

Gap dynamics of forest trees: A review with particular attention to boreal forests

John McCarthy

Abstract: Small-scale gap disturbance in forests is reviewed. Caused by the death of individual or multiple trees with subsequent fall from the canopy, gaps have been extensively studied in temperate deciduous and tropical forests for the past 20 years. This review considers much of this research with a view to assessing the importance of gap disturbance in boreal forests. Because of the ubiquity of large-scale, stand-initiating disturbances such as landscape-level fires, epidemic insect outbreaks, and periodic extensive windthrow events, gap processes in boreal forests have received little attention. Research in the Scandinavian and Russian boreal forest, as well as in high-altitude boreal “outliers” found in Japan and the United States, is showing that gap disturbance determines forest structure and processes to a greater extent than previously assumed. Boreal forests dominated by the shade-tolerant fir (*Abies*) – spruce (*Picea*) complex are particularly well-adapted to the development of long-term, old-growth continuity in the absence of large-scale disturbance.

Key words: gap dynamics, disturbance, boreal forests, temperate forests, tropical forests, silviculture.

Résumé : L’auteur présente une revue sur les ouvertures par perturbations à petite échelle en milieu forestier. Occasionnées par la mort d’un ou plusieurs arbres suivie de leur chute de la canopée, ces ouvertures ont été largement étudiées en forêts décidues tempérées et tropicales au cours des 20 dernières années. Cette revue prend en compte une bonne partie de cette recherche pour évaluer l’importance de l’ouverture par perturbation en forêts boréales. À cause de l’ubiquité des perturbations à grande échelle, initiatrices de peuplements, telles que les incendies au niveau du paysage, les épidémies d’insectes et les événements périodiques de grands chablis, les processus d’ouverture en forêt boréale n’ont reçu que peu d’attention. Des recherches conduites dans les forêts boréales de Scandinavie et de Russie, ainsi que dans des stations subalpines au Japon et aux États-Unis, montrent que l’ouverture par perturbation détermine la structure de la forêt et de ses processus beaucoup plus qu’on l’avait jusqu’ici assumé. Les forêts boréales dominées par le complexe sapin tolérant (*Abies*) – épinette (*Picea*) sont particulièrement bien adaptées au développement de forêts surannées en continuité et à long terme, en absence de perturbation à grande échelle.

Mots clés : dynamique des ouvertures, perturbation, forêts boréales, forêts tempérées, forêts tropicales, sylviculture.

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J. McCarthy.¹ Forest Sciences Department, Faculty of Forestry, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada.

¹ Present Address: 5935 Iona Drive, Vancouver, B.C. V6T 1J7, Canada (e-mail: jmccarthy@jesuits.ca).

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Introduction

The main objective of this review will be to focus on increasing evidence that points to the importance of small-scale gap dynamics in boreal forests. This will be accomplished by a general review of research on gap dynamics in tropical and temperate forests. Such research has confirmed the prevalence of gap dynamics in these forests. Insights on gap dynamics gained from this research will permit a focus on boreal forests. It is hoped that a review of this literature, as well as a consideration of the research conducted in boreal forests and the subalpine spruce (*Picea*) – fir (*Abies*) forests of Canada, the United States, and Japan, will serve to underline the general importance of gap dynamics in boreal forests. Given the prevalence of large-scale disturbance in boreal forests, it has been assumed that small-scale gap dynamics were not important in determining the structure and function of boreal forests. It is the intention of this review to question this assumption.

This review will focus on a particular type of forest disturbance termed “gap dynamics.” Gap dynamics is characterized by small- or micro-scale disturbance of the mature forest canopy. Trees die standing, snap off, or are blown to the ground, creating a “hole” in the canopy. The death of a single stem or a few stems releases available growing space (*sensu* Oliver and Larsen 1996). In time, this growing space is occupied by tree regeneration, usually a result of released advance regeneration or recruitment from buried or dispersed seed propagules. Considered as a key process in autogenic succession (Kimmins 1997), gap dynamics in forest ecosystems have become the focus of much investigation over the last two decades, particularly in tropical and temperate systems (Yamamoto 1992a).

Investigation of forest gap dynamics dates from the late 1970s. This research has underlined the ubiquity and importance of small-scale canopy disturbance in forests not subject to extensive, large-scale, catastrophic disturbance. The vast majority of research on tree fall and gap dynamics has been

conducted in tropical forests and in the temperate hardwood forests of the United States (Pickett 1983; Brokaw 1985a; Runkle 1985a; White and Pickett 1985; Denslow 1987; Platt and Strong 1989; Denslow and Spies 1990; Whitmore 1995). Significant work on gap disturbance has also been initiated in the *Nothofagus* forests of the southern Hemisphere (Veblen 1985a, 1985b, 1989; Stewart et al. 1991; Heinemann et al. 2000), temperate coniferous forests (Lertzman and Krebs 1991; Spies et al. 1990), subalpine spruce–fir forests of both the United States (Foster and Reiners 1986; Battles and Fahey 1996, 2000) and Japan (Yamamoto 1993, 1995), as well as in Japanese temperate forests (Yamamoto 1989, 1992b).

Except for recent work in Scandinavian and Russian forests (Liu and Hytteborn 1991; Kuuluvainen et al. 1998; Drobyshev 1999) little research has been conducted on gap dynamics in boreal forests. In the Canadian boreal forest, gap dynamics have been studied in spruce budworm (*Choristoneura fumiferana* Clem) – mediated balsam fir (*Abies balsamea* (L.) Mill.) forests (Kneeshaw and Bergeron 1998) and in old, uneven-aged aspen (*Populus tremuloides* Michx.) forests of northeastern Alberta (Cumming et al. 2000). Papers in special issues of both *Ecology* (Platt and Strong 1989) and the *Canadian Journal of Forest Research* dedicated to gap dynamics (Denslow and Spies 1990) did not address boreal forests. The same is true for published reviews that focus exclusively on temperate (Runkle 1985a; Veblen 1985b) and tropical forests (Hartshorn 1978; Whitmore 1978; Brokaw 1985a; Denslow 1987). The single known review of boreal forest gap dynamics (Kuuluvainen 1994) focuses solely on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) dominated forests of Finland. The current review attempts a more detailed analysis of gap dynamics in global boreal forests.

For purposes of this review, the geographical boundaries of the circumpolar boreal forest will be expanded to include the subalpine spruce–fir forests of both the Appalachians (Oosting and Billings 1951; McIntosh and Hurley 1964) and the northern islands of Japan (Kojima 1991, 1995). These “outlier” forests, dominated by the spruce–fir association, possess a physiognomy and floristics similar to the boreal forest of the northern latitudes. The high-altitude forests of Englemann spruce (*Picea engelmannii* Parry) – subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) found in western Canada (Coates et al. 1994) and the United States (Alexander 1987) will also be examined. While not considered boreal forests in the strict sense, these spruce–fir forests possess ecological characteristics similar to those found in the boreal forest.

This review will focus for the most part on gap dynamics of forest trees and the response of tree regeneration to canopy disturbance. Understory and gap vegetation other than trees will be considered only in terms of their effects on tree recruitment. For a consideration of canopy gaps and organisms other than trees, the reader is referred to Schemske and Brokaw (1981), Collins et al. (1985), Levey (1988), and Fuller (2000).

At this point, it is important to distinguish the difference between the terms “gap” and “patch” in this discussion of forest dynamics. The size of canopy openings obviously ranges from small openings created by the fall of individual trees or large branches to disturbances covering thousands or millions of hectares. Such a range of spatial scales will necessarily provoke changes in resource allocation and species response of a radically different nature. Unfortunately, both the terms “gap” and “patch” have been used in a synonymous or inconsistent manner in the forest ecology literature despite an explicit, if not implicit, recognition of their difference (White and Pickett 1985; Peterken 1996; van der Maarel 1996; Barnes et al. 1998). A distinction is important, for it is evident that patches resulting from large-scale fires or insect outbreaks in the boreal forest are certainly not “gaps” in the same sense as “gaps” created by treefalls in tropical and temperate forests.

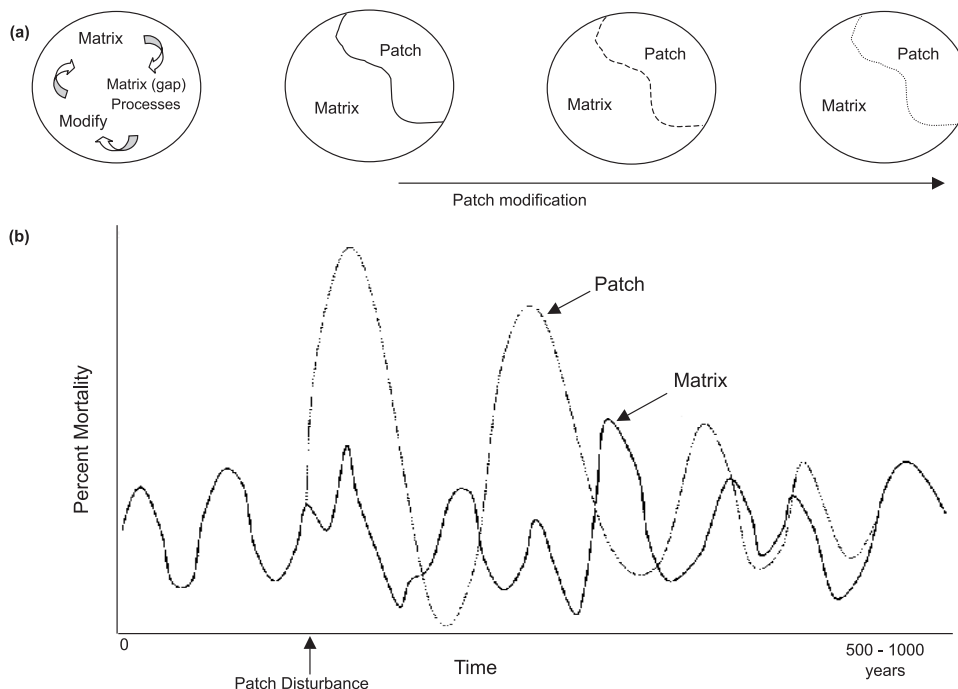
For the purposes of this review, gaps are defined as canopy openings not generally exceeding 200 m² in area. Tree death, normally on a single-tree or small group level, is caused by stem breakage due to root and butt diseases or windthrow in some instances. The continual production and filling-in of these small gaps may be termed a “matrix” process that dominates the disturbance regime in self-perpetuating, climax or near-climax, old-growth forests (Lewis and Lindgren 2000). Patches are larger openings in

Fig. 1. Conceptual model of gap (matrix) and patch processes and attributes (after K.J. Lewis and B.S. Lindgren, *The Forestry Chronical*, **76**(3): 433–443, 2000, figure 1).

Attribute or Process	Gap dynamics	Patch modifying	Patch dynamics
Spatial scale of change	Individual tree	←→	Stand or portion thereof
Size of canopy opening	≤ 200 m ²	←→	>200 m ²
Temporal scale of change	Slow change (10 to 100s years)	←→	Rapid, often catastrophic change
Type of change	Modification of original stand (quasi-constant tree recruitment and mortality)	←→	Initiation of new cohorts (episodic tree recruitment and mortality)
Change in resource availability	Little change	←→	Major change
Forest development	“Climax”, old-growth in quasi-equilibrium	←→	“Pioneer”, early successional or stand-initiation (<i>sensu</i> Oliver and Larsen, 1996)
Type of disturbance	Decay (root and butt rots) or single-tree windthrow	←→	Epidemic insect, fire, wind, avalanches, volcanoes
Stand structure	Often all-aged, reverse-J diameter distribution	←→	Even-aged or multi-cohort, normal diameter distribution
Regeneration strategies	Release of advance regeneration	←→	Seed propagule dispersal, seedbanks, vegetative propagation, as well as seedling bank release.
Forest structure	“Homogeneous” old-growth	←→	Mosaic of seral stages

the canopy caused by rapid, at times catastrophic, biotic and abiotic disturbances and may be described as a “relatively discrete spatial pattern” (White and Pickett 1985) that exhibits sufficient structural and behavioural differences from the surrounding matrix. See Fig. 1 for a conceptual differentiation of gap and patch processes. Figure 2 provides a spatial and temporal conceptual model of tree mortality effected by both gap and patch disturbance. The conceptual model begins with a homogeneous time-zero forest, the disturbance regime of which is characterized by small-scale gap or matrix processes. At a point in time, an exogenous disturbance produces large-scale mortality, which creates a patch. Processes operative within the patch are a combination of successional and stand developmental processes that effect gradual change over time. With time, the disturbance regime of the patch becomes more and more similar to that operative in the matrix (Lewis and Lindgren 2000). Forests dominated by patch disturbance are usually characterized, on the landscape level, by a mosaic of seral stages in various stages of stand development (*sensu* Oliver and Larsen 1996). No claim will be made for a review *in toto*. The already burgeoning and prolific literature on gap research in temperate and tropical systems continues to expand. After an initial historical overview of disturbance ecology, the review considers the reasons why there have been so few studies on gap dynamics in boreal forests. Subsequent sections review the investigations on gap dynamics carried out in tropical and temperate forests as well as in boreal forests. After a review of the etiology of gaps, research methodology will be considered. Gap size and geometry and the consequent differential fluxes of above- and below-ground resources that impact tree recruitment are subsequently covered. Final sections focus on characteristics of gap specialists and the feasibility of a gap-based silviculture. The review concludes with a presentation of some possible future research priorities (Fig. 3).

Fig. 2. Conceptual spatial (a) and temporal (b) models of mortality rate and patch appearance with various types of disturbances (after K.J. Lewis and B.S. Lindgren, *The Forestry Chronical*, **76**(3): 433–443, 2000, figure 2).



The purpose of such a synthesis is twofold: an examination of the occurrence and relative importance of gap dynamics in global forests, including the boreal forest, and the provision of an incentive for further work on boreal gap dynamics, particularly in the North American boreal forest.

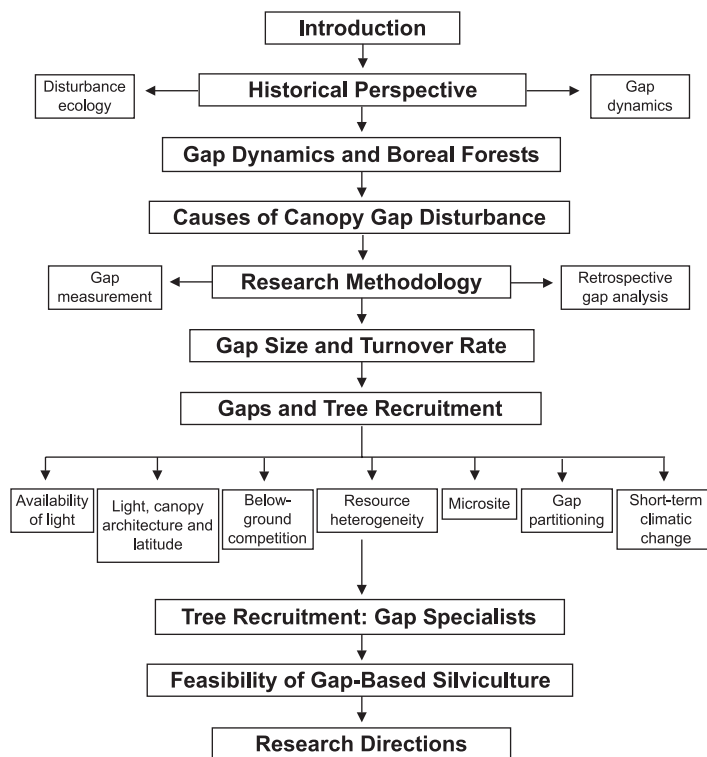
Historical perspective

Disturbance ecology

Disturbance is ubiquitous in forest ecosystems (Attwell 1994; Rogers 1996). Defined as “any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett 1985), disturbance determines forest species composition, structure, and process. Furthermore, disturbances exert their influence over a wide range of temporal and spatial scales. This disturbance, in turn, promotes changes in resource fluxes, changes that lead to some form of reorganization of the disturbed patch or gap at structural and functional levels that may be similar or dissimilar to predisturbance levels. Resource levels and inputs are changed and species respond accordingly.

The notion that disturbances are prevalent and even pandemic in all ecosystems was by no means always universally accepted. It is generally acknowledged that the pioneering work of Cowles (1899, 1911) did much to enhance the understanding of plant communities as essentially dynamic in nature (Cooper 1926). Succeeding decades would find researchers intent on describing identifiable temporal sequences of vegetation, a process that would eventually lead to the development of the theory of ecological succession. Of prime interest would be the amassing of evidence for the existence of a vegetation climax, a stable, self-reproducing plant community, whose species composition was determined solely by the local climate (Clements 1916). Using organismic terminology, Clements (1916) likened the se-

Fig. 3. Review of outline showing relationship among topics.



quence of successional stages to the developmental stages of an organism; just as an organism grows and passes from one stage towards another more advanced stage, the same with plant communities. Succession was clearly perceived as developmental in nature, with the stable climax phase regarded as the ultimate adult stage of the embryonic successional stages.

Due to this preoccupation with the climatically controlled climax, there existed relatively little appreciation for the role of natural disturbance in fashioning plant communities. Early dissenters of the strict view of climax as a final stage of plant community development included Tansley (1935), who proposed that certain ecosystems failed to attain a climatic climax because of the mitigating effects of edaphic and physiographic influences and disturbance events such as fire. In this case, climax is simply the culmination of the development of a system determined more directly by factors other than the regional climate. It was not that Clements and the early proponents of the classical monoclimate theory were not unaware of disturbance (cf. proclimax, subclimax (Clements 1936)), but that the theoretical framework was definitely dominated by the quintessential climax. Eventually, though, as communication increased among scientists, a consensus regarding the prevalence of ecological disturbance slowly developed. Jones (1945) questioned whether the term “climax forest” may exist only as a concept, never existing in reality because of the constant influence of catastrophic disturbance.

Recent commentators have gone so far as to describe the abandonment of the classical notion of a regional climax by modern ecologists (Pickett 1976) or cite the notion of climax as having been a “rather oppressive influence on the minds of many ecologists” (Sprugel 1976). On the other hand, White (1979), while acknowledging the problematic nature of the term “climax,” did not advocate its complete abandonment. Instead, he accepted the utility of the concept only if it was explicitly defined in terms of the disturbance dynamics and other dynamic properties of the particular ecosystem under

investigation. For example, the biogeoclimatic ecosystem classification of British Columbia accepts the polyclimax concept because of the preponderance of extensive areas of long-lived forests that have escaped catastrophic disturbance for extended periods (Pojar et al. 1987). However one views the term “climax,” research in disturbance ecology has repeatedly underlined the fact that attention to the intensity, scale, and frequency of disturbance events must always be maintained in any study of ecosystem structure and function (Mooney and Godron 1983; Pickett et al. 1989; Sprugel 1991; Rogers 1996; Parminter 1998). Various disturbance events such as fire, insect, disease, windthrow, and herbivory are subjects of studies that attempt to comprehend ways in which disturbance determines species composition, reproductive strategies, stand development, physiognomy, and evolutionary changes in ecosystems.

Gap dynamics

Alex Watt, in his 1947 presidential address to the British Ecological Society (Watt 1947), is generally credited with the first attempt to reconcile the notions of process and pattern in contemporary plant ecology (van der Maarel 1996). He attempted to move plant ecology beyond the purely descriptive stage by injecting dynamic principles into the study of plant communities. This new level of explanatory knowledge allowed a more comprehensive understanding of inter- and intra-specific interactions and the forces that determine the maintenance and regeneration dynamics of particular plant communities.

Watt (1947) thought it best to understand plant communities in terms of patches or phases. Considered as a developmental sequence of a particular plant community, each patch or phase is joined together in a mosaic and dynamically related to others in such a manner that the community patterns persist through time. In other words, the community passes through a series of developmental stages that repeat themselves in a cyclic fashion. This cycle is in turn determined by the extent, frequency, and magnitude of various disturbances that impact the plant community. Using the terminology of Watt (1947), we may say that both process and pattern influence each other in a dynamic manner.

Watt (1947) used seven different plant communities to develop his thoughts on pattern and process. Germane to our review is his description of gap-phase regeneration in European beech (*Fagus sylvatica* L.) forests. He defined the gap phase as that part of the forest developmental cycle dominated by the presence of tree regeneration, it being excluded from other phases. The gap phase may be initiated by small-scale disturbance such as tree-falls or by large-scale disturbance such as fire, insect or disease epidemics, and extensive windstorms. It is during the gap phase, when the mature canopy experiences sufficient disturbance, that the site is opened up, permitting the release of either advance regeneration or the recruitment of new regeneration. It should be noted that for Watt (1947) phases were synonymous with patches and that gap phase could be of widely varying spatial dimensions, it being defined simply as the stage of forest development in which regeneration was confined. As emphasized earlier, I will use the term “gap” in a more restrictive sense than was used by Watt (1947). Watt (1947) noted that regeneration may happen during the actual gap phase or during the phase corresponding to the mature phase. This distinction is important for it is well known that many shade-tolerant species are able to establish themselves as advance regeneration under a mature–overmature closed canopy that may be “losing its grip” on the growing space of the site (Oliver 1981; Oliver and Larson 1996). An early confirmation of Watt’s gap-phase dynamics was given by Bray (1956) for maple–basswood (*Acer saccharum* Marsh. – *Tilia americana* L.) forests of Minnesota.

Watt’s seminal idea of patch dynamics in vegetation ecology has subsequently been developed and promoted as workers have come to appreciate the degree of patchiness in ecological systems. Constituting a *grille de lecture*, the concept of patch dynamics has emerged as an intellectually satisfying and fruitful paradigm by which to understand plant community dynamics. Contemporary manifestations of Watt’s original insight have taken shape: dynamic landscape – succession model (Pickett 1976), mosaic phenomena of communities (Whittaker and Levin 1977), non-equilibrium coexistence hypothesis (Pickett 1980), shifting mosaic steady state (Bormann and Likens 1981), patch dynamics and disturbance (Sousa 1984; Pickett and White 1985), forest gap models (Shugart and Seagle 1985), mosaic-cycle

concept (Remmert 1991), and hierarchical patch dynamics (Wu and Loucks 1995). Regardless of the accepted nomenclature and theoretical perspective, it is evident that the paradigm of “patch dynamics” has provided significant insight into ecosystem structure and dynamics.

Gap dynamics and boreal forests

Why have boreal gap dynamics not been researched to the same extent that we witness in temperate and tropical forests? A prime reason is the generally felt assumption that gap dynamics cannot explain the initiation and maintenance of boreal forests. Instructive is the comment by Lorimer (1989), who stated that “while small gaps are not unknown in the boreal forest, it is unlikely that the origin of a sizable percentage of trees can be traced to such events.” Except for a single study of spruce budworm mediated gap dynamics (more correctly termed “patch dynamics”) in Québec’s southern boreal forest (Kneeshaw and Bergeron 1998) and gap dynamics in Albertan boreal aspen stands (Cumming et al. 2000), research on the actual prevalence of gap dynamics as a significant disturbance event in the Canadian boreal forest is non-existent.

This lacuna is understandable for the simple reason that boreal forest scientists have been preoccupied with the obvious large-scale, stand-initiating disturbances that dominate boreal systems, particularly fire, insect, and wind disturbances. Viewed from a perspective of “natural disturbance types,” the boreal forest is assumed to exemplify what is termed a natural disturbance type 3, which is defined as “ecosystems with frequent stand-initiating events” (British Columbia 1995). At the opposite end of the disturbance spectrum are natural disturbance type 1 ecosystems, which are characterized by “rare stand-initiating events” in which small-scale gap dynamics are the predominant disturbance events (British Columbia 1995). Rarely, however, have boreal forests been considered as natural disturbance type 1 ecosystems. In the 1999 Canadian Sustainable Forest Management sponsored conference entitled “Sustaining the Boreal Forest,” all of the nine papers devoted to natural disturbance in the boreal forest featured fire and insect herbivory, with fire clearly continuing to garner the most attention (Veeman et al. 1999). This is understandable given the fact that the boreal forest, particularly the vast tracts of relatively uninhabited Canadian and Russian boreal forest, are periodically disturbed by extensive landscape-level fires.

Wildfire is considered of paramount importance in controlling the dynamics of the boreal forest (Heinselman 1973; Rowe and Scotter 1973; Wein and MacLean 1983; Dyrness et al. 1986; Payette et al. 1989; Payette 1992; Dansereau and Bergeron 1993; Johnson et al. 1998). Johnson (1995) noted four characteristics of boreal fires that especially impact forest composition and successional dynamics: the occurrence of intense crown fires, the vast areas burnt, the frequency of occurrence, and the degree of forest floor combustion. Fires greater than 100 000 ha are common, with fires affecting over 1 000 000 ha not unknown. Average fire rotations (Heinselman 1973) or fire cycles (van Wagner 1978) (defined as the time period required to burn an area equivalent to the area under study) differ, depending on climate, lightning occurrence, and tree species. Fire rotation estimates of 50–100 years are given for the drier continental boreal forests of western Canada and Alaska (Heinselman 1981; Yarie 1981). Fire cycles of approximately 100 years are cited for Québec’s boreal forest (Bergeron 1991; Payette et al. 1989) and for the boreal forests of northern Sweden (Zackrisson 1977).

Insect disturbance in the boreal forest, especially by defoliators and bark beetles, is common and widespread (Holling 1992). Periodic insect outbreaks, especially of the spruce budworm and the hemlock looper (*Lambdina fiscellaria fiscellaria* Guen.) have caused extensive defoliation and stand mortality across the range of balsam fir in the eastern Canadian boreal forest (Carroll 1956; Blais 1965, 1983; Brown 1970; Otvos and Moody 1978; Otvos et al. 1979; Kettela 1983; Hardy et al. 1986; Ostaff and MacLean 1989; MacLean and Ebert 1999; Morin et al. 1993; Hudak et al. 1996; Morin 1998; Candau et al. 1998; Fillion et al. 1998; Simpson and Coy 1999). Starting about 1910, 1940, and 1970, three successive spruce budworm outbreaks in eastern Canada affected about 10, 25, and 57 million hectares of forest, respectively (Blais 1983; Morin and Laprise 1990). Recent work on spruce budworm – balsam fir dynamics has shown that spruce budworm outbreaks and balsam fir forests form a self-regulating

system that perpetuates itself through time (Baskerville 1975; MacLean 1984, 1988; Morin 1994; Leblanc and Bélanger 2000). In the boreal forests of western Canada, particularly those dominated by white spruce (*Picea glauca* (Moench) Voss), epidemic outbreaks of the spruce beetle (*Dendroctonus rufipennis* Kirby) are common and promote significant stand-initiating events (Werner et al. 1977; Werner and Holsten 1983; Holsten et al. 1995; Safranyik 1995; Werner 1996).

Given the ubiquity and intensity of fires and insect outbreaks and the common occurrence of fire-adapted species such as jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) B.S.P.), and trembling aspen, all of which may reach ages greater than the average fire rotation of 100 years, it is easy to understand why gap dynamics would not be considered an important disturbance factor in the Canadian boreal forest. Most of the forest would experience catastrophic stand-replacing fires and insect outbreaks before the onset of any old-growth stage, thus preventing the conditions conducive for gap-phase regeneration. The prevalence of large-scale disturbance would minimize the development of a self-replacing, steady-state forest.

An appreciation of the role of micro-scale disturbance in high latitude boreal forests is, however, slowly growing. Notable are the comments made by the organizing committee of the 1996 *Second International Workshop on Disturbance Dynamics in Boreal Forests*. They noted that “the role of fire may be overemphasized in boreal systems, and old-growth forests controlled by alternating disturbances may be more abundant than has been generally considered” (Bergeron et al. 1996). In fact, publication of the conference papers two years later confirmed that gap disturbance appears to be common in boreal forests and, in some forests, is probably more important than fire (Bergeron et al. 1998).

Even before Watt (1947) developed his theory of patch dynamics, Serander (1936) presented what he termed the “storm gap structure.” Working in old-growth Norway spruce forests of central Sweden, Serander (1936) understood the regeneration dynamics and mosaic structure of these forests to be determined by periodic gap-phase disturbance caused by treefalls. Recruitment in the gaps is facilitated by the release of suppressed advance spruce regeneration (“dwarf trees” according to Serander) to form the future canopy, which in turn is prone to gap formation. Serander’s storm-gap theory of spruce forest regeneration has been confirmed by contemporary quantitative studies of gap dynamics in the primeval forest reserve of Fiby urskog (Hytteborn and Packham 1985, 1987; Leemans and Prentice 1987; Leemans 1990, 1991; Hytteborn et al. 1991; Liu and Hytteborn 1991). Serander’s work has also been confirmed by research on gap dynamics carried out in northern Sweden (Hytteborn et al. 1987), Finland (Kuuluvainen 1994), and Russia (Kuuluvainen et al. 1998).

In the Canadian boreal forest, conditions exist that would promote the frequency of small-scale canopy disturbance. This is particularly true in areas of the boreal forest that have escaped large-scale disturbance for long periods of time. Specific climatic or edaphic conditions may prevent the periodic occurrence of fire or insect infestation. In the humid maritime boreal forests of eastern Canada, for example, fire frequency is much less than that documented for the continental boreal forest. Forest fires are relatively uncommon in southeast Labrador where Foster (1983) determined a fire rotation of approximately 500 years, a fire cycle much greater than the 200 years suggested by Heinselman (1981) for the high precipitation areas of eastern Canada. Although fire cycles are unknown, Meades and Moores (1989) considered the extensive balsam fir forests of western and northern Newfoundland to have had very little fire history (cf. Wilton and Evans 1974). Despite a natural fire cycle of 80–100 years in northern Sweden (Zackrisson 1977), areas of Norway spruce dominated fire-free refugia or areas of very low fire frequency do occur (Hansson 1992; Segerström et al. 1994, 1996). Using charcoal and pollen analysis, Ohlson and Tryterud (1999) documented long-term continuity (1700 years) in Norway spruce landscapes in southeastern Norway. Regeneration dynamics in these forests are characterized by small-scale gap dynamics (Steijlen and Zackrisson 1987; Liu and Hytteborn 1991; Hörnberg et al. 1995). Bergeron and Dubuc (1989), in a study of succession in the southern Québec boreal forest, concluded that in the absence of fire, gap dynamics could emerge as a driving force determining successional patterns, a trend confirmed by Kneeshaw and Bergeron (1998), who documented spruce budworm mediated gap

dynamics in old balsam fir forests in Québec. A reassessment of the dominance of fire in the boreal forest is also emerging from research in the Russian taiga where Syrjänen et al. (1994) suggested that in extensive mesic areas dominated by Norway spruce, small-scale gap dynamics determine regeneration patterns.

In the Canadian boreal forest, conditions that promote the maintenance of self-perpetuating forests through long-term gap dynamics certainly exist. Theoretically, boreal forests not disturbed by fire or insect herbivory for long periods of time will revert to multi-cohort, self-perpetuating, gap-driven forests. The boreal forests of eastern Canada, particularly those of Newfoundland that are influenced by a humid, maritime climate, are dominated by late succession balsam fir in the absence of periodic fires. The forests of western Newfoundland, for example, are dominated by balsam fir, with black spruce and white spruce being of lesser importance, their occurrence depending for the most part on topographic and edaphic influences. The predominance of balsam fir in this region indicates a fire rotation longer than the average of 100–150 years normally cited for the Canadian boreal forest. Balsam fir will not reproduce after fire, only becoming established in late successional, nonpyrogenic forests (Damman 1964; Furyaev et al. 1983; Viereck 1983). The increase in moisture gradient from western to eastern Canada is paralleled by a significant decline in forest fire frequency as one moves from the western to the eastern boreal forest (Johnson 1995). Therefore, eastern Canadian boreal forests that experience both significant oceanic influence and an absence of insect infestations are prime candidates for gap dynamics. Furthermore, the ability of balsam fir to regenerate well on a variety of microsites, high shade tolerance, and rapid growth after years of suppression (Ghent 1958) further enable the species to grow well in gap-driven forests.

Uneven-aged forests may even occur in forest areas traditionally assumed to be characterized by high fire frequencies. In both Saskatchewan (Dix and Swan 1971) and northwestern Ontario (Zoladeski and Maycock 1990), balsam fir forests were considered to be late successional forests capable of self-perpetuation in the absence of fire. On old burns in southeastern Labrador, Foster (1985) identified uneven-aged forests that developed through slow and progressive post-fire establishment of black spruce and balsam fir over a period of 70–100 years. Furthermore, the extremely long intervals between fires (500 years) documented for southeastern Labrador have produced a landscape dominated by old, multi-aged spruce–fir forests with individuals exceeding 250–300 years in age (Foster 1983, 1984). Even fire-prone lichen–spruce forests in central Labrador – Ungava may escape fire to produce multi-cohort stands exceeding 300 years in age and regenerating via gap dynamics (Treter 1995). Early studies in Labrador (Wilton 1959, 1965) and neighbouring Québec (Hatcher 1963) confirmed the presence of old, uneven-aged black spruce forests with a high proportion of balsam fir or late successional undisturbed forests dominated by balsam fir with minor components of white spruce and white birch (*Betula papyrifera* Marsh). Recent work by Groot and Horton (1994) in northeastern Ontario has identified old, uneven-aged black spruce forests characterized by age classes that span two to three centuries. Such forests, considered by Groot and Horton (1994) as a rarity in the boreal forest, were deemed able to perpetuate themselves in the absence of catastrophic disturbance. Gap dynamics of shade-tolerant spruce and fir combined with the ability of both spruce and fir to layer could certainly account for self-perpetuation in these forests.

In summary, evidence is mounting that indicates that, despite the ubiquitous nature of catastrophic disturbance in the boreal forest, such disturbances do not fully explain the range of observed structural and compositional patterns found in the boreal forest. Micro-scale gap dynamics seem to be a significant and often overlooked disturbance factor in boreal forests.

Causes of canopy gap disturbance

Gap disturbance is driven by treefalls and the production of standing dead trees. Trees die from insect, disease, and meteorological vectors, remain standing as snags or fall to the ground to create a

canopy gap. This single- or multi-tree gap may initiate a new period of recruitment depending on the presence of seed or advance reproduction and the degree to which site resources are released.

Trees die standing, snap off, or uproot. The particular process of death affects not only the spatial characteristics of gap formation, but also the type of microsite produced and the potential resources available to gap regeneration. Table 1 provides a summary of the mode of tree mortality for gapmakers in different forest ecosystems. Despite the wide variability in forest types studied, consistent patterns are evident. Tree mortality from stem-snapping is dominant, due no doubt to the prevalence of decay fungi as the determining disturbance agent in old-growth forests. Excluding the one study conducted on southern hemisphere *Nothofagus*, the amounts of standing dead are quite similar among all forest types, ranging from 14 to 17%. Mortality from uprooting ranges from 20 to 30% among all forest types.

Variation in the mortality of gap-makers is determined by a multitude of factors. Everham and Brokaw (1996), in their extensive review of treefalls, divided the factors that predetermine the type of tree mortality into two classes, biotic and abiotic. Biotic factors include stem size, stand conditions, species differences, and tree pathogens. Abiotic factors include storm intensity, timing, and associated precipitation, topographic features, edaphic conditions, and disturbance history. The complex interaction of a multitude of factors certainly accounts for the variability in gap-maker mortality in global forests. Putz et al. (1983) attempted to understand why trees uproot or snap in terms of their mechanical and architectural properties. Uprooted tropical trees tend to be stronger, larger, and shorter for a given stem diameter than trees that snap off.

An understanding of how trees have died is important in any study of gap dynamics. Gaps are created by individual tree mortality, the complexity of which has only recently been appreciated (Maser et al. 1988; Lugo and Scatena 1996). Pathogens may or may not play a role in tree death. Cause of mortality is important in assessing the degree to which site resources may be changed when a tree dies. A tree that dies and remains standing for a long time or that slowly breaks up over time will affect resource release and allocation differently than one that is suddenly snapped off or windthrown (Krasny and Whitmore 1992).

Of particular importance, but little studied, is the role of pathogens as a disturbance factor in forests. In Canadian boreal forests, extensive research has provided detailed understanding of the pathological vectors responsible for trunk and root rots in spruce and fir (Basham et al. 1953; Davidson 1957; Redmond 1957; Basham and Morawski 1964; Basham 1973a, 1973b; Whitney et al. 1974; Whitney 1976, 1995; Whitney and Myren 1978; Lavallée 1986, 1987). Much of this work, however, has focused on estimating the level of cull in commercial forests and on understanding the types of pathogenic decay fungi responsible for the loss of merchantable wood fibre. Therefore, little consideration was given to viewing tree stem and root decay as a mechanism of biotic disturbance in boreal forests. Results from studies on fir and spruce pathology repeatedly underline the importance of root and associated butt rots in determining growth increment patterns and timing and etiology of tree death (Whitney 1989, 1995; Whitney and MacDonald 1985). As root and butt decay progresses, trees are susceptible to windthrow and stem breakage, both of which determine the rate and type of gap disturbance in old boreal forests.

Worrall and Harrington (1988) examined the disease vectors responsible for canopy gaps in old-growth subalpine spruce–fir forests in New Hampshire. Biotic diseases (root and butt rots, stem decays, cankers, and dwarf mistletoe) accounted for up to 66% of the gap area at the lowest elevation. At higher elevations, chronic wind stress accounted for up to 72% of the gap area. Butt and root rots predisposed trees, particularly balsam fir, to stem breakage at ground level. The authors attributed the relative rarity of balsam fir at lower elevations to its high susceptibility to root pathogens. In a central British Columbia spruce (*Picea glauca* × *engelmannii*) – subalpine fir system, butt rots were deemed essential in determining the differential mortality of the shorter-lived subalpine fir and as agents of gap dynamics in these wet sub-boreal spruce forests (Lewis and Lindgren 1999). Heart rot fungi were responsible for the high degree of stem snap and associated gap dynamics in wind-sheltered old-growth western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests of southeast Alaska (Nowacki and Kramer

Table 1. Mode of mortality of gap-makers in gap-disturbed forests.

Location	Forest type	Mortality of gap maker (%)				Reference
		Standing dead	Snapped off	Uprooted	Other	
Boreal and subalpine forests						
Japan	Subalpine <i>Tsuga–Abies–Picea–Betula</i>	10.7	46.7	42.2	—	Kanzaki and Yoda 1986
Sweden	Primeval <i>Picea abies</i>	13	57	29	1	Liu and Hytteborn 1991; Hytteborn et al. 1991
Japan	Subalpine <i>Picea–Abies</i>	41.9	48.8	7.0	2.3	Yamamoto 1993
Japan	Sub-boreal <i>Picea–Abies</i>	<i>Picea</i> : 8 <i>Abies</i> : 17	<i>Picea</i> : 61 <i>Abies</i> : 45	<i>Picea</i> : 31 <i>Abies</i> : 38	—	Kubota et al. 1994
Japan	Subalpine <i>Picea–Abies</i>	43.7	41.7	13.1	1.4	Yamamoto 1995
Japan	Subalpine <i>Abies–Picea–Tsuga</i>	42.6	43.7	12.2	1.5	Yamamoto 1996
Temperate hardwood forests						
Tennessee	Mature hardwood	3	87	10	—	Barden 1981
United States	Old-growth mesic hardwoods	10	58	19	13	Runkle 1982
Japan	Primary evergreen broad-leaved	17.3	51.4	22.3	9.0	Yamamoto 1992b
Japan	Cool-temperate <i>Fagus–Quercus–Acer</i>	45.2	27.9	18.0	8.9	Yamamoto 1996
Japan	Warm-temperate <i>Castanopsis–Persea–Quercus</i>	17.3	51.5	22.3	8.9	Yamamoto 1996
Japan	<i>Fagus</i> : seral stages	39.2 ^c 47.0 ^c 44.5 ^c 42.9 ^c 20.0 ^a 5.0 ^a	13 35.3 22.2 50 40 75	17.4 11.8 33.3 7.1 36.7 20	25.9 5.9 — — 3.3 —	Yamamoto and Nishimura 1999
Temperate coniferous forests						
Oregon–Washington	Old-growth <i>Pseudotsuga–Tsuga</i>	55.4 ^a 73.8 ^b	17.9 13.8	26.7 12.4	— —	Spies et al. 1990
British Columbia	Subalpine old-growth <i>Abies–Tsuga</i>	24	13	6	57	Lertzman and Krebs 1991
British Columbia	Temperate rainforest	27.2	37.7	20.6	14.6	Lertzman et al. 1996

Table 1. (concluded)

Location	Forest type	Mortality of gap maker (%)				Reference
		Standing dead	Snapped off	Uprooted	Other	
Alaska	Old-growth <i>Tsuga</i>	0	95	5	0	Ott 1997
		15	64	19	2	
		4	69	25	2	
		6	76	17	1	
Tropical forests						
Panama	Tropical moist	14	60	17	9	Putz et al. 1983
Mexico	Tropical cloud	13.9	29.1	52.7	4.3	Arriaga 1988a
Mexico	<i>Pinus-Quercus</i>	26.4	39.5	20.5	13.6	Arriaga 1988b
Costa Rica	Cloud forest	2	39	41	18	Lawton and Putz 1988
Southern hemisphere forests						
New Zealand	Old-growth <i>Nothofagus</i>	31	41	24	4	Stewart et al. 1991
Summary statistics for Table 1 (range values; median values in parentheses)						
		Standing dead	Snapped-off	Uprooted	Other	
	Boreal and subalpine	8–44 (17)	42–61 (47)	7–42 (29)	0–2 (1)	
	Temperate hardwoods	3–45 (17)	28–87 (52)	10–37 (20)	0–13 (9)	
	Temperate coniferous	0–55 (15)	13–95 (64)	5–27 (19)	0–57 (2)	
	Tropical	2–26 (14)	29–60 (40)	17–53 (31)	4–18 (12)	
	Southern hemisphere	31	41	24	4	

^aOld-growth stands.

^bMature stands.

^cDeveloping stands.

1998). An early work pointed to the significant role of butt and root rots in the promotion of windthrow and stem breakage (Hubert 1918). The role of pathogens as gap makers, and therefore determinants of forest structure and dynamics, needs greater attention in gap studies (van der Kamp 1991; Castello et al. 1995; Hennon 1995). In boreal forests or high-altitude coniferous forests at lower latitudes, snow loading and ice damage may open up gaps in the forest canopy through top and stem breakage (Gill 1974). In subalpine coniferous forests in Japan, typhoon-mediated gaps are a common occurrence (Naka 1982; Kanzaki 1984; Kanzaki and Yoda 1986). Spruce budworm mediated small gap processes have also been documented for southern boreal forests in Québec (Kneeshaw and Bergeron 1998).

Research methodology

Gap measurement

How one defines a forest canopy gap is of the utmost importance. This is true especially if one wishes to quantify forest disturbance in terms of “turnover rates,” which are defined as the mean time between gap creation events at any point in the forest (Brokaw 1982; Green 1996). Both gap size and turnover rate are significantly influenced by the particular gap definition chosen (van de Meer et al. 1994). Comparisons among small-scale disturbance events in different forest types are valid only if researchers employ a standard methodology (Runkle 1992).

A number of gap definitions have been suggested. Working in old-growth mesic hardwood forests in the eastern United States, Runkle (1981, 1982) defined two types of gaps. The simplest to consider is the surface of the forest floor directly under the canopy opening. Additional areas of forest floor may be included in what has been termed the “expanded gap” that Runkle (1982) defined as the canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap. Trees growing in gaps were considered part of the surrounding canopy when they had reached heights of 10–20 m.

In tropical ecosystems, one of the earliest definitions of a canopy gap was provided by Brokaw (1982), who defined a gap as “a ‘hole’ in the forest extending through all levels down through an average height of 2 m above ground. The sides of forest openings are irregular in profile, but, for a workable definition, the sides of that space defined as a gap are vertical. The side at a particular place on the perimeter is located at the innermost point reached by foliage, at any level, at that place on the perimeter.”

It is often difficult to distinguish gaps in the field. Gaps, once formed, do not remain static but exist in various states of “filling in” that can range from a fresh, newly opened, relatively well-defined gap to one that for all intents and purposes is no longer a gap, having filled in from the growth of advanced regeneration or lateral branch growth of surrounding trees. A basic assumption is that gaps can be effectively and accurately distinguished from the surrounding background trees. Various researchers, depending on the type and height of the forest in question, have determined a critical regeneration height beyond which the gap is considered closed. This critical height will of course depend on the height of the dominant canopy and the practical difficulties of readily observing the canopy opening.

Most gap research involves ocular recognition of canopy gaps and use of either Brokaw’s or Runkle’s gap definition or some similar variant. Most forest stands of interest are subsampled for gaps using line intersect sampling or strip transects (Runkle 1985*b*, 1992). Gaps are often considered to approximate an ellipse and are measured accordingly. It has been noted, however, that such assumptions regarding the shape of gaps are often unfounded and appropriate adjustments must be taken if gap geometry and gap fraction are to be accurately determined (Battles et al. 1996).

Retrospective gap analysis

History of forest disturbance, including small-scale gap dynamics, may be inferred from retrospective studies (Lorimer 1985; Foster et al. 1996). The method of choice is determined by the questions

posed by each study, particularly the temporal and spatial scale for which information is required. Methods may include the analysis of age and size structure of stands (Whipple and Dix 1979; Ågren and Zackrisson 1990; Hiura et al. 1996), radial and height growth increment patterns (Lorimer 1985), stand reconstruction (Oliver and Stephens 1977; Suzuki et al. 1987; Deal et al. 1991), soil microtopography and coarse woody debris (Henry and Swan 1974), repeat measurements of permanent sample plots (Hofgaard 1993a), and even fine-resolution, stand-level pollen analysis (Mitchell 1988; Bradshaw and Zackrisson 1990; Foster and Zebryk 1993; Ritchie 1995). Each technique employed in the study of disturbance dynamics has its particular limitation. For example, good age data are often difficult and time consuming to gather, dendroecological techniques are restricted to surviving and decay-free trees, and pollen analysis may often be too coarse-filtered for a study of stand-level dynamics. Therefore, an integrated approach that uses a combination of techniques and data will often provide the best insight into stand dynamics. (Lorimer 1980; Foster 1988).

Spatial analysis of mapped tree stem data is assuming increasing importance in the analysis of small-scale canopy disturbance. Aside from the significant benefit achieved from the analysis of ecological systems using spatial data (Legendre and Fortin 1989; Rossi et al. 1992), the use of spatial analysis in studies of gap dynamics is important from a methodological point of view. Traditional studies of gap dynamics have been carried out in temperate and tropical forests characterized by closed canopies in which gap openings are generally easily verified and measured. However, despite the relative ease with which gaps are identified in these high forest canopies, methodological assumptions and sampling protocols are items of concern, especially in the determination of gap area. Furthermore, what a particular investigator measures in terms of gap structure may not be that to which individual trees are actually responding. As gap studies consider more patchy and open-canopied situations, such as may be found in slow-growing boreal forests, the use of traditional gap methodology ceases to be useful. In these forests, stands may not achieve anywhere near full crown closure, making the delineation of gap openings extremely problematic. A need, therefore, exists for some form of gap quantification that does not depend on the ocular measurement of holes in the canopy.

Characterization of gap structure and dynamics in old-growth stands has been achieved by the use of spatial analysis of stem-mapped point data (Leemans 1991; Moeur 1993, 1997; Chokkalingam 1998; Parish et al. 1999; Chen and Bradshaw 1999). The acquisition of stem map data may be time consuming, especially in multi-stage stands, but is facilitated by recent developments in hand-held laser technology (Peet et al. 1997). The stem map data may be analyzed by Ripley's univariate K function (Ripley 1977, 1981; Diggle 1983; Upton and Fingleton 1985; Cressie 1993), which compares the distances between all possible point pairs and tests whether an observed spatial pattern is random, aggregated, or regularly spaced. The null hypothesis is that the spatial pattern of measured points is not significantly different from that observed in a random population. Bivariate spatial interactions between two groups of trees may also be performed. The null hypothesis assumes complete spatial independence between the two populations in question. Both univariate and bivariate analysis are very useful in detecting spatial patterns associated with gap structure and dynamics across a continuum of spatial scales.

Interest has grown in the use of retrospective dendroecological techniques to describe and quantify small-scale forest disturbance history, particularly of old-growth forest systems (Fritts and Swetnam 1989; Schweingruber 1996). Tree ring patterns, particularly patterns in relative ring width, are able to provide information on the patterns of establishment, suppression, and release of individual trees. These patterns furnish essential clues to the disturbance history of forest stands (Lorimer 1985; Lorimer and Frelich 1989). Both annual growth increment and ring-width patterns of shade-tolerant species have been used as proxy evidence of past canopy disturbance caused by gap dynamics (Lorimer 1980; Canham 1985, 1990; Lorimer and Frelich 1989; Payette et al. 1990; Frelich and Lorimer 1991; Fajvan and Seymour 1993; Frelich and Graumlich 1994; Orwig and Abrams 1994, 1995; Parshall 1995; Cho and Boerner 1995; Abrams et al. 1995; Abrams and Orwig 1996a, 1996b; Cherubini et al. 1996; Daniels and Klinka 1996; Nowacki and Abrams 1997; Abrams et al. 1998; Ishikawa et al. 1999). In response to

the creation or infilling of canopy gaps, trees experience periods of release or suppression, evidence of which is preserved in the growth rings. The frequency, duration, and spatial pattern of the release and suppression events provide a helpful picture of historic canopy disturbance and recruitment dynamics.

Most dendroecological studies have been aspatial in nature, randomly sampling a select number of canopy and understory trees for radial growth analysis. The insights gained from such studies may be enhanced by including dendroecological data and spatial statistics on completely mapped tree point data (Payette et al. 1990; Chokkalingam 1998). This form of analysis provides added insight into the spatio-temporal dynamic of gaps across a continuum of spatial scales, allowing a fine-scale delineation of gaps through time and across the physical space of the plot.

Though employed more rarely, other methods in gap studies include repeated measurements in permanent sample plots (Nakashizuka et al. 1992), measurement of actual canopy height in a mapped stand (Parker et al. 1985), hemispherical photographs (Whitmore et al. 1993), repeat aerial photography (Tanaka and Nakashizuka 1997), and other remote sensing techniques (Bradshaw and Spies 1992; Blackburn and Milton 1996).

Gap size and turnover rate

As noted above in the discussion on methodology, the measurement of gap size and the calculation of gap turnover rates are heavily influenced by the gap definition employed. Combined with the inherent subjectivity in field assessment of gaps, this creates a difficulty in making comparisons among studies. However, a comparison among gap studies made in different forest ecosystems may be instructive (Table 2). Certain trends are evident and provide useful information on comparative forest gap dynamics, as described below.

Gap size is often used as an indicator of environmental heterogeneity and resource sequestration in gaps. The degree to which light, moisture, and nutrient resources are available to vegetation occupying a newly formed gap is often dependent on gap size. Furthermore, among other factors, gap dimensions often determine whether the available growing space will be occupied by early or late successional species (Pickett 1983; Denslow 1987).

Gap size will obviously differ depending on tree size and crown dimensions, whether gaps are formed from single- or multiple-tree falls, the age of the gap, as well as the methodology employed by the respective researcher. For the most part, gap-size distributions are negatively exponential in form, with the largest percentage of gaps in the lowest size range, indicating that small single-treefall gaps form more frequently than large multi-treefall gaps. Gap size for single treefalls normally ranges from 50 to 200 m² (Table 2). In old-growth Swedish boreal forests, Liu and Hytteborn (1991) found that 98% of the sampled gaps were smaller than 250 m². For subalpine coniferous forests, Yamamoto (1993) suggested an upper limit of 200 m² below which exists the vast majority of gaps. This would seem reasonable, given similar findings in work conducted in other boreal and subalpine coniferous forests (White et al. 1985a; Foster and Reiners 1986; Hytteborn et al. 1991; Yamamoto 1995; Battles and Fahey 1996). Median values of average gap size are lowest for tropical forests and highest for the temperate coniferous forests and southern hemisphere forests dominated by large-sized canopy trees.

Single-treefall gaps often enlarge as a result of subsequent fall of gap border trees. Thus many gaps measured in the field are the result of a series of treefall events covering a substantial period of time (Lertzman and Krebs 1991). Evidence for such multiple events includes the wide range in degree of necrotization in the gap-maker trees now forming part of the coarse woody debris. Liu and Hytteborn (1991) found that up to 65% of the sampled gaps contained more than one age-class of logs, indicating successive periods of gap enlargement. Working in tropical systems, Young and Hubbell (1991) found that gap-edge trees were much more likely to fall into pre-existing gaps than in other directions. The preponderance of asymmetrical crowns of gap-edge trees proved to be the main factor influencing direction of tree fall.

Table 2. Gap characteristics of gap-disturbed forests.

Location	Forest type	Gap fraction (%)	Average gap size (m ²)	Gap range (m ²)	Annual gap formation rate (%)	Turnover rate (years)	Reference
Boreal and subalpine forests							
New Hampshire	Subalpine <i>Abies–Picea</i>	24 ^a	—	—	—	—	Foster and Reiners 1983
Japan	Subalpine <i>Tsuga–Abies–Picea–Betula</i>	10.8–17.2	83.8–133.7	—	—	—	Kanzaki 1984
North Carolina – Tennessee	Old-growth subalpine <i>Picea–Abies</i>	36	66	15–150	0.6–0.9	111–178	White et al. 1985a
New Hampshire	Subalpine <i>Picea–Abies</i>	33	—	18 m ² – 12.2 ha	—	303	Foster and Reiners 1986
New Hampshire	Subalpine <i>Picea–Abies</i>	6–33	45–145 ^b	—	—	—	Worrall and Harrington 1988
		40–77 ^b	—	—	—	—	
Japan	Mixed <i>Abies</i> –hardwoods	21.5	141	22–318	—	—	Ishikawa and Ito 1989
Sweden	Old-growth <i>Picea abies</i>	28	100	71–139	—	—	Leemans 1990
Sweden	Primeval <i>Picea abies</i>	31	84.2	9–360	—	170–228	Liu and Hytteborn 1991; Hytteborn et al. 1991
Sweden	Old-growth <i>Picea abies</i>	—	—	—	—	200	Hofgaard 1993b
Japan	Subalpine coniferous	7.3–8.5	40.8–42.5	1.2–285	—	—	Yamamoto 1993
Japan	Subalpine <i>Picea–Abies</i>	19.3	—	5–1245	—	—	Kubota et al. 1994
New York	Subalpine <i>Abies–Picea</i>	15	72 ^c	—	—	—	Battles et al. 1995
Japan	Subalpine <i>Abies–Tsuga</i>	7.3	43.3	3.6–369.6	—	—	Yamamoto 1995, 1996
New York – New Hampshire	Subalpine <i>Picea–Abies</i>	15–42 ^b	25–93 ^{bc}	12–1135 ^b	—	—	Battles and Fahey 1996
Japan	Subalpine <i>Abies–Picea–Betula</i>	—	—	—	1.2–2.4	87–99	Hiura et al. 1996
Russia	<i>Picea abies</i>	35	<200 (95% of all gaps <100 (65%))	—	—	—	Drobyshev 1999
Temperate hardwood forests							
Indiana	Old-growth <i>Fagus–Acer</i>	—	101	22–252	—	—	Williamson 1975
Tennessee	Mature hardwoods	—	90 ^{cd}	8–404 ^d	—	—	Barden 1981
United States	Old-growth mesic hardwoods	—	200	28–2009	—	—	Runkle 1981

Table 2. (continued)

Location	Forest type	Gap fraction (%)	Average gap size (m ²)	Gap range (m ²)	Annual gap formation rate (%)	Turnover rate (years)	Reference
Japan	Evergreen broadleaf	20	92	19.5–390	0.56	180	Naka 1982
United States	Old-growth mesic hardwoods	9.5	28–69	25–1500	1	100	Runkle 1982
Japan	Climax <i>Fagus</i>	20	137	10–470	0.45–1.03	100–200	Nakashizuka 1984
Japan	Primary <i>Fagus</i>	—	—	54–144	—	—	Ohkubo et al. 1988
Indiana	Old-growth hardwoods	9	52.4	25–375	—	—	Ward and Parker 1989
Japan	Climax <i>Fagus</i>	12	92	≤728	—	134	Yamamoto 1989
Québec	Old-growth <i>Acer–Betula</i>	—	126	9–385	—	45	Payette et al. 1990
Ohio	Old-growth <i>Acer–Fagus</i>	7	≤200	—	0.8–0.9	110–125	Runkle 1990
		14.1 ^b	100–400 ^b	—	—	—	
Michigan	Old-growth <i>Acer–Tsuga</i>	—	—	—	0.57–0.69	145–175	Frelich and Lorimer 1991
New York	Mature northern hardwoods	8.4	42.8	—	—	—	Krasney and Whitmore 1992
		20.7 ^b	209.1 ^b	—	—	—	
Japan	Old-growth temperate deciduous	6.2	—	—	0.42	58–240	Nakashizuka et al. 1992
Japan	Primary evergreen broadleaf	15.7	80.3	—	—	—	Yamamoto 1992 ^b
North Carolina	Mixed <i>Quercus</i>	2	239	40–850	0.8	—	Clinton et al. 1993
North Carolina	Mixed <i>Quercus</i>	—	227	60–630	—	—	Clinton et al. 1994
Japan	Old-growth evergreen broadleaf	17	77.1	≤568.3	—	—	Yamamoto 1994
		8.3	55.8	≤181.5	—	—	
Japan	Old-growth temperate deciduous	—	70	5–330	—	—	Abe et al. 1995
Michigan	Old-growth <i>Acer–Tsuga</i>	—	—	—	0.54	186	Parshall 1995; Frelich and Graumlich 1994
Japan	Old-growth evergreen broadleaf	6.9	67.3	—	—	—	Tanouchi and Yamamoto 1995
Michigan	Old-growth <i>Acer–Tsuga</i>	—	44.8 ^f	—	0.78 ^f	128 ^f	Dahir and Lorimer 1996
		—	44.2 ^g	—	0.52 ^g	192 ^g	

Table 2. (continued)

Location	Forest type	Gap fraction (%)	Average gap size (m ²)	Gap range (m ²)	Annual gap formation rate (%)	Turnover rate (years)	Reference
Japan	Cool-temperate	13.8	92	—	—	—	Yamamoto 1996
	Warm temperate	17	77.1	—	—	—	
Japan	Old-growth temperate deciduous	8.8–20.2	103.6–189.9	—	0.78	127/162	Tanaka and Nakashizuka 1997
Great Smokey Mountains, U.S.A.	Old-growth temperate deciduous	10	—	—	—	—	Busing 1998b
Maine	Northern hardwood and mixedwood	—	38.6–57.9	4.1–712.6	1.05–1.27	<100	Chokkalingam 1998
Japan	<i>Fagus</i> chronosequence	1.7–4.6 ^h 9.5–20.0 ⁱ	19.4–40.0 ^h 65.0–162.8 ⁱ	— —	— —	— —	Yamamoto and Nishimura 1999
Temperate coniferous forests							
Oregon	Old-growth <i>Pseudotsuga</i>	—	—	—	—	—	Stewart 1986
Oregon–Washington	<i>Pseudotsuga</i> – <i>Tsuga</i>	13.1 ⁱ	85 ^{ci}	~25–380	0.2 ⁱ	—	Spies et al. 1990
British Columbia	Old-growth subalpine <i>Abies</i> – <i>Tsuga</i>	18.2 ^j	19 ^{cj}	—	0.3 ^j	—	
California	Old-growth mixed-evergreen	18	77	5–525	—	280–1000	Lertzman and Krebs 1991
British Columbia	Temperate rainforest	11.1	131	8–734	—	—	Hunter and Parker 1993
		14	—	—	—	350–950	Lertzman et al. 1996
Tropical forests							
Costa Rica	Tropical wet	3.6–7.5	54–120	—	0.72–1.3	80–138	Hartshorn 1978
Panama	Tropical moist	—	—	—	0.73	137	Lang and Knight 1983
Mexico	Tropical cloud	—	—	—	0.5	158	Arriaga 1988a
Costa Rica	Tropical cloud	—	—	>4–135+	0.8–1.4	95	Lawton and Putz 1998
Ecuador	Lowland rainforest	1.4	10	—	—	—	Kapos et al. 1990
		5.1	15	—	—	—	

Table 2. (continued)

Location	Forest type	Gap fraction (%)	Average gap size (m ²)	Gap range (m ²)	Annual gap formation rate (%)	Turnover rate (years)	Reference
Ivory Coast	Tropical moist	0.84	41	11–244	—	244	Jans et al. 1993
India	Tropical wet evergreen	3.6	—	≤500	1.13	83	Chandrashekara and Ramakrishnan 1994
Ivory Coast	Lowland evergreen	0.84	41	—	—	—	Poorter et al. 1994
Panama	Tropical moist	4.3	79	8–604	0.45–6.5	—	Yavitt et al. 1995
Panama	Lowland tropical	2.0 ^h	64 ^h	22–232 ^h	0.63 ^h	159 ^h	Brokaw 1996
		2.8 ⁱ	86 ⁱ	26–342 ⁱ	0.88 ⁱ	114 ⁱ	
Christmas Island	Tropical	—	45.9	17–700	—	—	Green 1996
French Guiana	Lowland rainforest	1.1	120	—	0.96	—	van der Meer and Bongers 1996a
French Guiana	Lowland rainforest	—	—	—	1.3–1.5	—	van der Meer and Bongers 1996b
Southern hemisphere forests							
Chile	Temperate rain forest	8.6 ^k	432 ^{bck}	120–1532 ^{bk}	—	392 ^k	Veblen 1985a
		3.3–6.6 ^l	151–200 ^{bcl}	66–1060 ^{bl}	—	633–794 ^l	
Argentina	Old-growth <i>Nothofagus</i>	—	102–603 ^{bc}	294–3462 ^b	—	—	Veblen 1989
New Zealand	Old-growth <i>Nothofagus</i>	—	—	—	—	—	Stewart and Rose 1990
New Zealand	Subalpine montane	2.8 ^m	39.5 ^m	—	0.28 ^m	360 ^m	Ogden et al. 1991
		2.5 ^k	67.8 ^k	—	0.25 ^k	400 ^k	
New Zealand	Old-growth <i>Nothofagus</i>	4–15	93 ^c	24–528	—	—	Stewart et al. 1991
Chile	Old-growth <i>Fitzroya</i>	—	143 ^c	37–736 ^c	—	—	Donoso et al. 1993
Argentina	Old-growth <i>Nothofagus</i>	15.6 ^c	106	19–372	—	320–448	Rebertus and Veblen 1993
		9.1	—	—	—	—	
		34.8	—	—	—	—	
		12.1	61	26–898	—	331–415	
		11.6	104	18–1476	—	346–519	
South Africa	Plateau	9.9	37.9	3.9–122.2	—	450	Midgley et al. 1995
		2.1	20.5	0.1–73.6	—	—	

Table 2. (concluded)

Location	Forest type	Gap fraction (%)	Average gap size (m ²)	Gap range (m ²)	Annual gap formation rate (%)	Turnover rate (years)	Reference
Summary statistics for Table 2 (range values; median values in parentheses)							
	Boreal and subalpine	6–36 (21)	41–141 (78)	15–1245	0.6–2.4 (1.0)	87–303 (174)	
	Temperate hardwoods	2–20 (10)	28–239 (79)	8–2009	0.4–1.3 (0.8)	45–240 (134)	
	Temperate coniferous	11–18 (14)	77–131 (85)	5–734	0.2	280–1000 (650)	
	Tropical	0.8–8 (4)	10–120 (50)	4–700	0.5–6.5 (1.0)	80–244 (137)	
	Southern hemisphere ⁿ	3–35 (8)	40–143 (93)	24–1476	0.25–0.28 (0.3)	320–794 (408)	

^aUnless otherwise noted, all gap measures refer to actual canopy gaps which are defined as the projection of the canopy edge on the forest floor (Runkle 1992).

^bExpanded canopy gap is defined as the area circumscribed by the boles of the canopy trees whose foliage borders the actual gap.

^cMedian values.

^dSingle-tree gaps.

^eMulti-tree gaps.

^fStands dominated by *Acer saccharum*.

^gStands dominated by *Tsuga heterophylla*.

^hDeveloping stands.

ⁱOld-growth stands.

^jMature stands.

^kMontane stands.

^lLowland stands.

^mSubalpine stands.

ⁿFigures for South Africa were excluded.

Gap turnover time will depend on the rate of gap infilling, the recruitment and growth of seedlings in the gaps, and the rate of gap expansion (Valverde and Silvertown 1997). In turn, the growth of seedlings, whether established before the gap event as advance regeneration or subsequently recruited after gap establishment, is determined by the rate and quantity of resource allocation in the newly acquired growing space. Closure of small gaps will depend to a large degree on lateral branch infilling by surrounding canopy trees, whereas closure of large gaps occurs more through the growth of released or newly recruited trees (Runkle 1990). Annual lateral growth rates of hardwoods have been calculated at 4–26 cm (Runkle 1985a), 18 cm (Runkle 1990), and 12 cm (Runkle 1998). Gaps were considered closed when hardwood saplings had reached a height of 10–20 m (Runkle 1981). This height growth, combined with the estimated rates of lateral infilling, resulted in a range of maximum possible gap ages of 10–40 years (Runkle 1982). In montane and lowland Chilean rain forests, gaps were determined to be no older than 32 and 50 years, respectively (Veblen 1985a). Gaps in old-growth Douglas fir were estimated to have begun at least 50 years ago, with gaps in the mature 140-year-old forest being much younger (Spies et al. 1990). The oldest gaps in a Swedish boreal forest were at most 70 years old (Liu and Hytteborn 1991).

Median values for the annual gap formation rate are quite similar for boreal, temperate hardwood, and tropical forests, ranging from 0.8 to 1.0% (Table 2). Both temperate coniferous and Southern hemisphere forests have lower gap formation rates of 0.2%. This translates into almost equal turnover rates for temperate and tropical forests (135 years) with a slightly higher figure of 174 years for northern boreal forests. Temperate coniferous forests and southern hemisphere *Nothofagus* forests exhibit the slowest turnover rates of 400 to 650 years (Table 2). Gaps are shorter lived in temperate and tropical forests, tending to fill in at a quicker rate. Slow turnover rates for the northern and southern hemisphere temperate rain forests are in part attributable to the relatively long life span of the respective tree species. It is interesting to note the generally large area in gaps documented for the Appalachian and Swedish boreal forests relative to other studies. Furthermore, these gaps tend to be much older than gaps in tropical and temperate forests. Gap recruitment and gap filling in cold, slow-growing northern forests are probably very slow compared with that occurring in most temperate and tropical forests. As expected, gap fraction is lowest in tropical forests.

Gaps and tree recruitment

Availability of light

Most studies on tree regeneration and gap structure have focused on the relationship among gap size, associated light levels, and regeneration success. Of particular interest has been the effect of gap size and gap position on the flux of solar radiation and its effect on the germination, survival, and growth of tree species. The spatial and diurnal flux of photosynthetically active radiation in forest gaps has been shown to be a pre-eminent factor in seedling survival and growth, particularly in tropical forests (Denslow 1987; Denslow and Hartshorn 1994; Nicotra et al. 1999). At any particular location, the amount of light entering the gap depends on the size and topographic position of the gap, the position within the gap, the height of the surrounding canopy, the sun angle, and sky conditions (Messier 1996).

Chazdon and Fetcher (1984), in their study of light fluxes in tropical forests, estimated total incident photosynthetically active radiation at 1–2% of full sunlight in the understory, 9% in the centre of a 200 m² gap, and 20–35% in a 400 m² gap. In similar forests, Denslow et al. (1990) determined the total incident radiation to be the highest in gap centres (9–23% of full sunlight). At the gap–forest edges, radiation was 3–11% of the full sunlight with the understory showing a low 0.4–2% of full sunlight.

Differential response of tree species to light flux under closed forest canopies and in gaps has long been known to foresters who have provisionally segregated tree species in terms of their ability to germinate, survive, and grow under varying degrees of shade (Baker 1949). Such defined differences in shade tolerance, though often expressed in relative, descriptive terms, have long provided a useful and functional foundation to silvicultural systems in many forest types around the world.

According to Marks (1974), forests respond to canopy openings from disturbance in two major ways: by responding through reorganization of vegetation established prior to disturbance or by responding as vegetation that becomes established following disturbance. The coupling of the long-held notions of shade tolerance with the recent interest in gap dynamics has emerged as workers attempt to relate gap physiognomy with differential recruitment of tree species. The size of gaps in closed forests has been shown to determine the type of trees recruited in the gaps. Small gaps coupled with advance regeneration of shade-tolerant species would favour the “reorganization” response as defined by Marks (1974). Seed colonization of large gaps by shade-intolerant species would define the other extreme.

Using extensive work in tropical forests as a basis, Whitmore (1978, 1989) and Brokaw (1985*b*) divided trees that colonize gaps into two contrasting ecologic groups: those termed climax or primary species (non-pioneer) and pioneer species. Despite the recognition that a continuum of regeneration strategies exist, the classification of trees into two regeneration types has proven quite useful. Climax or shade-tolerant species are able to establish themselves under shade as advance regeneration and will respond to small gaps. Light-demanding or pioneer species are often recruited only in larger gaps and are usually established after gap formation. Gap formation, therefore, not only drives the forest growth cycle but also determines forest floristics (Whitmore 1982). Gap regeneration behaviors have also been delineated for tree species in undisturbed primary forests in Japan (Yamamoto 1989, 1992*b*).

Gap research has focused heavily on the preference of different tree species for larger or smaller gaps in determining forest regeneration dynamics. It has been well established that gap size is a major factor determining post-disturbance tree species composition. Shade-intolerant and shade-tolerant species exhibit differential recruitment depending on the size of canopy gaps (Hartshorn 1978; Whitmore 1978; Barden 1979, 1980; Hibbs 1982; Runkle 1982; Pickett 1983; Nakashizuka 1985; Brokaw 1985*a*, 1985*b*, 1987; Denslow 1987; Bongers et al. 1988; Brokaw and Scheiner 1989; Raich and Gong 1990; Veblen 1992; Nakashizuka et al. 1992; Orwig and Abrams 1994; Abe et al. 1995; Tanouchi and Yamamoto 1995; Abe et al. 1998). Species considered intolerant are relatively more abundant in large gaps while tolerant species often grow more abundantly in smaller gaps. Large gaps in old-growth stands are generally considered essential for the establishment of shade-intolerant species such as tulip tree (*Liriodendron tulipifera* L.) (Buckner and McCracken 1978; Runkle 1984; Clebsch and Busing 1989; Busing 1995). Pin cherry (*Prunus pensylvanica* L.f.) and paper birch both require conditions associated with larger gaps relative to beech (*Fagus grandifolia* Ehrh.) and sugar maple, which are usually considered as adapted to conditions characteristic of small gaps (McClure and Lee 1993). Busing (1994), in a study of old-growth Appalachian cove forests, determined that a gap size of 0.04 ha was a threshold size below which intolerant species were not able to establish. Although able to germinate in a shaded understory, seedlings of the Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.) need gaps greater than 95 m² to survive and grow into saplings (Myers et al. 2000).

In general, shade-tolerant species, usually existing as advance regeneration, have a greater chance of responding to small gap openings or even to small increases in ambient light levels from diffuse radiation. The physiological and morphological plasticity of shade-tolerant species allows rapid response to increased light environments. Less tolerant species, on the other hand, may still persist in canopies of shade-tolerant forests because of their opportunistic exploitation of larger gaps. A diversity of gap sizes may therefore be significant in the maintenance of canopy diversity in old-growth forests (Barden 1979, 1980, 1981; Runkle 1982; Canham 1989; Clebsch and Busing 1989; Ward and Parker 1989; McClure and Lee 1993; Tanouchi and Yamamoto 1995; Busing and White 1997; Busing 1998*a*, 1998*b*).

Much study has been made of the compositional stability of beech – sugar maple forests (Poulson and Platt 1996) and the hemlock (*Tsuga canadensis* (L.) Carr) – beech – maple forests in the Great Lakes region (Frelich and Lorimer 1991; Frelich et al. 1993; Tyrrell and Crow 1994*a*). Allogetic coexistence of shade-tolerant species is explained by a long-term disturbance regime characterized by small light gaps. Beech, maple, and hemlock, being able to persist as advance regeneration in the shaded conditions of the dominant canopy, may fluctuate in relative dominance, but will maintain control of the canopy.

This self-replacement of beech, sugar maple and eastern hemlock via small-scale gap dynamics has been noted by a number of workers (Brewer and Merritt 1978; Woods 1979; Woods and Whittaker 1981; Runkle 1981, 1984, 1990, 1998). Under present climatic conditions, gap-phase dynamics is sufficient to maintain canopy species composition. Small gap maintenance of canopy compositional stability has also been reported for several forest types in Japan (Shimizu 1984; Hara 1985). Catastrophic canopy disturbances would be required to significantly change canopy species composition.

Along with gap size, heterogeneity of light flux, and regeneration response are also dependent on gap position and orientation. In the northern hemisphere, the north end of an open gap is subject to higher light fluxes than the more shaded southern edge. Coates (1998, 2000), in a study of tree response to gaps in partially cut western red cedar (*Thuja plicata* Donn) – hemlock forests, demonstrated an increase in light gradients throughout the growing season from the southern to the northern edge of gaps. Emergence and early survival of all species were greatest in the shade of the south gap edge, a fact attributed to the negative effects of direct sunlight in the northern gap edges. For planted seedlings, however, the best growth was found in the sunnier middle to northern ends of the gaps. Such discordance between regeneration niche and growth niche is common among forest tree species of western North America (Coates 1998). Differential patterns of tree growth in different gap positions have also been determined for *Nothofagus* species in New Zealand (Runkle et al. 1995), old-growth eastern hardwoods of Michigan (Poulson and Platt 1989), and for Norway spruce in Sweden (Dai 1996).

Other than the study by Dai (1996), no detailed work seems to have been done on the relationship among gap geometry, light availability, and tree recruitment in boreal forests. Work to date has focused, for the most part, on confirming the importance of canopy gap size for seedling recruitment and growth in old-growth boreal forests (Leemans 1990; Liu and Hytteborn 1991; Drobyshev 1999; Drobyshev and Nihlgård 2000).

Light, canopy architecture, and latitude

Light regimes under gaps and forest canopy are significantly affected by both canopy architecture and latitude (Poulson and Platt 1989; Canham and Burbank 1994; Lieffers et al. 1999). One would expect that single tree gaps formed in tall, closed-canopy tropical forests would produce different light regimes than gaps formed in more open, boreal conifer forests growing at high latitudes. Canham et al. (1990), in their comparative study of light regimes in gap-disturbed temperate and tropical forests, were able to demonstrate the significant effect of latitude and canopy architecture on gap light regimes. The high ratio of tree height to crown width in old-growth Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, for example, minimized any change in gap light regimes. Gaps of up to 500 m² had little effect on light levels on the forest floor. Similar effects of the height and architecture of the gap periphery trees on gap light regimes were noted in montane rain forests of Costa Rica (Lawton 1990).

In northern latitude boreal forests, where canopies may be more open because of slow growth rates and nutrient limitations, the interaction of the gap aperture and the low angle of solar radiation produces a different gap light regime than that found in temperate or tropical forests. Canham et al. (1990) demonstrated the significant penetration of light into the understory adjacent to a gap (extended gap), particularly at high latitudes. In a study of gap dynamics in high latitude *Larix gmelini* old-growth in northeastern China, Ban et al. (1998) found that obliquely projected gaps were more important than vertically projected gaps in explaining regeneration patterns. Direct beam radiation is less intense and able to spread through the stand much beyond the actual vertical gap. It has been suggested that the transition to narrow crowned, strongly epinastic boreal forests in the high latitudes is partly a function of the greater ability of vertically extended crowns to use photosynthetically active radiation compared with the broad, horizontally stratified crowns of the lower latitudes (Kuuluvainen 1992). In high latitudes, vertical crown growth is seen as the prime mechanism enabling trees to capture a greater amount of the low angle radiation. Developers of recent gap light models have recognized the critical importance of latitude in determining gap light regimes (Canham 1988a; Dai 1996; Weishampel and Urban 1996).

Gaps in boreal forests are therefore not the same environments as gaps in lower latitudes in terms of changed gap light regimes. Overall, high light levels should occur under much more restricted conditions in boreal forests. This lower light flux, however, is offset by the generally broader transmission of light through conifer canopies, the photosynthetic significance of sunflecks, and specific adaptive mechanisms of northern conifers to low light availability.

Below-ground competition

The majority of gap studies have focused on changes in light availability with gap formation. Concurrent with the changes in the above-ground plant competitive environment may be changes in the below-ground competitive environment (Casper and Jackson 1997). The flux and heterogeneity of solar radiation across the gap–non-gap interface is important in determining regeneration dynamics in many forest types. Little work, however, has been conducted on the effect of gap formation on below-ground competition. An emphasis on the relationship between gap dynamics and below-ground competition may be particularly fruitful, especially in sub-boreal or boreal forests. The generally open nature of many old-growth boreal forests (Liu and Hytteborn 1991; Kneeshaw and Burton 1997) and the well-established acceptance of boreal forests as nitrogen limited (Krause et al. 1978) both support the hypothesis that reduction in root competition with tree death and fall is a major determinant of regeneration dynamics in these forests.

In open-grown, nutrient-poor, boreal forests where the canopy never closes, the overstory trees may be expected to suppress any advance regeneration through extensive root competition (Ågren and Zackrisson 1990; Tilman 1997). In such open forests at high latitudes, one would not expect light to be the dominant limiting factor. Even in light openings, seedlings and saplings may remain in a suppressed state for long periods of time, waiting for sufficient reduction in root competition before being released. Evidence is accumulating that below-ground competition for nutrients is a major factor affecting growth on nutrient-poor Scots pine (Kuuluvainen et al. 1993; Kuuluvainen 1994) and black spruce sites (Newton and Jolliffe 1993). Trenching studies in temperate forests have confirmed the importance of significant below-ground competitive effects (Toumey and Kienholz, 1931; Korstian and Coile 1938; Christy 1986; Coomes and Grubb 2000).

Actual measurements of temporal and spatial dynamics of nutrient fluxes under distinct gaps in boreal forests are not available. Work to date has focused on tropical and temperate forests, but conclusions are not entirely consistent. Early work in tropical forests by Vitousek and Denslow (1986) and Uhl et al. (1988) failed to detect consistent, significant differences in nutrient levels in gaps relative to closed canopy. Recent work by Denslow et al. (1998) found that increases in nitrate-N and extractable phosphate-P in artificially created gaps may enhance growth rates of pioneer tree species. Zhang and Liang (1995) and Zhang and Zak (1995), working in subtropical forests in China, observed that a gap threshold of about 15 m in diameter was critical in determining the rate of nutrient release from plant decomposition. Below this gap size, decomposition processes were not affected. Above this gap size, however, nutrient release from litter decomposition was strongly inhibited. In single-treefall gaps in hemlock and sugar maple stands, differences in nitrogen dynamics were significant (Mladenoff 1987), with the doubling of nitrate levels in the hemlock gaps of greatest import. Palik et al. (1997) also found increased nitrogen levels in the centres of large openings in generally open-canopied longleaf pine (*Pinus palustris* Mill.) stands in Georgia. Seedling growth was related to both light and below-ground nitrogen levels. Similarly, in lodgepole pine (*Pinus contorta* Dougl.) forests, root gaps were detected in artificially created light gaps of at least 30 trees (Parsons et al. 1994a) with increases in mineralized nitrogen evident in gaps created by the removal of at least 15–30 trees (Parsons et al. 1994b). In German beech forests, root gaps were present up to 3 years after the creation of artificial gaps 30 m in diameter (Bauhus and Bartsch 1996). Below-ground root gaps were also found under experimentally created canopy gaps in deciduous forests (Wilczynski and Pickett 1993) and in naturally uneven-aged longleaf pine forests in Florida (Brockway and Outcalt 1998). In tropical forests, conflicting results have emerged

with tree falls either creating root gaps (Sanford 1989; Ostertag 1998) or having no effect on below-ground root distribution (Sanford 1990). In a single study in the boreal forest, no evidence was found for reduction in fine root production in small (<100 m²) above-ground gaps (Campbell et al. 1998).

Despite the somewhat ambiguous results, partly explained no doubt by high soil variability, diverse methodological procedures, and inherent problems encountered in studying below-ground structure and processes, it is clear that changes in forest stand structure and density can significantly affect below-ground nutrient processes and plant competitive relationships. On nutrient-limited sites in generally open-grown boreal forests, competition for nitrogen rather than light may play a more significant role in determining regeneration recruitment and growth. Loss of mature trees from the canopy may reduce competition for nitrogen and promote release of previously suppressed seedlings. Reduction of intense below-ground competition in combination with increased light levels in canopy gaps may promote seedling establishment and release of suppressed trees.

Resource heterogeneity

The preceding discussion has emphasized the relationship between gap size and geometry and light resources in the determination of the species composition of forest gaps. Many other factors, however, determine which individuals or species are able to successfully establish themselves in forest gaps. Hartshorn (1978) recognized the importance of variables other than gap size that influence the successful regeneration of tree species in gaps. These included (1) time of gap occurrence, (2) proximity of seed source to gaps and mechanism of seed dispersal, (3) substrate conditions, and (4) plant–herbivore relations. Furthermore, Bazzaz (1996) described a number of plant traits that even further complicate gap dynamic processes: (1) many shade-tolerant species require gaps in the canopy to reach maturity, (2) understory seedlings may experience damage or mortality in response to sudden increases in light flux, (3) some pioneer species may be able to take advantage of diffuse radiation, whereas many shade-tolerant species are dependent on some brief period of direct radiation, and (4) even when resources such as light and nutrients are limiting, tree seedlings may not always respond to increased resource levels.

Bazzaz and Wayne (1994) stressed the complicated nature of resource heterogeneity across the gap–non-gap continuum. Because spatiotemporal heterogeneity is scale dependent, it may not be obvious which scale is appropriate to detect meaningful variation that is causing differences in species composition and density. Furthermore, Bazzaz and Wayne (1994) distinguished between what they termed “measured” and “functional” heterogeneity. Measured heterogeneity is what ecologists record with their instruments in the field. Functional heterogeneity, on the other hand, is what plants actually respond to. The gradients, therefore, of one or several variables measured across the gap – closed canopy continuum may not correspond to the actual gradients experienced by different species, genotypes, or phenotypes. For example, changes in gap size may not result in concomitant changes in gap microclimate (Brown 1993) or resource allocation (Kuuluvainen et al. 1993). It is with caution, therefore, that one accepts the simple gap–non-gap or “Swiss cheese” description of forest ecosystems (Lieberman et al. 1989).

While cognizant of this fact, however, the vast majority of gap researchers have focused on the resource gradient and species response across the gap–understory continuum. Bazzaz and Wayne (1994) described it succinctly: “The primary questions we focus on (in gap dynamic research) are: What are the ecologically relevant quantitative and (or) qualitative differences in the microenvironmental conditions at different points across the gap–understory continuum, and what are the physiological and demographic characteristics of species’ seedlings that occupy different portions of the continuum?” It is evident, however, that an understanding of the gap–non-gap interface as a continuum is somewhat limited. Resources do not necessarily display a gradual continuum in flux and concentration but are inherently heterogeneous from the gap centre into the closed forest. A prime determinant of such heterogeneity is the microsite.

Microsite

Of particular importance in determining seed germination and early tree establishment in gaps is the nature and abundance of forest floor substrates or microsites found in subcanopy and open gap positions (Zasada et al. 1992; Duchesneau and Morin 1999; Greene et al. 1999). Tree recruitment is often more dependent on microsite quality, which may override the effect of standing tree basal area, gap size, and resource gradients in gaps (Houle 1992; Lundqvist and Fridman 1996; Gray and Spies 1997), especially for shade-tolerant fir and spruce. Microsite variability may be a factor of forest floor disturbance and the presence of exposed mineral soil, amount and type of coarse woody debris, and degree of competing vegetation.

Recent studies have emphasized the role of coarse woody debris as an important structural component of balsam fir forests (Lang 1985; Sturtevant et al. 1997), northwest coniferous forests (Sollins 1982; Spies et al. 1988), old-growth Scandinavian boreal forests (Linder et al. 1997; Jonsson 2000; Siitonen et al. 2000), European mixedwood forests (Falinski 1978), and old-growth hemlock–hardwood forests (Tyrrell and Crow 1994*b*). The amount, type, and degree of decomposition of coarse woody debris on the forest floor significantly determine seed germination and survival and growth of tree seedlings in many forest ecosystems (Harmon et al. 1986). Fallen logs, upon suitable decay, act as nurse logs or preferred sites of germination. Fallen wood, although making up only a small percentage of the microsites, accounts for a disproportionate percentage of established seedlings. This phenomenon is well documented for a variety of forest types, including the temperate rainforests of western North America (Christy and Mack 1984; Harmon and Franklin 1989; Deal et al. 1991) and Chile (Lusk 1995), Rocky Mountain spruce–fir forests (Knapp and Smith 1982), balsam fir forests (McLaren and Janke 1996), Japanese spruce–fir forests (Takahashi 1994), and Scandinavian Norway spruce dominated forests (Sirén 1955; Jonsson 1990; Hofgaard 1993*b*; Hörnberg et al. 1997). Similarly, Szewczyk and Szwagrzyk (1996) observed that spruce and fir seedlings were much more pronounced on rotten wood compared with mineral soil. Such differentiation in density and species composition on rotten wood has been attributed to the reduced competition from herbs and mosses on the raised surfaces of the coarse woody debris (Harmon and Franklin 1989) and retention of favourable moisture supplies (Place 1955). Well documented is the observation that spruce seedlings, when compared with fir seedlings, show a preference for coarse woody debris as a site of germination and early growth (Bedell 1948; Rowe 1955; Day 1964; Wagg 1964; DeLong et al. 1997; Hörnberg et al. 1997). Fir seedlings, while possessing the ability to germinate on decayed wood, are also able to germinate on a variety of other microsites, including thick litter layers and sites dominated by mosses (Nakamura 1992; Simard et al. 1998). This is generally attributed to the more robust nature of the fir seedling, which possesses greater root growth and deeper penetration than spruce seedlings (Place 1955).

Uprooting of trees normally exposes the mineral soil and disrupts the soil profile (Brown 1977; Bormann et al. 1995). Treefalls that expose mineral soil and produce pit and mound topography create a diversity of microsites conducive to the establishment and growth of particular tree, moss, and herbaceous species (Beatty and Stone, 1986; Schatzl et al. 1989 *a*, 1989*b*; Jonsson and Esseen 1990; Jonsson and Dynesius 1993; den Ouden and Alaback 1996; Rydgren et al. 1998; Ulanova 2000). The etiology of any particular gap-maker (Putz et al. 1983) should significantly affect resource heterogeneity and flux in the gap. Whether a tree dies and remains standing for a significant period of time, breaks off above the ground, or uproots to create forest floor and soil disturbance will determine the type of microsite available for subsequent colonization.

The pit and mound topography characteristic of uprooting may persist for centuries (Lyford and MacLean 1966; Schatzl and Follmer 1990). The pit and the mound act as unique microsites that can determine tree species composition, growth, and density (Peterson and Pickett 1990; Peterson et al. 1990). Trees classified as pioneers are often found regenerating preferentially on disturbed soil in treefall gaps (Henry and Swan 1974; Putz 1983; Nakashizuka 1989). Hence, so-called “early successional species” are able to persist in the canopy dominated by late successional species because of periodic

tree uprooting. This is quite evident in the boreal forests of Newfoundland where shade-intolerant white birch persists in the mature canopy of old-growth balsam fir – spruce forests. This is due, probably, to the prolific seedling and robust dissemination of white birch and its ability to germinate well on the exposed mineral soil of root mounds (Marquis et al. 1964; Safford et al. 1990).

Non-tree vegetation may often respond to the increased resource fluxes in gaps and act as an important factor mitigating against the successful response of tree species. Trees may not respond, therefore, in a predictable fashion to gap openings because of above- and below-ground competition effected by a flourishing ground vegetation. Response of competing vegetation may depend on gap size. Single elm (*Ulmus americana* L.) tree gaps resulted in the regeneration of canopy dominants whereas multiple-tree gaps enhanced successful shrub regeneration, effectively suppressing regeneration of the tree dominants (Huenneke 1983). On productive sites in boreal and hardwood forests, red raspberry (*Rubus isaeus* L.) may germinate profusely from the abundant forest floor seed bank in response to canopy disturbance and quickly occupy the growing space (Ruel 1992; Osawa 1994; Ricard and Messier 1996), effectively competing with conifer regeneration (Lautenschlager 1999). Bamboo species may act as effective competitors of fir in Chinese, Japanese, and Himalayan forests (Taylor and Zisheng 1988a; Kojima 1995; Gratzner et al. 1999). In boreal forests, competition from members of the Ericaceae (e.g., *Vaccinium*, *Kalmia*, *Empetrum*) is common, particularly on the generally poorer, late successional sites. These shrubs possess strong ability to negatively affect the successful establishment of conifer seedlings (Damman 1967; Meades 1983; Jäderlund et al. 1997; Zackrisson et al. 1997). Most of these studies showing intense competitive effects of the Ericaceae, however, have been conducted on open sites, often after significant site disturbance such as clear-cutting. In small gap disturbance, however, advance tree regeneration may respond more vigorously than any shrubs that are present, effectively minimizing any potential competitive interactions (Alaback and Tappeiner II, 1991).

Herb patches have also been shown to exercise significant effects on the density and distribution of seedlings of canopy dominants (Maguire and Forman 1983). In hardwood forests, herb density, leaf cover, and species richness have increased in response to forest gaps (Moore and Vankat 1986; Goldblum 1997). Studies that included the creation of artificial gaps have shown both positive response (Reader and Bricker 1992) or no real response (Collins and Pickett 1987, 1988a, 1988b) of herbs to canopy openings. The short time span of various studies, a lack of soil disturbance in artificially created gaps, and a host of other constraints on herb response in gaps may account for the ambiguous results (Collins et al. 1985).

Gap partitioning

The gap partitioning hypothesis was initially proposed as a mechanism to help explain the well-known difference in species diversity between tropical and temperate forests (Ricklefs 1977; Denslow 1980). It was proposed that the gradients of environmental heterogeneity between closed forest canopy and gaps within the canopy were much steeper or broader in tropical forests compared with temperate forests. It was thought that the greater micro-heterogeneity found in tropical gaps would promote increased niche specialization (Grubb 1977), resulting in greater species diversity in tropical forests. The hypothesis assumes that generalist species are not common, but that species have evolved to take advantage of the range of resource fluxes found in the gap-closed forest continuum. Species are not generally able to take full advantage of the wide gradient of resources available across the gap. Instead, species differ in habitat preference and therefore perform differentially in different positions in the gap. In other words, species have the potential to partition the gap understory environment (Bazzaz 1996).

Despite the theoretical recognition of the possibility of gap partition, results in field situations have proved inconsistent, with no clear picture of gap partitioning emerging. Concerns surround methodology, particularly control over field experiments. Sipe and Bazzaz (1995) noted that an adequate experimental test of gap partitioning would have to include simultaneous measurements of field microclimates, species ecophysiology, and growth responses over time in a fully controlled field experiment. Studies

supporting the theory of gap partitioning in tropical systems have based their conclusions on floristic analysis of recognized zones in gaps (Brandani et al. 1988; Núñez-Farfán and Dirzo 1988). Other studies characterized by a stronger, more controlled experimental methodology failed to find adequate evidence that different tree species consistently favoured distinct gap positions (Whitmore and Brown 1996). Acknowledging a photosynthetic potential for gap partitioning among species of New England *Acer* (Sipe and Bazzaz 1994), limited evidence of gap partitioning was identified (Sipe and Bazzaz 1995). Both Barton (1984) and Gray and Spies (1996) provided limited evidence of gap partitioning, while Wright et al. (1998) noted little evidence of gap partitioning in interior cedar–hemlock forests of northwest British Columbia. As far as is known, no study of gap partitioning has been conducted in boreal forests.

Short-term climatic change

Gap disturbance occurs within the context of changing climatic parameters. In northern boreal forests, climate–vegetation interactions are significant (Bonan and Shugart 1989). Recent research has treated the advance and retreat of tree-line forests as proxy indicators of long-term millennial climatic change (Payette and Lavoie 1994). It has been noted, however, that boreal forests, at both the tree line and in denser forests to the south, are able to undergo important decadal-level changes in regeneration, mortality, and canopy structure in response to climatic variability (Hofgaard 1997). Of note is the documented phenotypic plasticity of spruce canopies (Hofgaard et al. 1991) and tree forms (Lavoie and Payette 1992, 1994) in response to climatic variability, a phenomenon of importance for the long-term understanding of gap dynamics in northern boreal forests. Annual variations in snow loads, mean summer temperatures, and winter frost injury, for example, have been implicated in significant structural and mortality changes in boreal forests. Recent studies in high elevation spruce–birch and pine forests in the Swedish Scandes demonstrate the relatively rapid change in forest structure induced by short-term climatic disturbance (Kullman 1989, 1991, 1996; Kullman and Högberg 1989).

Other studies in the Scandinavian boreal forest have emphasized the importance of relatively short-term climatic influences in determining forest development and regeneration. Steijlen and Zackrisson (1987), in their investigation of virgin pine–spruce–birch forests in northern Sweden, concluded that the regeneration dynamics and age structure were influenced by low-frequency climatic fluctuations. Snow-rich winters promoted spruce establishment with the recruitment of Scots pine favoured by warm summer temperatures. Climatically induced regeneration and mortality events seem to determine the gap-phase replacement of these northern forests. Multi-modal age structures of Scots pine stands on poor sites in northern Sweden provide further evidence of climatically induced regeneration pulses in boreal forests (Zackrisson et al. 1995). Distinct pulses of pine regeneration occurred during the mid-1970s, mid-1800s, and during the 1930s–1940s, known periods of general warming throughout Scandinavia. Between these temporal pulses, the absence of pine regeneration was noticeable. Seed crops in boreal Sweden are significantly affected by climatic periodicity (Hofgaard 1993c), a fact which probably explains the synchronous regeneration patterns found in the pine stands. The age class structure did not exhibit the classical reverse-J distribution characteristic of continuously recruiting gap-driven forests. In any study of gap dynamics in boreal forests, due recognition must be given to the possible complicating influence of short-term climatic changes on gap dynamics and stand recruitment.

Tree recruitment: gap specialists

Different tree species have been identified as either small gap or large gap specialists. In tropical forests, large gap specialists have been defined as species that “require the high light intensities and temperatures of large gaps for germination and seedling establishment. Early growth is rapid, and saplings are able to reach the upper forest strata during the lifetime of a single gap” (Denslow 1987). On the other hand, small gap specialists “germinate in the understory or in small clearings. Saplings are able to survive understory light conditions owing to low respiration rates and low light requirements at

saturation, but they are dependent on some canopy opening for substantive growth and reproduction.” (Denslow 1987). Typical small gap specialists found in temperate forests include eastern hemlock (Busing 1994), sugar maple (Runkle 1984, 1990; Canham 1985), and beech (Canham 1988*b*, 1990). Shade-tolerant species are able to respond to minimum levels of increased light and often experience several periods of suppression and release before reaching the canopy (Canham 1985, 1989, 1990).

Small and large gap specialists may also be differentiated in terms of their respective growth patterns. Early successional or large gap specialists exhibit what is termed a “height-growth type” that is characterized by greater photosynthetic allocation to plant height growth than to construction of lateral branches and foliage. Late successional or small gap specialists, on the other hand, are termed “crown growth type” in which photosynthate is allocated preferentially to the construction of lateral branches and foliage rather than to plant height growth. This distinction in plant assimilate partitioning is paralleled by differences in successional status, shade tolerance, and gap reproductive success (Marks 1975; Boojh and Ramakrishnan 1982*a*, 1982*b*).

Relative to tropical and temperate forest systems, less work has been conducted on the relationship between forest composition and gap dynamics in boreal and sub-boreal forests. Evidence, however, points toward the recognition of both small and large gap specialists in forests dominated by fir, spruce, and birch species. Both fir and spruce are generally able to perpetuate themselves in forests dominated by single tree gaps, with the less shade-tolerant birch maintaining itself only in larger-sized gaps. This is no doubt attributable to the contrasting growth patterns and life history traits of fir and birch (Hara et al. 1991). In Swedish forests, Leemans (1991) found that smaller gaps caused by the death of one or two trees promoted directional succession towards a forest dominated by shade-tolerant Norway spruce. Large patches (up to 1 ha) resulting from large-scale disturbance allowed the recruitment of both late successional and early successional birch species. Coexistence of fir and birch (Taylor et al. 1996) and pine and birch (Kuuluvainen and Juntunen 1998) was mediated by the tendency for birch to regenerate in large-sized gaps. Furthermore, tip-up mounds associated with the gap disturbance generally provide excellent microsites for birch germination and early development (Carlton and Bazzaz 1998). In spruce-dominated systems in Sweden (Liu and Hytteborn 1991) and British Columbia (Kneeshaw and Burton 1997), micro-scale gap disturbance effectively maintained spruce dominance in the canopy. Although gap dynamics were not explicitly studied, Bergeron and Dubuc (1989) and Bergeron (2000) also noted the successional convergence of southern boreal forests in Québec toward shade-tolerant conifer-dominated forest. Work in the same area of Québec confirmed that spruce budworm mediated patch dynamics promoted a gradual transition to fir-dominated forests (Kneeshaw and Bergeron 1998).

Most fir species, especially balsam fir, are classified as shade tolerant (Baker 1949; Frank 1990). Their ability to germinate under a closed canopy, to persist as a seedling bank (advance regeneration) for decades, often in a suppressed state, and then to respond to increases in light levels allow them to self-perpetuate in forests characterized by small gap disturbance (Messier et al. 1999). Balsam fir possesses the three characteristics deemed essential for a seedling bank species: a narrow range of heights in the shade, persistence in the shade, and the retention of the capacity to grow rapidly in height once light levels have increased after some degree of canopy disturbance (Morin and Laprise 1997; Marks and Gardescu 1998). True firs exhibit a high degree of morphological and physiological plasticity in response to light gradients (Klinka et al. 1992; Mitchell and Arnott 1995; Parent and Messier 1995; Sprugel et al. 1996; King 1997). Under low understory light levels, the growth of lateral branches is favoured at the expense of height growth, a growth strategy ostensibly favouring light sequestration under shaded conditions and minimizing respiration losses from non-photosynthetic tissues. As well, needles generally assume a more horizontal display, maximizing reception of incoming radiation. Highly suppressed fir seedlings, therefore, generally exhibit a characteristic umbrella-shaped form (Kohyama 1980; Takahashi 1996). Similar suppression-induced phenotypic plasticity also occurs in Norway spruce (Greis and Kellomäki 1981). Suppression of balsam fir may occur for decades, even up to 100 years (Morris 1948). Characteristic of this period of intense suppression are reductions in photosynthate

production and allocation resulting in many missing and partial rings. Missing rings are characteristic of understory suppressed trees (Turberville and Hough 1939; Bormann 1965; Lorimer et al. 1999). When released after years of suppression, such seedlings respond vigorously and often grow at rates equal to that of seedlings that did not experience suppression (Hatcher 1960; Logan 1969; Crossley 1976; Hatcher 1964; Herring 1977; Seidel 1977, 1980; Ferguson and Adams 1980; Alexander 1987; Tucker et al. 1987; Kneeshaw et al. 1998; Antos et al. 2000). Fir species may thus be considered small gap specialists, but not in an obligate sense, for fir will grow rapidly and vigorously in large patches created after removal of the parent canopy as a result of clearcutting (Vincent 1956; Hughes 1964), insect outbreaks (Vincent 1962; Fye and Thomas 1963; Bakuzis and Hansen 1965), windthrow (Kimura et al. 1986), stand attrition and breakup (Baskerville 1965), and wind-induced wave forests in high-altitude fir forests (Iwaki and Totsuka 1959; Sprugel 1976).

Black spruce, often growing in association with balsam fir, is also adapted to forests characterized by gap disturbance. Though generally considered to be less shade tolerant than balsam fir, black spruce may form abundant advance growth that can develop in as little as 10% of full sunlight (Viereck and Johnston 1990). Furthermore, the well-known ability of black spruce to reproduce vegetatively through layering (Kenety 1917; Stanek 1961) in the moist feathermoss and *Sphagnum* moss carpets commonly associated with black spruce sites produces mature stands with abundant advance growth. The majority of young trees respond well to release, both after cutting (Doucet 1990; Paquin and Doucet 1992) and in response to small-scale canopy disturbance in multi-cohort stands (Groot and Horton 1994). Furthermore, the competitive ability of black spruce to persist under cold, wet, nutrient-poor edaphic conditions (Newton and Jolliffe 1998) and its phenotypic plasticity under changing climatic conditions (Lavoie and Payette 1992, 1994) makes it particularly suitable for self-perpetuation in gap-driven forests. Under marginal climatic conditions commonly found in the northern fringes of the boreal forest, the climatically controlled accumulation of peat under both balsam fir and black spruce promotes reproduction principally by layering (Sirois 1997). Under such conditions, self-perpetuating old-growth forests driven by gap dynamics may dominate the forested landscape.

It is instructive to note some of the studies that have examined the recruitment of fir and spruce species in forests dominated by small gap disturbance processes (Table 3). Due to their shade tolerance, both fir and spruce are able to self-perpetuate in forest systems dominated by small gap disturbance regimes. Note that Englemann spruce – subalpine fir forests are included in Table 3. Much research has been devoted to the successional relationship between fir and spruce in these generally cold, high-altitude forests. While little actual work has been conducted on the role of gap dynamics in these forests, pathological, autecological, and successional studies would seem to indicate that, between long fire return intervals of 500–1000 years, fungal-induced gap dynamics may play a significant role in the perpetuation of the spruce–fir complex. Subalpine fir, despite its greater shade tolerance and predominance in the regenerating layer, is usually not able to achieve canopy dominance because of the greater longevity of spruce and the shorter pathological rotation of fir (Hanley et al. 1975; Alexander 1985; Veblen 1986a, 1986b; Aplet et al. 1988; Lewis and Lindgren 1999).

Feasibility of gap-based silviculture

The goals and methods of contemporary forestry practice are undergoing a paradigmatic shift. Notwithstanding the early recognition of the need to develop a “nature-based” silviculture (Smith 1962), contemporary forestry is experiencing a radical shift in perspective. The change is characterized by a shift in emphasis on single commodity goods from forests to a recognition of management foci that address the ecological integrity of the natural ecosystem being managed. The traditional emphasis on wood production, for example, required a silviculture that focused on the techniques required to maximize a forest owner’s rate of return through a series of interventions in the development of a stand. Whether silviculture worked with nature, improved on nature, or deviated from nature was often of little

Table 3. *Abies* and *Picea* forests dominated by gap disturbance.

Location	<i>Abies</i> species	<i>Picea</i> species	Associated species	Reference
Spain	<i>Abies pinsapo</i>	—	—	Arista 1995
China	<i>Abies faxoniana</i>	—	<i>Betula utilis</i>	Taylor and Zisheng 1988a, 1988b
China	<i>Abies faxoniana</i>	<i>Picea purpurea</i>	<i>Betula albosinensis</i> <i>Betula utilis</i> <i>Larix potaninii</i> <i>Sabina saltuaria</i>	Taylor et al. 1996
Japan	<i>Abies sachalinensis</i>	—	<i>Acer mono</i> <i>Quercus mongolica</i> <i>Tilia japonica</i>	Ishikawa and Ito 1989
Japan	<i>Abies sachalinensis</i>	<i>Picea jezoensis</i> <i>Picea glehnii</i>	<i>Betula ermani</i>	Kubota et al. 1994 Hiura et al. 1996
Japan	<i>Abies mariesii</i> <i>Abies veitchii</i>	<i>Picea jezoensis</i>	<i>Tsuga diversifolia</i> <i>Betula corylifolia</i> <i>Betula ermani</i>	Kanzaki 1984 Yamamoto 1993, 1995, 1996
Northern Appalachians, U.S.A.	<i>Abies balsamea</i>	<i>Picea rubens</i>	<i>Betula papyrifera</i> var. <i>cordifolia</i> <i>Betula lutea</i>	Foster and Reiners 1983, 1986 Worrall and Harrington 1988; Perkins et al. 1992; Battles et al. 1995; Battles and Fahey 1996, 2000
Southern Appalachians, U.S.A.	<i>Abies fraseri</i>	<i>Picea rubens</i>	<i>Betula lutea</i> <i>Betula alleghaniensis</i>	White et al. 1985a, 1985b Busing 1996; Wu et al. 1999
Québec	<i>Abies balsamea</i>	<i>Picea mariana</i> <i>Picea glauca</i>	<i>Betula papyrifera</i> <i>Populus tremuloides</i> <i>Pinus banksiana</i> <i>Thuja occidentalis</i>	Kneeshaw and Bergeron 1998
British Columbia	<i>Abies amabilis</i>	—	<i>Tsuga heterophylla</i> <i>Tsuga mertensiana</i> <i>Chaemaecyparis</i> <i>nootkatensis</i>	Lertzman 1992
British Columbia	<i>Abies lasiocarpa</i>	<i>Picea engelmannii</i> × <i>glauca</i>	<i>Pinus contorta</i> <i>Populus tremuloides</i>	Kneeshaw and Burton 1997

Table 3. (concluded)

Location	<i>Abies</i> species	<i>Picea</i> species	Associated species	Reference
Western Canada (Alberta) – United States (Wyoming, Colorado)	<i>Abies lasiocarpa</i>	<i>Picea engelmannii</i>	—	Oosting and Reed 1952; Day 1972; Whipple and Dix 1979; Veblen 1986a, 1986b; Aplet et al. 1988; Roovers and Rebertus 1993
Finland	—	<i>Picea abies</i>	<i>Pinus sylvestris</i>	Kuuluvainen 1994
Sweden	—	<i>Picea abies</i>	<i>Pinus sylvestris</i> <i>Betula pendula</i> <i>Betula pubescens</i> <i>Populus tremula</i>	Serander 1936 Hytteborn and Packham 1985 Hytteborn et al. 1987, 1991; Leemans 1990, 1991; Liu and Hytteborn 1991; Hofgaard 1993d
Russia	<i>Abies siberica</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	Syrjänen et al. 1994
Russia	—	<i>Picea abies</i>	<i>Betula pubescens</i>	Kuuluvainen et al. 1998; Drobyshev 1999; Drobyshev and Nihlgård 2000

concern. Emphasis was placed, instead, on the maximization of wood of a certain quality within the economic, political, and social constraints operative at the time.

Under the current umbrella of forest ecosystem management, silviculture is being defined more broadly. Forest ecosystem management is predicated on the assumption that present patterns of productivity, resilience, and biodiversity developed within the context of recurrent, historical disturbance patterns. Such patterns are to be respected, therefore, if both flow of desired goods from the forest and ecological integrity of the forests are to be maintained. If such values are to be preserved into the future and intergenerational needs assured, then silvicultural practices must somehow “mimic” the intensity, frequency, and scale of natural disturbance patterns (Kohm and Franklin 1997).

Such forms of “naturalistic silviculture” are of critical importance in uneven-aged, old-growth forests maintained by disturbance patterns characterized by gap dynamics. Complex structural heterogeneity such as standing dead snags, coarse woody debris, multi-storied canopies, and presence of canopy gaps plays a significant role in both long-term ecosystem functioning and the maintenance of biological diversity (Peterken 1996; Voller and Harrison 1998). Contemporary approaches to forest landscape management focus on the desire to “mimic” or emulate the spatial and temporal characteristics of the natural disturbance regimes of the particular landscape in question (Angelstam 1998*a*, 1998*b*; Niemelä 1999). While this is no easy task, indicator species, structure, and processes are being identified for the range of disturbances such that forest management options are being clarified. In the case of old-growth stands slated for harvesting, a particular challenge consists in being able to maintain an acceptable flow of wood, while at the same time maintaining old-growth characteristics considered essential for the preservation of biodiversity and the conservation of significant structural features or biological legacies. Under current systems of clear-felling and even-aged management, such structural heterogeneity and maintenance of the potential for biodiversity is minimized. In boreal forests, many of which are even-aged from extensive, catastrophic insect outbreaks and fires, the dominant silvicultural system of clearcutting may be considered ecologically viable and sustainable (Weetman 1995). It would be unrealistic, however, to think that large, extensive clearcuts with removal of most of the biomass essentially mimics natural processes such as fire and extensive insect herbivory. In other forest ecosystems, including areas of the boreal, where mixed-aged and old-growth, uneven-aged, structurally diverse forests predominate, alternative silvicultural methods are being considered. Silvicultural options needed to meet these goals, while specific to different forest types, may include long rotations, various types of patch cutting, and degrees of variable retention and promotion of all-aged stand structures (Alexander 1987; Runkle 1991; Kimball et al. 1995; Franklin et al. 1997; Coates and Steventon 1995; Bergeron et al. 1999; Burton et al. 1999; Lähde et al. 1999).

Research in gap dynamics has increased our understanding of small-scale disturbance in many forest ecosystems. Given the growing desire to emulate natural disturbance patterns in forest activities, new attention is being given to gap-based silvicultural systems. Such systems attempt to mimic the natural gap size and frequency in gap-disturbed forests through judicious use of well-planned partial cutting. Coates and Burton (1997), in their study of undisturbed interior cedar-hemlock forests of northwestern British Columbia, found that a gap-based partial cutting silvicultural system is particularly effective, allowing for timber extraction while at the same time maintaining mature or old-growth structure and process. Similarly, in uneven-aged Norway spruce sites in Sweden, Fries et al. (1997) recognized that traditional clear-cutting and shelterwood regeneration methods were not able to maintain significant historic structures and processes that promoted biodiversity. Proposed management options included a shift to selection systems or even no cutting in gap-driven forests. The feasibility of gap-based silviculture as an effective management option in Indonesian dipterocarp forests (Tuomela et al. 1996), Peruvian tropical forests (Hartshorn 1989), and Southern Cape forests in South Africa (Geldenhuys and Maliepaard 1983) has also been examined. Uneven-aged management and appropriately devised selection systems are receiving increasing interest in North America as well (Nyland 1996, 1998; Emmingham 1997, 1998; Guldin and Baker 1998; Long 1998; O’Hara 1998; Seymour and Kenefic 1998).

The natural filling-in of gaps with regeneration of trees would appear to suggest that silviculture prescriptions should logically follow this natural precedent. Such reasoning, along with the increasingly accepted notion that forest management should produce “natural-looking” forests, has invigorated the long tradition of uneven-aged silviculture (cf. Emmingham 1997) that has been traditionally practiced in mountainous forests of central Europe under the rubric of selection systems and irregular shelterwoods. The classic selection silvicultural system as originally devised in Europe (Knuchel 1953; Kostler 1956) was based on a gap-replacement scenario. The shade-tolerant species mix of silver fir (*Abies alba* Mill.), European beech, and Norway spruce, along with economic, ecological, and cultural incentives provided the *raison d'être* for the successful, though geographical limited, implementation of uneven-aged silviculture in central European forests (Kenk 1995). Early attempts to transfer European silvicultural ideas (i.e., uneven-aged selection systems) into North America were made by Meyer (1952) and Meyer et al. (1961).

Under uneven-aged management using variations of the selection system, there exists a traditional reliance on advance regeneration that will release into the gaps created by canopy removal. The selection silvicultural system is characterized by continuous forest cover, continuous or episodic advance regeneration, little or no relationship between individual tree size and tree age because of long periods of suppression, and continuous harvest removals. Such stands are traditionally characterized by reverse-J (Meyer 1952; Leak 1996) or reverse sigmoidal (Goff and West 1975; Goodburn and Lorimer 1999) diameter class distributions. Under *BDq* regulation (basal area level (*B*), maximum diameter (*D*), and a *q* factor that defines the regular change of numbers across consecutive diameter classes), periodic harvests are carried out in such a manner that an uneven-aged, reverse-J residual stand is created and maintained, theoretically providing for a sustained yield of wood volume (Nyland 1996).

Although boreal forests are usually even-aged in structure, with normal diameter distributions due to catastrophic stand-initiating events such as fire, insect outbreaks, and blowdown, multi-cohort forests do persist where these events are rare. This situation is most common at high elevations and where climatic and edaphic conditions prevent the spread of fire or the development of insect outbreaks. In boreal spruce–fir and northern conifer cover types, attempts have been made to use classic *BDq* regulation with gap regeneration as a silvicultural system (Frank and Bjorkbom 1973; Frank and Blum 1978; Seymour and Kenefic 1998) or more rudimentary variations of the selection system (Groot 1995). On harsh sites where regeneration is slow to occur and where survival may depend on overstory protection, uneven-aged management with selection cuts may be the only successful way to maintain forest cover protective functions.

Despite the biological feasibility of some form of gap-based silvicultural system in the boreal forest, classical selection forestry has not been generally accepted or even perceived to be of relevance. This is understandable given the fact that the boreal forest is generally even-aged, having originated from massive fires and insect outbreaks. Furthermore, the common occurrence in Canada of extensive areas of old, unmanaged forests subject to high risk from fire and insects has mitigated against the use of selection silvicultural systems that have generally assumed detailed inventories, individual tree selection, extensive road access, and a detailed understanding of individual stand structure and dynamics. Wedeles et al. (1995), in their assessment of various silvicultural systems in the boreal mixedwoods of Ontario, pointed to the uncertainty over patterns and composition of regeneration and stand dynamics as well as operational and economic constraints as important factors preventing acceptance of the selection system. In the Canadian boreal forest, commercial volumes and assessed values of timber are often low, providing little financing or incentive for the development of alternative silvicultural systems. The contemporary focus is on the protection of advanced regeneration under conditions of mechanized harvesting. This reliance on advance regeneration, often gap-related, has initiated debate concerning the degree to which residual advance growth is abundant enough, vigorous enough, and spatially distributed such that future stands of desirable volume and species composition are realized under even-aged management.

Despite the institutional disincentives for gap-based silvicultural systems in the Canadian boreal forest, there is growing public pressure to employ selection and shelterwood systems that are based on

gap dynamics. Currently, forestry, including boreal forestry, is marked by a struggle between biologists and foresters. The former are concerned with maintenance of biodiversity and the development of naturally based silvicultural systems that maintain natural disturbance regimes. The forester, particularly when it comes to the boreal forest, is saddled with the task of rationalizing harvesting and silviculture for a large, publicly owned forest characterized by high risk factors, old age, and usually unbalanced age class distributions (Weetman 1995). The public desire for forest ecosystem management is calling them together.

Research directions

Multi-cohort stands and associated gap dynamics are much more common in boreal forests than previously assumed. Most of our understanding of gap structure and dynamics in boreal forests has originated from work carried out in Scandinavia and Russia and in the subalpine boreal “outliers” found in Japan and American Appalachia. To date, the vast amount of disturbance dynamics research in the Canadian boreal forest has focused on fire and insect disturbance. The reasons for such a focus are obvious given the frequency, scale, and economic importance of such disturbance events.

This review suggests a number of possible research priorities. Of first importance is the definition of what constitutes old-growth boreal forest. Our contemporary understanding of what constitutes old-growth has, for the most part, emerged from research in the temperate coniferous forest of western North America and from remnant old-growth hardwood forests throughout the United States. Structural parameters and gap-related processes need to be determined for old-growth boreal forests. Secondly, once identifying parameters have been established, landscape-level identification and mapping of old-growth areas may be initiated. Many government and industrial forest inventories would have to be updated, given the prevailing even-aged assumptions common to many inventory systems.

The increased focus on ecosystem management, maintenance of species- and landscape-level biodiversity, identification of representative protected areas, and natural disturbance-based forest management has initiated a renewed interest in understanding the full range of disturbance processes at play in the boreal forests of Canada. As already noted, disturbance in the boreal forest is assumed to be characterized by catastrophic, stand-replacing events such as fire and insect outbreaks. This assumption may be too simplistic for slow-growing, maritime and more northern regions of the boreal forest. A greater appreciation for the dynamics of these regions of the boreal forest is important, especially if we wish to conduct forest harvesting and develop a protection strategy that maintains the natural productive dynamics and biodiversity of these primary forests. Contemporary forest management in many parts of the boreal forest is predicated on a scenario of even-aged forest dynamics. Such a fundamental assumption of forest dynamics has in turn produced relatively simple even-aged silviculture and growth and yield modeling. In many cases, this form of management results in a simplification of forest structure and diminution of species- and landscape-level biodiversity.

The dynamic relation among different disturbance regimes needs attention. Attention is often focused on one or the other disturbance regime without consideration of the temporal and spatial links to other disturbance events. While this focus is methodologically obvious and often necessary, it is essential to relate the frequency and extent of disturbance from fire, insects, wind, fungi, not to mention harvesting and management activities such as fire suppression and silviculture. Furthermore, we are increasingly aware of the overarching and complicating impact of rapid climate change on forest disturbance history.

The etiology of gap dynamics is poorly understood. Much of the work in forest pathology has focused on the identification of fungal decay agents responsible for the loss of merchantable wood. It will be important to build on this wealth of knowledge by examining the role played by these biotic factors in the development and maintenance of what may be termed “fungal-driven” forests. We need to view fungi as disturbance vectors much as we do fire, wind, and insects.

An understanding of the temporal persistence of gap-driven forests is needed. Stand-level pollen records may prove helpful in the retrospective reconstruction of gap forests, giving insight into the

long-term continuity of old-growth forests. Related to this temporal continuity are the floristic and faunal complexity and assemblages. Gap-driven forests, given their structural complexity and temporal stability, may provide regeneration niches not found in forests that experience regular large-scale disturbance.

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Glossary

Advance regeneration: Seedlings or saplings that germinate and grow in the understory of a closed canopy. They gradually grow into the canopy as canopy disturbance provides sufficient growing space. Usually associated with shade-tolerant trees such as the true firs, sugar maple, western red cedar, eastern cedar, hemlocks, and American beech (Barnes et al. 1998).

Disturbance: Any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985).

Gap: The physical or growing space occurring in forest stands due to individual or small group mortality, blowdown, or stem breakage. Canopy opening usually $\leq 200 \text{ m}^2$ (adapted from Helms 1998).

Gap phase: A term first coined by Watt (1947) who accepted “phase” and “patch” as synonyms. Gap phase is a stage of forest stand development to which tree regeneration is confined, it being excluded from other phases.

Gap dynamics: The change in space and time in the pattern, frequency, size, and successional processes of forest canopy gaps caused by the fall or death of one or more canopy trees. Small- or micro-scale disturbance of the forest canopy in which the gaps formed by single tree or small group mortality release sufficient growing space that is subsequently occupied by tree regeneration, usually a result of released advance regeneration or seedling recruitment from buried or dispersed seed propagules. Tree mortality initiated by decay (root and butt rots) or individual tree blowdown (adapted from Helms 1998).

Patch: The physical or growing space occurring in forest stands due to the mortality of a stand or forest or part thereof. A relatively discrete spatial pattern with no constraint on upper limit of patch size, internal homogeneity, or discreteness. Patch implies a relationship of one patch to another in space and to surrounding, unaffected or less affected matrix. Canopy opening usually $> 200 \text{ m}^2$ (adapted from White and Pickett 1985).

Patch dynamics: Forest disturbance on the forest or stand level or portion thereof in which new tree cohorts are initiated producing a mosaic of cohort patches of different sizes and discreteness across the forest landscape. Usually associated with large-scale disturbances such as fire, insect outbreaks, and windstorms.

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