchronous disturbances (patch-dynamic ecosystems). The long-term effects of this paradigm shift are difficult to predict, although jack pine and other species dependent on recurrent catastrophic fires will most certainly be adversely affected (Heinselman 1973). Frelich & Reich (1995) propose that fire suppression has increased the importance of canopy gap succession dynamics. However, the natural disturbance history of boreal forest ecosystems has favoured the evolution of 'ruderal' rather than 'competitor' life history strategies (sensu Grime 1977). As a result, few boreal forest tree species are 'secondary' colonizers adapted to establishing and growing under a forest canopy or invading small gaps (Rowe 1961). Balsam fir has such 'secondary' characteristics, but generally only forms stands in more mesic, mesotrophic environments. Not coincidentally, such environments are less prone to catastrophic fires. In the absence of fire, black spruce may come to dominate both upland and lowland oligotrophic boreal habitats.

8. Modelling Boreal Forest Dynamics

The vegetation at a given site is a function of a number of factors, including time since last catastrophic disturbance, site disturbance history, propagule availability, non-catastrophic disturbances (herbivory, granivory, pests and pathogens), edaphic factors, physiography, and climate. As a result, the boreal forest landscape consists of a complex mosaic of plant communities at varying successional stages. Modelling such a system is a formidable challenge, particularly given our state of knowledge of boreal forest dynamics and the probable importance of both persistence and chaotic dynamics. Despite these challenges, predictive models of boreal forest dynamics are required for management purposes. Pickett et al. (1987) developed a comprehensive hierarchical framework that includes three "general causes" of succession: site availability, differential species availability, and differential species performance. We briefly summarize these three causes as they relate to boreal forest dynamics.

Site Availability

The process contributing to site availability is 'coarse-scale' ecosystem disturbance (Pickett et al. 1987). The size, intensity (severity), frequency and timing of fire are of overriding importance in boreal ecosystems, although spruce budworm infestation is a consideration in some areas.

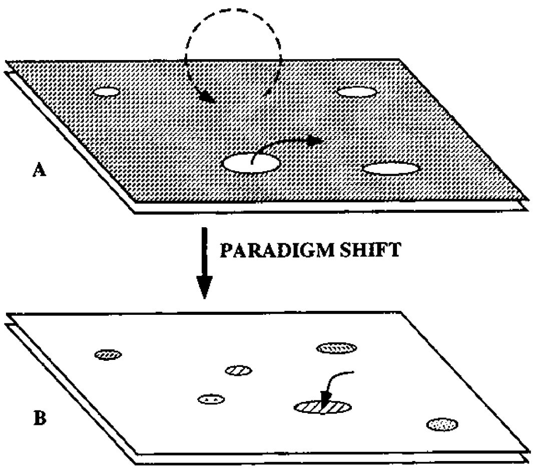

Figure 3. Paradigm shift in boreal forest dynamics. Under the usual synchronous catastrophic fire regime (A), most of the landscape is burned (shaded areas) although some regions escape fire (unshaded areas). Regularly burned areas quickly reestablish from serotinous seeds or vegetative regrowth (dotted arrow). Later-successional species present in the unburned areas colonize the reestablished stands (arrow), but are normally extirpated by a second catastrophic fire. The landscape is therefore dominated by disturbance-tolerant pioneer species (shaded areas), while late-successional species are restricted to infrequently burned areas (unshaded areas). With fire suppression, a paradigm shift in disturbance dynamics occurs (B). The shaded area in A is eventually colonized by later-successional species. Disturbances are local and asynchronous (various shadings in B); the system is now driven by forest gap dynamics (arrow), and pioneer species are eventually extirpated.

Landscape physiography will affect the size, intensity and frequency of catastrophic fires. Scaling effects, and the cumulative effects of recurrent disturbance events, must also be considered. While some investigators have examined boreal forest succession at a coarse spatial scale (e.g. Carleton & Maycock 1978; Cogbill 1985; Zoladeski & Maycock 1990), others have focussed on smaller regional landscapes (e.g. Dix & Swan 1971; Heinselman 1973, 1980; Bergeron & Dubuc 1989; Grigal & Ohmann 1975). Local models are not robust, but more global models offer poor prediction at the stand level.

Differential Species Availability

Factors affecting species availability include propagule dispersal into a site, the propagules available at a site, and site resource availability (Pickett et al. 1987). The available propagule pool is the most important factor in sites subject to recurrent catastrophic fires. Species that quickly recolonize a site are favoured: recolonization may be from buried seed, from serotinous seeds dispersed a short distance (e.g. jack pine), or from underground vegetative parts (e.g. trembling aspen). The available species pool is largely a reflection of site disturbance history. Propagule dispersal into a site is more important if a fire is very severe, and during later stages of boreal forest succession. Species that are not well adapted to recurrent catastrophic fires (e.g. white spruce, balsam fir) produce prodigious amounts of wind-dispersed seed that may invade into older stands. The rate and degree of invasion are largely a function of seed source availability (Galipeau et al. 1997). In general, greater landscape complexity results in a greater juxtapositioning of stand types and higher seed source availability. By contrast, the vast uniform stands of early-successional species that dominate regions of low landscape complexity are very slowly (if at all) invaded by later-successional species (Carleton 1982). Propagule availability may also be affected by herbivore-granivore activity. Edaphic conditions may also be important. Much of the boreal forest occurs on young, poorly-developed soils of low nutrient status, but relatively few species have adapted to such conditions. Species requiring higher nutrient levels generally have much more restricted distributions within the boreal forest. Climatic extremes may further limit species distributions in the boreal forest.

Differential Species Performance

Differential species performance includes factors such as ecophysiology (germination requirements, growth rates), life-history strategies, environmental stress, competition and allelopathy, herbivory, and pest and pathogen attack (Pickett et al. 1987). Fire suppression results in a shift in the processes controlling boreal forest dynamics, increasing the importance of competition and other mechanistic processes. Numerous boreal forest succession studies have revealed some general trends in species performance. The following summary is based on the available literature, and on our recent studies in northwest Ontario and western Manitoba.

Jack Pine Stands

These stands generally occur on excessively-drained, oligotrophic habitats such as sandy substrates and rock outcrops. In highly xeric habitats, jack pine stands often 'degenerate' over time, becoming open and savannah-like with only very limited recruitment by black spruce and balsam fir (Carleton & Maycock 1978). In less xeric habitats black spruce often regenerates beneath jack pine, but regeneration patterns vary widely (Carleton 1982; Kenkel 1986; Zoladeski & Maycock 1990). Mixed jack pine-black spruce stands are thought by many scientists to represent a successional stage toward fir-spruce dominance (Ritchie 1956; Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990). Balsam fir recruitment often does not occur until at least 30 years following stand initiation, and may increase over time (Foster & King 1986; Frelich & Reich 1995; Galipeau et al. 1997). However, balsam fir rarely enters into the canopy due to the combined effects of low nutrient availability, ungulate herbivory, and spruce budworm infestation (Blais 1983; Bergeron & Dansereau 1993). Because jack pine is a pioneer pyric species, the species is locally extirpated if fire cycles exceed 200 years (Heinselman 1973; Cogbill 1985; Bergeron & Dubuc 1989).

Black Spruce Upland Stands

These stands usually occur on acidic, oligotrophic, mesic substrates. Such stands often become more open with time, but undergo little compositional change as they age (Carleton & Maycock 1978; Zoladeski & Maycock 1990). Some stands show limited recruitment of balsam fir and white birch at later successional stages (Cogbill 1985), and more mesotrophic sites may be invaded by white cedar (Grigal & Ohmann 1975; Bergeron & Dubuc 1989). Oligotrophic and acidic substrate conditions lead to increased dominance of black spruce and ericaceous shrubs over time, and the accumulation of feathermosses.

Black Spruce Bogs

These stands occur on deep, moist peat-organic substrates where oligotrophic and acidic conditions prevail. Black spruce bogs become more open over time as peat mosses and ericaceous shrubs become increasingly dominant. Black spruce regenerates well through layering, but few other tree species are able to establish in these environments (Cogbill 1985; Zoladeski & Maycock 1990). Eastern larch is a highly shade-intolerant species that is rarely present in older bogs, although saplings may be encountered if sufficient light is available. White cedar may occur in less acidic, mesotrophic sites that are subject to water-level fluctuations (Kenkel 1987).

Mixed Wood (Fir-Spruce-Birch) Stands

These stands are typically found on fine-textured, slightly acidic to basic soils of moderate nutrient status. They are characterized by continuous, high recruitment of balsam fir, and low to moderate recruitment of white and black spruce (Zoladeski & Maycock 1990). It has been hypothesized that white birch stands represent an earlier successional variant, since balsam fir recruitment into birch stands is often high (Carleton & Maycock 1978; Frelich & Reich 1995). In Saskatchewan, balsam fir rarely occurs in the upper canopy although it is often frequent in the lower canopy (Dix & Swan 1971). White spruce is a long-lived species that has characteristics of both a colonizer and 'climax' species (Dix & Swan 1971; Lieffers et al. 1996). It rarely forms pure stands, however.

Trembling Aspen Stands

These stands typically occur on moderately-drained sandy loams and finer-textured soils of moderate nutrient status. Trembling aspen is the dominant deciduous tree species in the North American boreal forest. It remains the canopy dominant for at least 100 years (Heinselman 1973; Cogbill 1985). However, aspen regeneration beneath a closed canopy is low since the species is highly shade-intolerant. Propagation is mainly from vegetative root-suckers that are produced for 250 years or more (Kneeshaw & Bergeron 1996). However, aspen suckers are a favoured ungulate browse, which may limit successful regeneration of the species (Peterson & Peterson 1992). Pure stands of trembling aspen gradually deteriorate and may become "decadent", showing sparse tree regeneration and increased shrub dominance (Zoladeski & Maycock 1990). Alternatively, stands may be invaded by shade-tolerant conifers such as balsam fir and white spruce (Carleton & Maycock 1978; Cogbill 1985). Early recruitment of white spruce into aspen stands occurs if there is a nearby seed source. Otherwise, recruitment is delayed and tends to be highly episodic (Lieffers et al. 1996). Similarly, recruitment of balsam fir into aspen stands is highly dependent on seed source proximity (Carleton & Maycock 1978; Frelich & Reich 1995; Galipeau et al. 1997).

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References

Belovsky, G.E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020-1030.

Bergeron, Y. & J. Brisson. 1990. Fire regime in red pine stands at the northern limit of the species range. Ecology 71: 1352-1364.

Bergeron, Y. & P-R Dansereau. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. J. Veg. Sci. 4: 827-832.

Bergeron, Y. & M. Dubuc. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79: 51-63.

Bergeron, Y., A. Leduc, H. Morin, & C. Joyal. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. 25: 1375-1384.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13: 539-547.

Bonan, G.B. & H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Ann. Rev. Ecol. Syst. 20: 1-28.

Carleton, T.J. 1982. The pattern of invasion and establishment of *Picea mariana* (Mill.) BSP. into the subcanopy layers of *Pinus banksiana* Lamb. dominated stands. Can. J. For. Res. 12: 973-984.

Carleton, T.J. & P.F. Maycock. 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56: 1157-1173.

Cattelino, P.J., I.R. Noble, R.O. Slatyer & S.R. Kessel. 1979. Predicting the multiple pathways of succession. Environ. Manage. 3: 41-50.

Clayden, S. & A. Bouchard. 1983. Structure and dynamics of conifer-lichen stands on rock outcrops south of Lake Abitibi, Quebec. Can. J. Bot. 61: 850-871.

Clements, F.E. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Cogbill, C.V. 1985. Dynamics of the boreal forests of the Laurentian Highlands, Canada. Can. J. For. Res. 15: 252-261.

Collins, S.L., S.M. Glenn & D.W. Roberts. 1993. The hierarchical continuum concept. J. Veg. Sci. 4: 149-156.

Connell, J.H. & R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Cook, J.E. 1996. Implications of modern successional theory for habitat typing: a review. For. Sci. 42: 67-75.

Cowles, H.C. 1899. The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. 27: 95-117, 167-202, 281-308, 361-391.

DeGrandpré, L., D. Gagnon & Y. Bergeron. 1993. Changes in the understory of Canadian boreal forest after fire. J. Veg. Sci. 4: 803-810.

Delcourt, P.A. & H.R. Delcourt. 1987. Long-term forest dynamics of the temperate zone. Springer, New York.

Dix, R.L. & J.M.A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49: 657-676.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition. A factor in old-field development. Vegetatio 4: 412-417.

Finegan, B. 1984. Forest succession. Nature 312: 109-114.

Foster, D.R. & G.A. King. 1986. Vegetation pattern and diversity in S.E. Labrador, Canada: *Betula papyrifera* (birch) forest development in relation to fire history and physiography. J. Ecol. 74: 465-483.

Frelich, L.E. & P.B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. 65: 325-346.

Galipeau, C., D. Kneeshaw & Y. Bergeron. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. 27: 139-147.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. Club 53: 7-26.

Godfray, H.C.J. & B.T. Grenfell. 1993. The continuing quest for chaos. Trends Ecol. Evol. 8: 43-44.

Grigal, D.F. & L.F. Ohmann. 1975. Classification, description, and dynamics of upland plant communities within a Minnesota Wilderness Area. Ecol. Monogr. 45: 389-407.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Hastings, H.M. & G. Sugihara. 1993. Fractals: a user's guide for the natural sciences. Oxford Univ. Press, Oxford, England.

Heilman, P.E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47: 825-831.

Heilman, P.E. 1968. Relationship of availability of phosphorus and cations to forest succession and bog formation in interior Alaska. Ecology 49: 331-336.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3: 329-382.

Heinselman, M.L. 1981. Fire and succession in the conifer forests of northern North America. Pages 374-406 in West, D.C., H.H. Shugart & D.B. Botkin (eds.). Forest succession: concepts and applications. Springer-Verlag, New York.

Hirsch, K.G. 1991. A chronological overview of the 1989 fire season in Manitoba. For. Chron. 67: 358-365.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60: 695-713.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4: 1-23.

Holling, C.S. 1992. The role of forest insects in structuring the boreal landscape. Pages 170-191 in Shugart, H.H., R. Leemans, & G.B. Bonan (eds.). A systems analysis of the global boreal forest. Cambridge Univ. Press, New York.

Horn, H.S. 1976. Succession. Pages 187-204 in May, R.M. (ed.). Theoretical ecology. Saunders, Philadelphia.

Host, G.E., K.S. Pregitzer, C.W. Ramm, J.B. Hart & D.T. Cleland. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern lower Michigan. For. Sci. 33: 445-457.

Hurtt, G.C. & S.W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. J. Theor. Biol. 176: 1-12.

Huston, M. & T. Smith. 1987. Plant succession: life history and competition. Am. Nat. 130: 168-198.

Johnson, E.A. 1979. Succession: an unfinished revolution. Ecology 60: 238-240.

Johnson, E.A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge.

Jonsson, B.G. & M. Dynesius. 1993. Uprooting in boreal forests: long-term variation in disturbance rate. Can. J. For. Res. 23: 2383-2388.

Kenkel, N.C. 1986. Structure and dynamics of jack pine stands near Elk Lake, Ontario: a multivariate approach. Can. J. Bot. 64: 486-497.

Kenkel, N.C. 1987. Trends and interrelationships in boreal wetland vegetation. Can. J. Bot. 65: 12-22.

Kneeshaw, D.D. & Y. Bergeron. 1996. Ecological factors affecting the abundance of advance regeneration in Québec's southwestern boreal forest. Can. J. For. Res. 26: 888-898.

La Roi, G.H. 1967. Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monogr. 37: 229-253.

Larsen, J.A. 1980. The boreal ecosystem. Academic Press, New York.

Lenihan, J.M. 1993. Ecological response surfaces for North American tree species and their use in forest classification. J. Veg. Sci. 4: 667-680.

Lieffers, V.J., K.J. Stadt & S. Navratil. 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26: 1002-1007.

Liu, K-B. 1990. Holocene paleoecology of the boreal forest and Great Lakes-St. Lawrence forest in northern Ontario. Ecol. Monogr. 60: 179-212.

May, R.M. 1976. Simple mathematical models with very complicated dynamics. Nature 261: 459-467.

McCook, L.J. 1994. Understanding ecological community succession. Vegetatio 110: 115-147.

McCune, B. & T.F.H. Allen. 1985. Will similar forests develop on similar sites? Can. J. Bot. 63: 367-376.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Québec. Can. J. For. Res. 24: 730-741.

Muir, P.S. & J.E. Lotan. 1985. Disturbance history and serotiny of *Pinus contorta* in western Montana. Ecology 66: 1658-1668.

Naiman, R.J. 1988. Animal influences on ecosystem dynamics. Bioscience 38: 750-752.

Noble, I.R. & R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21.

Ohmann, L.F. & D.F. Grigal. 1981. Contrasting vegetation responses following two forest fires in northeastern Minnesota. Am. Midl. Nat. 106: 54-64.

Par, D., Y. Bergeron & C. Camir. 1993. Changes in the forest floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. 4: 811-818.

Pastor, J., R.H. Gardner, V.H. Dale & W.M. Post. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. Can. J. For. Res. 17: 1394-1400.

Payette, S. 1992. Fire as a controlling process in the North American boreal forest. Pages 144-169 in Shugart, H. H., R. Leemans & G.B. Bonan (eds.). A systems analysis of the global boreal forest. Cambridge Univ. Press, New York.

Peterson, E.B. & N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton. Spec. Rep. 1.

Pickett, S.T.A. 1976. Succession: an evolutionary interpretation. Am. Nat. 110: 107-119.

Pickett, S.T.A., S.L. Collins & J.J. Armesto. 1987. Models, mechanisms and pathways of succession. Bot. Rev. 53: 335-371.

Prentice, I.C. 1986. Vegetation responses to past climatic variation. Vegetatio 67: 131-141.

Prescott, C.E., J.P. Corbin & D. Parkinson. 1989. Input, accumulation, and residence times of carbon, nitrogen, and phosphorus in four Rocky Mountain coniferous forests. Can. J. For. Res. 19: 489-498.

Ritchie, J.C. 1956. The vegetation of northern Manitoba: I. Studies in the southern spruce forest zone. Can. J. Bot. 34: 523-561.

Ritchie, J.C. 1986. Climate change and vegetation response. Vegetatio 67: 65-74.

Ritchie, J.C. & G.A. Yarranton. 1978. The late-Quaternary history of the boreal forest of central Canada. Ecology 66: 199-212.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests in northwestern Alberta. Can. J. Bot. 39: 1007-1017.

Rowe, J.S. & G.W. Scotter. 1973. Fire in the boreal forest. Quat. Res. 3: 444-464.

Schroeder, M. 1991. Fractals, chaos, power laws: minutes from an infinite paradise. Freeman, New York.

Shafi, M.I. & G.A. Yarranton. 1973. Vegetational heterogeneity during a secondary (postfire) succession. Can. J. Bot. 51: 73-90.

Su, Q., D.A. Maclean & T.D. Needham. 1996. The influence of hardwood content on balsam fir defoliation by spruce budworm. Can. J. For. Res. 26: 1620-1628.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852.

Van Cleve, K., C.T. Dyrness, L.A. Viereck, J. Fox, F.S. Chapin III & W. Oechel. 1983. Taiga ecosystems in interior Alaska. Bioscience 33: 39-44.

Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. Pages 202-220 in Wein, R.W. and D.A. MacLean (eds.). The role of fire in northern circumpolar ecosystems. Wiley, New York.

Watt, A.S. 1947. Pattern and process in the plant community. J. Ecol. 35: 1-22.

Wein, R.W. & D.A. MacLean. 1983. The role of fire in northern circumpolar ecosystems. J. Wiley and Sons, New York.

Willis, K.J., M. Braun, P. Sümegi & A. Tóth. 1997. Does soil change cause vegetation change or vice versa? A temporal perspective from Hungary. Ecology 78: 740-750.

Wilson, J.B., H. Bitay, S.H. Roxburgh, W.M. King & R.S. Tangney. 1992. Egler's concept of initial floristic composition in succession-ecologists citing it don't agree what it means. Oikos 64: 591-593.

Wright, H.E. & M.L. Heinselman. 1973. The ecological role of fire in natural conifer forests of western and northern North America: Introduction. Quat. Res. 3: 317-328.

Zasada, J.C., T.L. Sharik & N. Markku. 1992. The reproductive process in boreal forest trees. Pages 85-125 in Shugart, H.H., R. Leemans & G.B. Bonan (eds.). A systems analysis of the global boreal forest. Cambridge Univ. Press, New York.

Zoladeski, C.A. & P.F. Maycock. 1990. Dynamics of the boreal forest in northwestern Ontario. Am. Midl. Nat. 124: 289-300.