Journal of Vegetation Science 9: 463-610, 1998

SPECIAL FEATURE

Key issues in disturbance dynamics in boreal forests

Editors

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Based on contributions presented at the IAVS Workshop on Disturbance Dynamics in Boreal Forests, held at the University of Québec in Abiti-Témiscamingue in Rouyn-Noranda, Canada, August 26-30, 1996

Contents

Key issues in disturbance dynamics in boreal forests: Introduction

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In 1989, when the idea of this workshop first seeded in our minds, our objective was to build bridges between researchers mainly from North America and northern Eurasia working in the boreal forest. The idea stemmed from the fact that a limited number of researchers were working in the boreal forest on both sides of the Atlantic, and that there was a need to attain a critical mass of scientists with a common interest in boreal ecosystems. We selected disturbance dynamics as the theme because it was clear at that time that disturbance was increasingly recognized as the driving ecological force in all ecosystems (Pickett & White 1985), and especially in boreal systems (Shugart et al. 1992). Since the first workshop (Engelmark & Bradshaw 1992; Engelmark et al. 1993), many developments can be seen which contribute to the success of our enterprise. The workshop papers (Bergeron & Frisque 1996) and this Special Feature include a large spectrum of research dealing with disturbances in the boreal forest. Some major themes emerge from this collection.

Conjunctive changes in climate and disturbance

Model predictions that climate change will strongly affect boreal ecosystems have focused attention on the need for more research in the northern hemisphere. Although disturbances are regarded as a major impetus of forest dynamics, their effects are constrained by the climate. Northern ecosystems have a long history of variations between warm and cold stages, at least since the beginning of the Quaternary era. Much of current research has focused on how present and future climate changes may affect plant distribution, composition and disturbance regimes in the boreal zone, in the case of a general warming or cooling trend. Furthermore, one must keep in mind that climate change may be spatially dependent; that is, the climate may simultaneously be warm in some areas and cool in others. Such spatial variability would also be expected to have different impacts in different ecological regions. Fire and herbivory are key disturbances in the boreal forests and, as suggested by Davis & Botkin (1985) and Fleming (1996), the effects of climate change on these disturbances and thereby on ecosystems, might be greater than the ecosystem changes due to climate change *per se*. Effects of climate change on fire regimes are still uncertain as studies undertaken in different regions have led to contradictory conclusions (*Flannigan et al.* this issue). Naturally, such changes in disturbance regimes may bring major changes in forest structure and composition (*Flannigan & Bergeron* this issue. For example, Landhäusser & Wein (1993) suggested, for the western Canadian Arctic, that an eventual warming involving more frequent fires, would cause the treeline to move progressively northward, with each fire providing a favourable seedbed. Regeneration close to the tundra is delicately balanced by fire and climate interaction (see also *Lavoie & Sirois* this issue). Climate effects could eventually lead to more extensive insect outbreaks (Fleming 1996), although changes in forest composition due to changes in fire regimes could also lead to a decrease in outbreak severity (*Bergeron & Leduc* this issue).

Within a long temporal perspective, the northern climate alternates between glacial and interglacial eras.

Independent of what future climatic trend will prevail in the boreal zone during the rest of the present interglacial, the Holocene, it will probably differ from what has occurred in the past. Climatic conditions will, instead, create new disturbance patterns and ecological responses, perhaps very different from the post-disturbance dynamics we have observed until now. The transient character of synergistic disturbances having partly unpredictable, yet long-lasting effects on ecosystems, will have to be addressed. Hence, it is crucial to focus studies on new disturbance patterns, in order to provide a more complete picture of the ever-changing biome we presently call 'boreal' and to contribute to the sustainable management of the natural resources in the North.

The stress-disturbance continuum

The studies reported during the workshop provide examples of a variety of disturbance types operating over a wide range of temporal and spatial scales. It is worth recalling the most commonly accepted definition of disturbance in the ecological context: "A disturbance is any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment" (Pickett & White 1985). Whatever the scale in which it operates, the rapidity with which the changes are brought upon a plant's resources and the detectable responses of the plants are generally viewed as the main determinants of an ecological disturbance (Bazzaz 1996) (*Skre et al.* this issue). However, plants also respond to gradual changes in the fluxes of chemical and physical factors of their environment.

While the response of plants to environmental stress may not be as readily detectable as their response to disturbance, a given level of stress may enhance disturbance intensity and modify plant response after disturbance. For example, at the stand level, stress induced by light, soil moisture and nutrient regime influences the response of plant populations to disturbance (*Messier et al.*; *Roberts et al.* this issue. On the global level, the boreal forest is submitted to temperature and precipitation gradients which largely control the range of major tree species (Nikolov & Helmisaari 1992; Payette 1993) and the distribution of the main boreal zones (Hustich 1966). Daily weather variations and long-enduring fluctuations in climate may potentially stress a tree's vital functions. Such stress may not have any detectable, direct effects because of the homeostatic control that many forest systems exert on their own environment. However, there is a growing body of evidence suggesting that the inertia of forests to a given stress may be levelled off by a disturbance because of the reduced resilience caused by a stress-inducing environment (Davis & Botkin 1985; Sirois et al. 1994; Arseneau & Payette 1992). Environmental stresses, operating on a daily to long-term basis, appear therefore intimately linked to disturbances as an important determinant of forest structure and function at the stand and landscape levels.

Disturbances in the boreal forest: more than fire

Fire is the most important disturbance in the boreal forest. This statement, supported by a dramatic image of wildfire, provided the introduction to many of the talks during the workshop. Fire remains the most popular disturbance theme among boreal forest scientists, but studies on insects and wind-related disturbances were also presented during the workshop. Fire is of course important - we now have a great deal of evidence from a wide range of ecosystems around the world. However, the role of fire may have been overemphasized in boreal systems. For example, old-growth forests controlled by other disturbances are more abundant than is generally expected. Gap disturbance appears also to be common in boreal forests (e.g. *Ban et al.*; *Campbell et al.*; *Kneeshaw et al.* this issue; Hofgaard 1993; Kuuluvainen 1994; Kneeshaw & Bergeron 1997; Kneeshaw & Burton 1997). These types of disturbance have proven to be very important and, in some situations, even more important than fire (*Kuuluvainen & Junuunen*; *Kuuluvainen et al.*; *Simard et al.* this issue). Among alternative disturbances are the action of insects, wind, various pathogens, snow and ice and large animals (cf. *Engelmark et al.* this issue; Engelmark in press). An example is the eastern spruce budworm (*Choristoneura fumiferana*).

Forests of eastern North America dominated by *Abies balsamea* (Balsam fir) and *Picea rubens* (Red spruce) are characterized by low fire frequency and here spruce budworm outbreaks are considered as the most important disturbance. In the last 70 years in Canada, 48 % of the boreal forest was disturbed by fire, 39 % by insects (mainly spruce budworm in the east) and 10 % by logging (Kurz & Apps 1996). Interestingly, by the time ecologists realized that forest dynamics could not be fully understood without including fire as a major disturbance, forest researchers studying boreal forests with *A. balsamea*, began to realize the necessity of studying the chronology and impact of spruce budworm outbreaks in order to understand forest dynamics. This is simply because spruce budworm outbreaks, sometimes associated with subsequent blow-down, create characteristic canopy gaps, the main disturbance that controls the structure and regeneration in the *A. balsamea* forest (MacLean 1988; Morin 1990, 1994). A cyclic mechanism in which the spruce budworm kills overstory trees, thus releasing a generally abundant seedling bank from suppression and regenerating the forest has been described for many of these forests. The importance of eastern and western spruce budworm (*Choristoneura occidentalis*) outbreaks has been documented in eastern North America by Blais (1983) and in the West by Swetnam & Lynch (1993) using dendro-ecological techniques. However, we do not yet have a large amount of reliable information on history and impact of these insects for the entire Holocene period. We are beginning to understand the mechanisms involved in recurrence of spruce budworm epidemics (Régnière & Sharov 1997). However, much work needs to be done to understand the relationships among interacting factors and to predict effects which are synergistic with other disturbances.

Of course, spruce budworm is not the only insect to have an impact on forest growth and structure. Larch sawfly (*Pristiphora erichsonii*), hemlock looper (*Lambdina fiscellaria fiscellaria*) in boreal coniferous forests and the forest tent caterpillar (*Malacosoma disstria*) in boreal deciduous forests are also very important in eastern North America. At present, many studies address forest dynamics in relation to the outbreaks of these insects. Wind-related disturbances, often involving several factors and forming a complex network of causes and effects, are now also recognized as being important, especially in exposed environments where fire is not important or has been removed from the system (Quine 1996; Ruel 1996).

Disturbance dynamics and forest management

Our increased understanding of natural disturbance dynamics in the boreal forest should ultimately lead to improvements in silvicultural and forest management strategies at the stand and regional scales which, in turn, should have an impact on the global level. For example, Norokorpi (1992) and *Angelstam* (this issue) have proposed a variety of silvicultural systems for northern Europe based on stand composition, structure and natural dynamics. These include a 'continuous cover' method for all-sized mixed-wood forests aimed at maintaining a minimal level of broad-leaved species, and small clearcuts in old *Picea abies* stands to permit invasion of beneficial hardwoods. Similarly, silvicultural approaches based on natural succession and disturbance regimes have been proposed for the Canadian boreal mixedwood forest by MacDonald (1995), Lieffers et al. (1996), and Bergeron & Harvey (1997). These strategies include using partial- and clear-cutting on mixed-wood sites to harmonize harvesting interventions with natural renewal processes and dynamics of species replacement from intolerant hardwoods to mixed stands and tolerant softwoods.

Johnson et al. (this issue) discuss the importance of a fair knowledge of natural regimes as a prerequisite for implementing such an approach. Delong & Tanner (1996) stressed the importance of modelling forest harvest patterns more closely in relation to the more complex patterns created by wildfire; this may include creating a greater range in patch sizes, more irregular disturbance boundaries and more patches of residual forest. The imperative of the landscape-level perspective in evaluating forestry impacts on ecosystem diversity has been demonstrated by Pastor & Mladenoff (1993), among others, and there is growing evidence to demonstrate that maintaining forest composition, age structure and ecosystem processes at equilibrium with the regional natural disturbance regime is a logical strategy for maintaining ecosystem integrity and biological diversity. Gauthier et al. (1996), for example, have shown how long-term management goals may be set within a conceptual framework based on natural fire cycles and regional geomorphological conditions. This approach can provide objectives for forest composition and ageclass structure that are at equilibrium with the natural disturbance regime. While this strategy appears to have much potential, considerably more effort needs to be invested in testing the idea.

These four themes are not exhaustive; however, they describe relatively well the major issues that emerged from the workshop and they stress the need for more research on disturbance dynamics in the boreal forest. The papers presented in this Feature further emphasize pertinent questions and detailed findings within this spectrum. Finally, growing concern about the maintenance of biodiversity has highlighted the importance of the boreal forest as one of the largest biomes on Earth. Our main challenge is to determine how to preserve biodiversity in an ecosystem which is constantly affected by both natural and human disturbances.

Acknowledgements. We would like to thank our partners: Université du Québec, International Association for Vegetation Science (IAVS), Sustainable Forest Management Network of Centres of Excellence, Fonds pour la formation des chercheurs et l'aide à la recherche (FCAR), Ministère des Ressources naturelles du Québec, Canadian Forest Service, Swedish Council for Forestry and Agricultural Research, the Edlund Brothers Donation Fund, Association forestière de l'Abitibi-Témiscamingue, Hydro-Québec and our sponsors: Caisse Populaire de Rouyn-Noranda, Ville de Rouyn-Noranda, Norbord Industries, Matériaux Blanchet, Domtar Forest Products and Donohue Forest Products. We would also like to thank all the workshop participants and contributors to this special issue. A special thanks to Gilles Frisque for the organisation of the workshop and to Eddy van der Maarel and Graciela Rusch for their contributions in the preparation of this Special Feature.

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