Dissertationes Forestales 100

Tree mortality and deadwood dynamics in late-successional boreal forests

Tuomas Aakala

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

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Author: Tuomas Aakala

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Thesis supervisor:
Prof. Timo Kuuluvainen
Department of Forest Sciences, University of Helsinki, Finland

Pre-examiners:
Dr. Shawn Fraver
Northern Research Station, Forest Service, United States Department of Agriculture, USA
Dr. Ken-Olaf Storaunet
Norwegian Forest and Landscape Institute, Norway

Opponent:
Prof. Yves Bergeron
Université du Québec en Abitibi-Témiscamingue, Canada

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Here I aimed at quantifying the main components of deadwood dynamics, i.e. tree mortality, deadwood pools, and their decomposition, in late-successional boreal forests. I focused on standing dead trees in three stand types dominated by *Picea mariana* and *Abies balsamea* in eastern Canada, and on standing and down dead trees in *Picea abies*-dominated stands in three areas in Northern Europe.

Dead and living trees were measured on five sample plots of 1.6-ha size in each study area and stand type. Stem disks from dead trees were sampled to determine wood density and year of death, using dendrochronological methods. The results were applied to reconstruct past tree mortality and to model deadwood decay class dynamics.

Site productivity, stand developmental stage, and the occurrence of episodic tree mortality influenced deadwood volume and quality. In all study areas tree mortality was continuous, leading to continuity in deadwood decay stage distribution. Episodic tree mortality due to either autogenic or allogenic causes influenced deadwood volume and quality in all but one study area. However, regardless of productivity and disturbance history deadwood was abundant, accounting for 20–53% of total wood volume in European study areas, and 15–27% of total standing volume in eastern Canada. Deadwood was a persistent structural component, since its expected residence time in early- and midstages of decay was 18 yr even in the area with the most rapid decomposition.

The results indicated that in the absence of episodic tree mortality, stands may eventually develop to a steady state, in which deadwood volume fluctuates around an equilibrium state. However, in many forests deadwood is naturally variable, due to recurrent moderate-severity disturbances. This variability, the continuous tree mortality, and variation in rates of wood decomposition determine the dynamics and availability of deadwood as a habitat and carbon storage medium in boreal coniferous forest ecosystems.

Keywords: dendrochronology, old-growth, coarse woody debris, stage-based model, forest dynamics, forest structure

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Viikki, February 2010

Tuomas Aakala

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles referred to in the text by their Roman numerals I–V:

I Aakala, T., Kuuluvainen, T., De Grandpré, L., and Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests in Quebec: spatial patterns, rates and temporal variability. Canadian Journal of Forest Research 36(1): 50-61. doi:10.1139/X06-201

II Aakala, T., Kuuluvainen, T., Wallenius, T., and Kauhanen, H. 2009. Contrasting patterns of tree mortality in *Picea abies*-dominated late-successional forests in two regions in northern boreal Fennoscandia. Journal of Vegetation Science 20: 1016-1026. doi:10.1111/j.1654-1103.2009.01100.x

III Aakala, T., Kuuluvainen, T., Wallenius, T., and Kauhanen, H. Episodic tree mortality in the pristine *Picea abies*-dominated taiga in the Arkhangelsk region, Northern Europe: drought as a primary disturbance agent in a mesic boreal forest. Manuscript.

IV Aakala, T., Kuuluvainen, T., Gauthier, S., and De Grandpré, L. 2008. Standing dead trees and their decay class dynamics in northeastern boreal old-growth forests of Quebec. Forest Ecology and Management 255: 410-420. doi:10.1016/j.foreco.2007.09.008

V Aakala, T. Coarse woody debris in three late-successional *Picea abies* forests in Northern Europe: variability in volume and models of decay class dynamics. Manuscript.

AUTHORS’ CONTRIBUTIONS

Tuomas Aakala was responsible for the summary of this thesis and for **V**. He is the main author of all the articles, and was responsible for the analyses of the data. In **I** Timo Kuuluvainen, Louis De Grandpré and Sylvie Gauthier developed the ideas and field methods, and participated in writing the article. In **II** Tuomas Aakala, Timo Kuuluvainen, and Heikki Kauhanen planned the research. All authors participated in the fieldwork, and Timo Kuuluvainen and Tuomo Wallenius participated in writing the article. In **III** Tuomas Aakala was responsible for planning the research, while all coauthors participated in planning the research and in conducting fieldwork. Timo Kuuluvainen and Tuomo Wallenius participated in writing the article. In **IV** Sylvie Gauthier was responsible for the idea, and all authors participated in the fieldwork and in writing the article.

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TERMINOLOGY

Allogenic disturbance: Disturbances that originate from outside the stands, e.g. storms, droughts, insect outbreaks (Kuuluvainen 2002).

Autogenic disturbance: Local-scale disturbances that originate from within the stands, e.g. pathogenic fungi or competition (Kuuluvainen 2002).

Background tree mortality: Tree mortality, not related to any distinct episodes (Franklin et al. 1987). Defined in this thesis as annual tree mortality not significantly above long-term average (European study areas), or as annual mortality rate of below 5% (eastern Canadian study areas) (Lugo and Scatena 1996).

Disturbance regime: Type, extent, severity, and frequency, as well as their variation in the occurrence of natural disturbances.

Down woody debris: Fallen deadwood, with stump height less than 1.3 m, or inclining at greater than 45° from the vertical.

Episodic tree mortality: Tree mortality aggregated in time, so that annual tree mortality rates in a stand rise above the background rates (Franklin et al. 1987). In this thesis, episodic tree mortality is defined as annual mortality significantly above long-term average (European study areas), or as annual mortality rate of over 5% (eastern Canadian study areas) (Lugo and Scatena 1996).

Expected residence time: In the decay class dynamics model, years since tree death to a point in time when 50% of the number of trees, deadwood volume, or deadwood mass that was given as input at time zero has decayed past the last decay class included in the model.

Historical range of variability: "The spatial and temporal variation of the ecological variable considered, in conditions that are relatively unaffected by people within a given period of time and geographical area appropriate to an expressed goal" (Landres et al. 1999). The range of variability is dependent on time- and spatial-scales of observation. In this thesis they are limited to late-successional forests at stand scale in the long-term absence of stand-replacing disturbances, and to time periods covered by the disturbance history reconstructions (i.e. approximately 200 years).

Late-successional forests: Forests whose developmental stage is far removed from stand-initiating disturbance. Following the terminology by Oliver and Larson (1996), these include both transitional and true old-growth forests.

Natural disturbance: Discrete events that are not primarily of human origin and that alter ecosystem structure and resource availability (White and Pickett 1985, Lindenmayer and Franklin 2002).

Quasi-equilibrium state: Relative structural and species compositional equilibrium, where stand structural attributes fluctuate around an equilibrium state (Shugart 1984). The quasi-equilibrium concept is scale-dependent. Although often considered at landscape-scale, quasi-equilibrium state is theoretically applicable also to stand-scale in late-successional forests driven by small-scale dynamics (cf. Bormann and Likens 1979).

Saproxylic organisms: Deadwood-dependent organisms. These are dependent, during some part of their life cycle, on deadwood or the presence of other saproxylics (Jonsson et al. 2005).

Snag: Standing deadwood, either intact or snapped, such that the height of the standing part is over 1.3 m, and inclining less than 45° from the vertical.

Susceptibility: Probability that a tree or a stand is being influenced by a disturbance; e.g. susceptibility describes the probability of a forest being attacked by spruce budworm (MacLean 1980).

Vulnerability: Probability of tree mortality resulting from a given level of allogenic disturbance; e.g. during spruce budworm outbreaks the probability of tree mortality with a given level of defoliation (MacLean 1980).

INTRODUCTION

Disturbance dynamics in boreal forests

The development of boreal forests under negligible human influence is often regarded as governed by large-scale high-severity disturbances, mainly forest fires (Zackrisson 1977, Bonan and Shugart 1989, Payette 1992). These disturbances cause abrupt large-scale tree mortality and dramatic changes in forest structure, initiating new stand successions. However, the occurrence of fire and other disturbances is not uniform over the boreal zone, due to broad variability in climatic and edaphic conditions (Bergeron 1991, Engelmark 1994, Granström 2001). For instance, in continental areas, such as in the central parts of North America, stand-replacing fires occur frequently (Payette 1992). In contrast, in more humid maritime climates such as those found in Northern Europe and eastern Canada, large areas of the boreal forest experience mixed-severity fires with cycles that can be several centuries long (Syrjänen et al. 1994, Gromtsev 2002, Wallenius et al. 2005, Cyr et al. 2007).

When stand-replacing disturbances are rare, boreal landscapes consist to a large degree of late-successional forests (Pennanen 2002, Wallenius et al. 2005, Boucher et al. 2006). The dynamics of these forests are driven by small-scale disturbances of low severity, leading to tree mortality at the scale of individual to small groups of trees (Kuuluvainen 1994, McCarthy 2001). In addition, recent research has suggested that the occasional moderate-severity disturbances that lead to episodic tree mortality may also play an important role in the dynamics of late-successional boreal forests (Fraver et al. 2008). The influence of these types of disturbances on stand structure is less dramatic than with large stand-replacing disturbances, but they nevertheless strongly influence stand structure, long-term stand developmental trajectories, and the creation of deadwood (Franklin et al. 1987). These processes create forests that are characterized by high structural complexity (Franklin et al. 2002).

Tree death and wood decomposition

In late-successional forests, allogenic disturbances can lead to abrupt tree mortality, in which the relationship between tree death and its cause is apparent. However, tree death is often a complex process that involves multiple factors. In either case, the death of a single tree is influenced by predisposing factors (following the terminology for decline disease theory by Manion 1991) that define the susceptibility of a tree to disturbances. Predisposing factors include tree species, age, size and canopy position of the tree, as well as competitive status and site conditions (Sprugel 1976, Bormann and Likens 1979, Harcombe 1987, Peet and Christensen 1987, Waring 1987, Bergeron et al. 1995, Ryan and Yoder 1997, Yoshida and Noguchi 2009). Depending on the predisposition, disturbance agents, such as storms, insect outbreaks, or droughts, may then either kill a tree directly or weaken its physiological state (inciting factors, *sensu* Manion 1991, McDowell et al. 2008). In the latter case, the tree becomes more vulnerable to further damaging agents (contributing factors, *sensu* Manion 1991), because they lower the severity of a further disturbance agent required to kill the tree (Oliver and Larson 1996). These agents, such as bark beetles or wind, may thus determine the exact timing of tree mortality (Edman et al. 2007) and be the most apparent cause of death, although the predisposing and inciting factors may have played a decisive role in the process of tree mortality (Manion 1991). In many cases, these factors also make tree mortality a lengthy process, in which the weakening of the physiological state of the tree can occur over decades (Waring 1987, Manion 1991, Pedersen 1998, Lännenpää et al. 2008). This also makes the causal agents responsible for the tree death difficult to distinguish.

Tree death leads to the creation of deadwood, irrespective of its causes (Franklin et al. 1987). However, the causes determine the type of deadwood structures created, i.e. the ‘mode of mortality’ (Kneeshaw and Bergeron 1998, Gale and Barfod 1999). A dead tree may remain standing intact, be partly snapped, or fall entirely on the forest floor (Tyrrell and Crow 1994, Hennon and McClellan 2003). These deadwood structures then gradually decompose, which in the boreal forest is primarily due to microbial respiration, fragmentation, and to a lesser extent leaching (Mackensen et al. 2003, Bond-Lamberty and Gower 2008, Cornwell et al. 2009).

The causal factors governing wood decomposition are still poorly understood (Cornwell et al. 2009). The decomposer community, climate, position of the tree (standing or down), and chemical and physical properties of the wood are known to influence the decay rates (Mackensen et al. 2003). Climatic factors determine the temperature and moisture regimes in the woody material. These affect the biological activity of the decomposing organisms. This effect is apparent in the generally positive relationship between mean annual temperatures and decay rates, when the differences in tree species-specific decay resistance are taken into account (Alban and Pastor 1993, Chambers et al. 2000, Yatskov et al. 2003, Laiho and Prescott 2004).

The position of the tree, whether standing or lying on the forest floor, similarly influences the decay rates. In snags the moisture content is much lower than in down woody debris that is in contact with the forest floor. Down woody debris thus has a more beneficial environment for decomposer activity than snags (Johnson and Greene 1991, Fraver et al. 2002, Wang et al. 2002). Therefore, the mode of tree death influences the longevity of the deadwood created. Deadwood can be expected to be a long-lived structural component in the boreal zone, because the low temperatures and short growing seasons limit the biological activity of decomposers.

Deadwood dynamics

On a stand scale, the dynamics of deadwood, i.e. fluctuations in its volume and quality, are determined by tree mortality and decomposition over time (Grove 2002, Jonsson et al. 2005). When the weakening stress factors are taken into account, tree death can be a lengthy process. However, from the ecosystem perspective the transition from living to dead wood occurs rapidly (Franklin et al. 1987), in comparison to the gradual process of wood decomposition. Thus the fluctuations in deadwood volume at the stand scale are primarily dependent on the temporal patterns of tree mortality (Greif and Archibold 2000).

After a stand-replacing disturbance, deadwood volume is in general assumed to follow a U-shaped pattern (Lang 1985, Spies et al. 1988, Sturtevant et al. 1997, Clark et al. 1998, Siitonen 2001; however, see Hély et al. 2000, Fraver et al. 2002). This is primarily a reflection of the patterns of tree mortality that change with stand succession (Franklin et al.

1987). Deadwood is usually highly abundant after a stand-replacing disturbance, but then its volume begins to decrease due to decomposition. Tree mortality in regenerating stands and during the stem-exclusion stage produces mainly small-diameter wood. The deadwood volume begins to increase only after larger trees of the pioneer cohort begin to die. Toward the late-successional or old-growth stages, deadwood becomes a major structural ecosystem component (Sirén 1955, Franklin et al. 1987, Franklin et al. 2002, Spies 1998, Luyssaert et al. 2008).

Theoretically, deadwood volume along the forest succession in coniferous forests can be expected to peak when the cohort of trees originating from the last stand-replacing disturbance reaches senescence and gradually breaks down (Sirén 1955, Bormann and Likens 1979, Janisch and Harmon 2002). In the absence of distinct disturbances, autogenic stand development is expected to lead to gap dynamic systems, in which causes intrinsic to the stand are the main determinants of both the timing and characteristics of tree mortality. Stand dynamics are then primarily driven by small-scale tree mortality (Kuuluvainen 1994, McCarthy 2001). This so-called background mortality and deadwood decomposition may eventually become balanced. Then the stand deadwood pool is expected to reach a ‘quasi-equilibrium’ state, in which deadwood volume and quality show only minor fluctuations around an equilibrium condition (Bormann and Likens 1979, Hofgaard 1993a, Janisch and Harmon 2002, Storaunet 2006).

However, a moderate-severity disturbance, either due to an allogenic disturbance agent, or a proportion of trees with increased vulnerability to specific disturbance agents, can cause episodic tree mortality. In such instances, a large number of trees are killed during a relatively short period of time (Mueller-Dombois 1987, Lugo and Scatena 1996). This type of tree mortality results in deviations from the expected autogenic stand development, and leads to a non-equilibrium state and fluctuations in deadwood volume (Hély et al. 2000, Fraver et al. 2002). In the short term, these fluctuations are directly due to the trees killed in the episode and their decomposition. In the longer term, episodic mortality influences deadwood dynamics by reducing the quantity of larger mature trees susceptible to disturbance agents and altering the predisposition to subsequent tree mortality by altering age- and size structure and species composition (Oliver and Larson 1996). For instance, outbreaks of insects preferring mature trees may deplete their host trees in severely impacted stands, changing the stand-level susceptibility to future outbreaks for decades (MacLean 1980, Berg et al. 2006).

The role of deadwood in boreal forest ecosystems

In forest ecosystems deadwood and its decomposition play significant roles in many fundamental ecological processes by forming the bases for cycling of photosynthetic energy, carbon, and nutrients stored in woody material. Deadwood also contributes to soil formation and soil profile development, and has functions such as erosion control (Harmon et al. 1986, Hyvönen and Ågren 2001). Moreover, in many forest types deadwood plays a pronounced role in stand dynamics in facilitating arboreal regeneration (Franklin et al. 1987, Kuuluvainen and Kalmari 2003, Lonsdale et al. 2008).

Currently, the importance of deadwood is emphasized for its role in the maintenance of biodiversity (Berg et al. 1994, Brassard and Chen 2008, Lonsdale et al. 2008, Bradshaw et al. 2009). Deadwood offers habitats for a variety of organisms, and a large number of organisms are in turn associated with these deadwood-dwelling species (Grove 2002, Jonsson et al. 2005). These saproxylic species include vertebrates (Ecke et al. 2001, Vaillancourt et al. 2008), invertebrates (Martikainen et al. 2000, Vanderwel et al. 2006a), fungi (Bader et al. 1995, Siitonen 2001), lichens and bryophytes (Crites and Dale 1998, Kuusinen and Siitonen 1998), as well as vascular plants (Gustafsson 2002).

In a given stand, the volume of deadwood is an important determinant of saproxylic species richness (Martikainen et al. 2000, Penttilä et al. 2004, Lonsdale et al. 2008). However, the value of an individual unit of deadwood is also influenced by its quality. Important variables include unit size, decay stage, position (standing vs. down), and tree species (McComb and Lindenmayer 1999, Jonsson et al. 2005, Lonsdale et al. 2008). The value of deadwood is thus dependent on the distribution of a given quantity among different qualities (Hottola et al. 2009).

Deadwood is also a major component of ecosystem carbon storage and cycling (Goodale et al. 2002, Janisch and Harmon 2002, Cornwell et al. 2009). Although the carbon pools in the organic matter in boreal soils are considerably larger (Dixon et al. 1994, Hyvönen et al. 2007), the woody biomass is important for carbon fluxes, due to its more rapid turnover rates compared with the soil carbon pool (Janisch and Harmon 2002).

Large areas of boreal forests still remain unmanaged and play an important role in the global carbon cycle (Bradshaw et al. 2009). The structure and regeneration of these forests and their disturbance regimes are linked – either directly or indirectly – to climatic variability (Hofgaard 1993a, Soja et al. 2007). Increased temperatures and longer growing seasons due to global warming can influence both tree growth and decomposition, although their exact influence is complex and uncertain, especially in the long run (Hyvönen et al. 2007). However, more abrupt changes in deadwood and stand dynamics can be expected from changes in the disturbance regimes. It is evident that climatic warming may alter the frequency and severity of episodic tree mortality events, including those caused by prolonged and higher-severity insect outbreaks (Berg et al. 2006, Soja et al. 2007, Gray 2008). However, recent studies suggest that the warming climate may influence background rates of tree mortality as well (Van Mantgem et al. 2009). These changes have implications for carbon cycling, because changes in disturbance frequency and severity (and thus stand and deadwood dynamics) may alter the ecosystems’ capacity to store carbon (Knohl et al. 2002, Smithwick et al. 2007, Luyssaert et al. 2008).

Deadwood in forest management

Intensive use of forest resources has led to reductions in deadwood volume and changes in its quality in managed forests (Siitonen 2001, Vaillancourt et al. 2008). These changes are especially large when managed forests are compared with late-successional stages of unmanaged forests (Bergeron et al. 2001, Kuuluvainen 2002). Currently, the importance of deadwood for the maintenance of biodiversity and ecosystem functioning is widely recognized, and deadwood is considered a critical component for the long-term sustainability of forest management. Integration of deadwood into forest management is thus seen as an important objective (Lindenmayer and Franklin 2002, Lonsdale et al. 2008, Bradshaw et al. 2009).

To facilitate this integration, forest management based on emulating natural processes and structures has been suggested as a potential solution (Bergeron et al. 2002, Gauthier et al. 2009, Kuuluvainen 2009). Natural forest conditions are seen as those conditions to which organisms are adapted. Thus the presence of natural structures is considered the key to the maintenance of biodiversity and ecosystem functioning (Seymour and Hunter 1999, Lindenmayer and Franklin 2002). The rationale is that the human impact on biodiversity is smaller if changes due to management occur within the limits of the natural range of variability of forest structure (Seymour and Hunter 1999, Lindenmayer and Franklin 2002, Angelstam and Kuuluvainen 2004, Gauthier et al. 2009).

Regarding deadwood, this emulation has two requirements. First, natural forests provide an indispensable reference with which to compare forest management alternatives and a set of hypothetical target states considering for the range of variability in deadwood volume and quality (Kuuluvainen 2002, Nilsson et al. 2002, Keeton 2006, Lonsdale et al. 2008, Gauthier et al. 2009). The second prerequisite is the ability to predict the dynamics of deadwood. This is important in terms of both habitat value and carbon dynamics (Bradshaw et al. 2009). This pre-requisite can be met through modeling the longevity of deadwood and rates of decomposition (Kruys et al. 2002, Vanderwel et al. 2006b, Drapeau et al. 2009).

A problem in determining the ‘natural’ reference levels of deadwood volume is the general lack of information concerning deadwood structures in different ecosystem types in the boreal zone (Brassard and Chen 2008). Deadwood volume in coniferous boreal forests are reported to vary widely (Krankina and Harmon 1995, Linder et al. 1997, Sippola et al. 1998, Siitonen et al. 2000, Nilsson et al. 2002), and thus any generalities in the patterns of deadwood dynamics in late-successional forests are poorly demonstrated (Spies et al. 1988). This is due to the lack of information regarding the input of deadwood through tree mortality as well as its decay rates (Jonsson et al. 2005, Storaunet 2006). Indeed, deadwood is often considered a static structural feature, despite its obvious dynamic nature (Lang 1985).

Thesis aims

My aim was to study the dynamics of deadwood in late-successional coniferous forests in the boreal zone. The research was carried out in stands that were located in four different areas representing distinct geographic locations and contrasting disturbance histories, but that had all developed for a long time in the absence of stand-replacing disturbances and direct human influence. Specifically, the aims were 1) to reconstruct the patterns of recent tree mortality by quantifying tree death rates and their interannual variability (I–III), 2) to quantify ecosystem dead wood pools (IV, V), and 3) to develop models of decay class dynamics for studying the residence times of deadwood as ecosystem components (IV, V). Using this information, the aim was to identify any general patterns of deadwood dynamics in late-successional boreal forests.

STUDY AREAS

Geography, climate, and soils

The studies were conducted in four different areas in the boreal zone (Fig. 1): in the North Shore region in northeastern Quebec, Canada (I, IV) and in three areas in Northern Europe (II, III, V). In the North Shore region, the study included three different stand types, based on the species composition of canopy-dominant trees: black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg)-dominated, balsam fir (*Abies balsamea* [L.] Mill.)-dominated, and mixed stands with shared dominance of the two species. The Northern European study areas were all dominated by Norway spruce (*Picea abies* [L.] H. Karst.).

The North Shore study areas were located within two bioclimatic subdomains: the balsam fir-white birch near the shoreline and the black spruce-moss subdomain elsewhere (Robitaille and Saucier 1998). The Northern European study areas differed in their climatic conditions (according to Ahti et al. 1968). Two of these areas were located within the northern boreal zone in the Pallas-Ylläs National Park in northwestern Finland (II, V) and in the Kazkim river area in the Laplandsky Forest –conservation area, Murmansk Province, Russia (II, V). The third area belonged to the middle boreal zone, and was located in the large forest massif between the Dvina and Pinega rivers in the Arkhangelsk Province, Russia (III, V).

Table 1. Study area coordinates, key climatic figures, and dominant tree species.

Area	Coordinates	Annual / July temperature	Precipitation	Dominant species
North Shore, Canada	49°30’-50°00’N, 67°30’-69°00’W	0.9°C / 15°C	1200 mm	*Picea mariana, Abies balsamea*
Pallas-Ylläs, Finland	67°40’N, 24°22’E	-1.1°C / 14°C	500 mm	*Picea abies*
Kazkim, Russia	68°18’N, 30°22’E	-1.2°C / 13°C	550 mm	*Picea abies*
Dvina-Pinega, Russia	63°00’N, 44°10’E	1.5°C / 17°C	670 mm	*Picea abies*

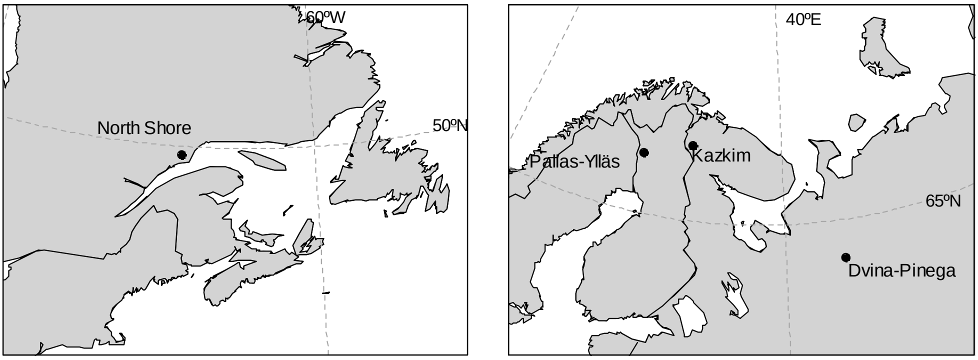

Figure 1. Study area locations.

All the study areas were in humid climates (i.e. precipitation exceeded evapotranspiration). The mean annual temperatures ranged from -1.2 ºC to 1.5 ºC and precipitation from 500–650 mm in the European study areas to 1200 mm in the North Shore in eastern Canada.

Soils in the study areas are formed of quaternary glacial deposits. In the North Shore region these consist primarily of thin to moderately thick layers of undifferentiated tills overlying the Canadian Shield (Robitaille and Saucier 1998). The northern boreal study areas in the Pallas-Ylläs and Kazkim areas are on the Fennoscandian Shield, where the *Picea abies* stands are commonly found on thin undifferentiated tills. The middle boreal Dvina-Pinega area is located on the East European plains, and in contrast to the other areas, the stands are in deep soils, consisting of tills with a high proportion of gleyic fraction (Batjes 2005). Topographically, the North Shore is rugged, with hills of moderate slopes. The northern boreal study areas in Pallas-Ylläs and Kazkim are located on the lower slopes of gentle hills. The middle boreal Dvina-Pinega study area is topographically flat.

Main tree species and disturbance regimes

The study areas in eastern Canada were dominated by *Picea mariana* and *Abies balsamea*. Both species are shade-tolerant and are dominant species in late-successional forests in the region (Robitaille and Saucier 1998). The proportion of *Abies balsamea* tends to increase with site productivity, whereas pure stands of *Picea mariana* are found on poorer sites (Bergeron and Dubuc 1989, Boucher et al. 2006). The maximum age normally attained is app. 200 yr for *Abies balsamea* and 250 yrs for *Picea mariana* (Nikolov and Helmisaari 1992).

Similar to the eastern Canadian *Picea mariana* and *Abies balsamea*, the *Picea abies* that dominates the European study areas is a shade-tolerant species (Nikolov and Helmisaari 1992). It is usually the dominant species on mesic sites, especially in late-successional stages. Compared with the Canadian *Picea mariana* and *Abies balsamea*, it is a longer-living species, with a normally attained maximum age of app. 300–350 yr (Sirén 1955, Wallenius et al. 2005).

The fire cycles in the North Shore region, as well as in the *Picea abies*-dominated sites in Northern Europe can be several centuries long (Wallenius et al. 2005, Cyr et al. 2007). Other disturbances are therefore more important factors for stand dynamics. In eastern Canadian boreal forests, recurrent outbreaks of the eastern spruce budworm (*Choristoneura fumiferana* [Clemens]) are a major disturbance factor. In the North Shore region, the last outbreak occurred from 1975 to the early 1990s and resulted in patchy tree mortality over large areas (De Grandpré et al. 2009). The main host species of the budworm is *Abies balsamea,* although *Picea mariana* also suffers mortality and growth reductions during the outbreaks (Nealis and Regniere 2004). Previous outbreaks in the 20th century recorded elsewhere in Quebec apparently had a minor influence on the North Shore (Blais 1983). Thus, the majority of these forests has been characterized by gap and patch dynamics, driven by wind and factors related to tree senescence, in addition to the spruce budworm outbreaks (Pham et al. 2004, Périgon 2006).

The European boreal forests lack similar large-scale biotic disturbance agents comparable to the spruce budworm in eastern Canada. In late-successional forests, smaller-scale disturbances due to wind, insects, fungi, and senescence-related tree deaths drive stand dynamics (Sernander 1936, Kuuluvainen 1994), in addition to infrequently occurring moderately-severity disturbances due to windstorms (Qinghong and Hytteborn 1991, Syrjänen et al. 1994, Gromtsev 2002, Fraver et al. 2008).

Stand selection

In the European study areas and in the three stand types in eastern Canada, five stands were selected based on forestry maps, aerial photographs, and satellite images. The criteria for selection were characteristics typically associated with unmanaged late-successional forests, including volume of deadwood, an uneven size structure, and the absence of direct signs of human influence (i.e. cut stumps).

All the stands selected were estimated visually to be relatively homogeneous regarding edaphic conditions and needed to be large enough to contain the 1.6-ha sample plot. Large plot size was considered necessary to adequately sample deadwood, which is often characterized by high spatial variability at fine scales (Harmon et al. 1986).

The question of how representative and comparable the sampled stands are requires some attention (cf. Fraver et al. 2009). In the North Shore, cuttings during recent decades have influenced the landscapes studied, and the selected stands were remnant patches of previously larger untouched forests. The forests in northern Finland have in general a long utilization history, mainly by selective cuttings. It is not known why the Pallas-Ylläs stands have originally been left outside the cuttings (see Angelstam and Kuuluvainen 2004). In contrast, the study areas in Kazkim and Dvina-Pinega were located in remote areas, where prior human influence has been negligible. In these areas, stand selection was limited primarily by logistic limitations in the roadless wilderness. Despite these uncertainties, the sampling procedures were considered to facilitate meaningful comparisons of the main ecological features of the stands.

METHODS

Quantification of stand structure (IV, V)

Dead and living trees were measured and mapped on sample plots of 40 x 400 m. In the North Shore all living trees with a minimum breast-height diameter (1.3 m height, DBH) of 20 cm and snags with a minimum DBH of 10 cm were recorded. In the European study areas the sampling was extended to all trees (including down woody debris) with a minimum DBH of 10 cm. In all study plots, tree heights were measured on a subsample of trees (app. half of the trees) and estimated for the remainder, using regression models between DBH and tree height (IV, V).

Dead trees were classified into decay classes. The decay classification applied in the North Shore followed that by Imbeau and Desrochers (2002). It was modified for the European study areas by simplifying the classification of snags and including classes for down woody debris (II, III, V; Fig. 2). This classification relied primarily on the presence/absence of branches of a certain order that has been found useful in determining the time since tree death (Storaunet 2004). Although a number of previous studies have successfully applied differing classifications of down woody debris in modeling decay class dynamics or determining their time since death (e.g. Storaunet and Rolstad 2002, Kruys et al. 2002), they are problematic in that their performance assessments have not considered bias related to the subjectivity of the classification. This is most likely a small problem when the same persons familiar with the classification classify the trees, but the repeatability of such classifications in other studies is uncertain (Larjavaara and Mueller-Landau, submitted manuscript). This applies especially to classifications that contain contradicting criteria (e.g. the criteria include both bark and branch characteristics that are not necessarily consistent in all cases). To minimize these potential problems, the simplified classification was applied in the current work.

Wood volumes were calculated using volume integrals of taper equations by Laasasenaho (1982) for *Picea abies*, Scots pine (*Pinus sylvestris* L.) and deciduous trees (taper equations for European white birch *Betula pendula* [Roth]). *Picea mariana* and *Abies balsamea* volumes were calculated with taper equations by Sharma and Zhang (2004). This approach also allowed us to estimate the volume for snapped trees (IV, V).

In the European study areas the biomass in deadwood was determined from the average wood density in each decay class (V). Selection of the trees for sampling wood density was done, using random sampling stratified by decay classes. From the trees selected, a sample disk (stem cross-section) or a partial disk was extracted and its dry mass/green volume was determined. The decay class-specific estimates were multiplied by the volume in each class to provide an estimate of biomass in coarse woody debris (V). It was assumed that some part of the recently dead snags had not lost their density due to decomposition. The mean of the top-10 highest densities was therefore used as the wood density of living trees to compare the biomass in deadwood with the total woody biomass.

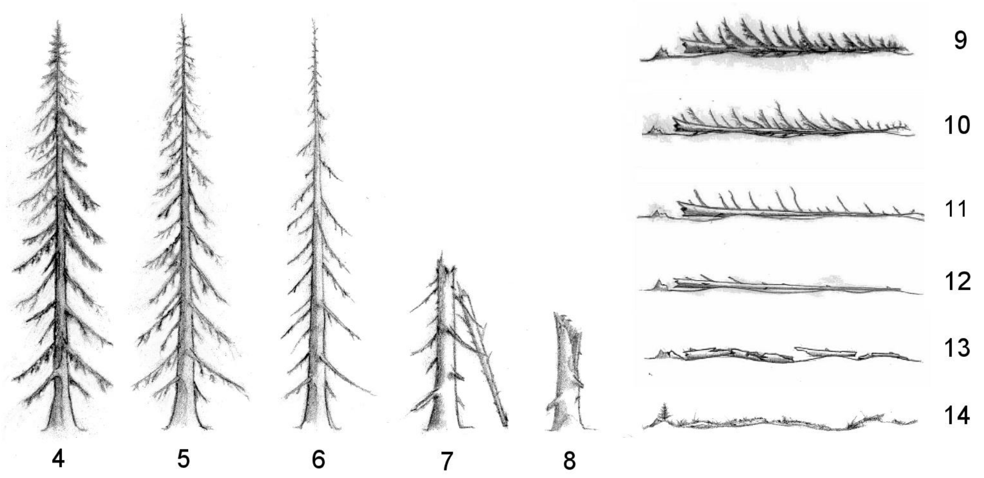

Figure 2. Illustration of decay classes for snags (classes 4-8) and down woody debris (classes 9-14; see II, III, V for detailed description). Classes 1-3 were reserved for living trees and were not used in this study. Illustrations by Ilkka Aakala.

Reconstruction of past tree mortality and disturbance history (I–III)

Patterns of tree mortality were determined, using dendrochronological cross-dating (Fritts 1976, Mast and Veblen 1995). For this, sample disks were extracted from dead trees, and the calendar year of the formation of the last ring was determined, using the marker-ring method (Yamaguchi 1991). Tree rings were then measured and the visual cross-dating results verified statistically against a master chronology for each study area (Holmes 1983). The calendar year of the last ring was interpreted as the year of tree death. This information was then used in reconstructing the annual tree mortality rates (I–III).

The year of the last ring may not correspond to the actual year of tree death, for two reasons. First, in decayed trees that have lost their bark, the outer rings may erode, and second, trees that have weakened prior to their death may have missing rings (Cherubini et al. 2002). The first uncertainty was avoided by sampling trees at a point where bark or bark remnants were visible. The second uncertainty was minimized by confirming the last ring on 2 or 3 radii on the same sample disks, so that partial rings were accounted for. Although inaccuracies may still have occurred between tree death and the calendar year of the formation of the last tree ring, the calendar year of the last ring was always used as the year of tree death.

The tree-ring data were also used for reconstructing the long-term disturbance history for the Dvina-Pinega stands, based on growth release analysis (III). In this, the ring-width measurements were investigated for patterns of growth release. These were then interpreted as a sudden increase in available resources for growth that resulted from the death of a nearby tree (Black and Abrams 2003, Splechtna et al. 2005).

In the European study areas the time since the last stand-replacing disturbance was assessed, using tree age distributions, fire scars, and charred woody material. The age structure was determined by systematic sampling of living trees on each sample plot (II, III). In the Kazkim area several fire scars were recovered from the vicinity of the sample plots on *Pinus sylvestris* snags. The years of formation of these fire scars were cross-dated against a 2000-yr chronology (Lindholm and Eronen 2000). In addition, several pieces of charred wood were recovered from the Kazkim and Pallas-Ylläs areas, and were radiocarbon-dated. In the Dvina-Pinega area no signs of fire were found, and the time since the last stand-replacing disturbance relied on the ages of the oldest trees, which give the minimum time since the last stand-replacing disturbance (Wallenius et al. 2005).

Models for decay class dynamics (IV, V)

Stage-based matrix models were constructed to assess the transition rates between decay classes and the longevity of deadwood as ecosystem structure (IV, V). First, the time period the trees stay in each decay class (class residence time) was determined from the time since tree death data, derived from the cross-dated sample trees. Annual transition probabilities between decay classes were then calculated from this data (Kruys et al. 2002). These annual transition probabilities were converted to 5-yr intervals (IV, V), during which a tree can remain in the same decay class *i*, move to class *i*+1, or move to class *i*+2. In the present study, these models were modified for snags by including the possibility of snag failure (i.e. height reduction of the stand part to below 1.3-m height; IV, V), and also degradation (i.e. height reductions above 1.3-m height; V). This was done by assigning the snags a probability of leaving the system through failure (IV) or by making a transition to a corresponding down woody debris class (V). For the European study areas the models were further developed to include the down woody debris decay class transitions. Wood density losses were incorporated in the models for the European study areas (V). This was done by multiplying the volume of wood in each class with the class-specific mean density at each step of the model run.

Comparisons of deadwood longevity and decay rates were done, based on the expected residence time (or half-life, IV). In the eastern Canadian study areas the expected residence time refers to the point in time when 50% of the number of trees killed standing at year zero have undergone failure or decayed past the last decay class included in the model (IV). In the European study areas the expected residence time refers to the point in time when 50% of the volume or mass input at time zero has decayed past the last decay class included in the model (V). These residence times were estimated separately for snags (expected snag residence time), down woody debris (expected down woody debris residence time), and for trees that die standing and are followed through snag degradation, snag failure, and the decay of fallen parts as down woody debris (expected total residence time) (V).

RESULTS AND DISCUSSION

Contrasting patterns of tree mortality were due to autogenic disturbance factors in northern boreal Fennoscandia (II)

The temporal patterns of tree mortality (Fig. 3) were contrasting between the northern boreal *Picea abies* forests in the Pallas-Ylläs and Kazkim study areas. Although in both areas tree mortality was continuous, the average tree mortality rates and their interannual variability were much higher in the Kazkim area (II). These stands had experienced elevated tree mortality rates, including episodic tree mortality in 1986, during which app. 7% of the trees died (II). Tree death rates were also elevated in the years prior to and after this peak, and app. 13% of the trees died during 1983–1986 (II). The average tree mortality rate for the past 15 yr (outside of the distinct episode) was 0.9% in the Kazkim area. This was still three times the longer-term mortality rate in the Pallas-Ylläs stands, with an average annual tree mortality rate of 0.3% (II), although the most important causes of tree death were the same in both areas: heartrot fungi that predisposed the trees to wind-induced mortality (Lännenpää et al. 2008).

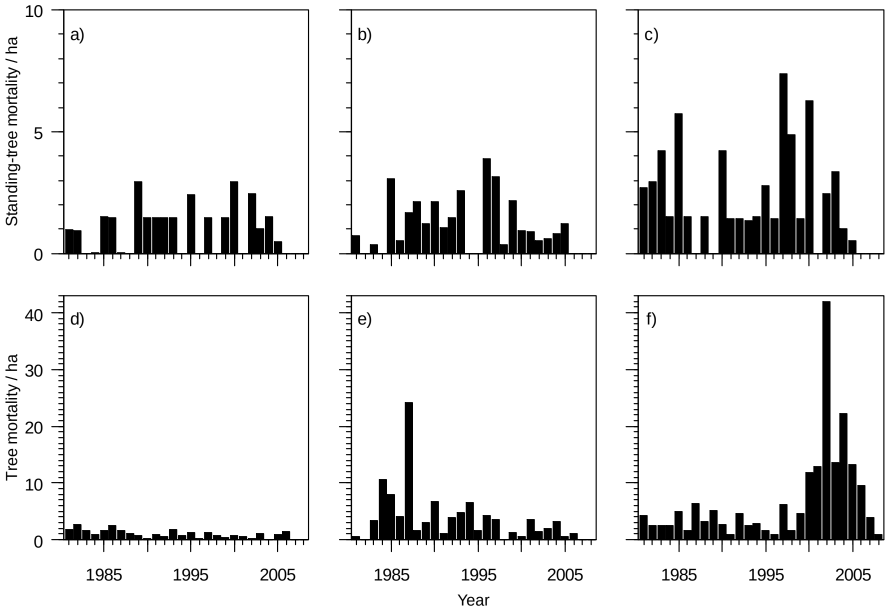

Figure 3. Annual tree mortality reconstructions for standing-tree mortality in the *Picea mariana* (a), mixed (b), and *Abies balsamea* stands in the North Shore, and both standing and down tree mortality in the *Picea abies*-dominated European study areas of Pallas-Ylläs (d), Kazkim (e), and Dvina-Pinega (f).

The contrasting temporal patterns of tree mortality were attributed to the differences in the tree age structure (II). The Pallas-Ylläs stands were uneven aged, whereas the Kazkim stands were old and even aged. Judged by the cross-dated fire scars and the tree age structure, the majority of the trees in the Kazkim stands had originated following a stand-replacing forest fire that occurred in 1689 (II). These trees were now close to or over the 300 years of age considered as the normally attained maximum age for *Picea abies* (Sirén 1955, Wallenius et al. 2005). The proportion of decayed stems increases with age in these stands (Norokorpi 1979), which makes the stand age structure a major determinant for the stand-scale vulnerability to wind-induced tree mortality. This autogenic predisposition has probably been the most important determinant for tree mortality, although the occurrence of high winds has determined the exact timing of tree death (Edman et al. 2007). In the Pallas-Ylläs area, only a small proportion of trees was similarly predisposed to the disturbances due to the uneven age distribution. The type of elevated tree mortality documented in the Kazkim area that is related to the senescence and breakdown of a cohort of trees approaching its maximum age was also documented in earlier studies from northern boreal spruce forests (Sirén 1955), as well as in other forest types (Mueller-Dombois 1987).

The tree mortality rates in northern boreal *Picea abies* forests were previously documented from northern Sweden, and were 0.5% and 0.6% (Hofgaard 1993b, Fraver et al. 2008). These values were derived from uneven aged stands and are thus more comparable with those of the Pallas-Ylläs stands. The rates in the Swedish studies were calculated from re-measured permanent sample plots over relatively long remeasurement periods, and the factors responsible for the higher rates than in the Pallas-Ylläs stands are not known.

A long-term reconstruction of disturbance history was available for the Pallas-Ylläs area (Caron et al. 2009). This reconstruction was consistent with the findings in the present study. In this area, tree mortality was continuous and although some fluctuations were evident, the forests had escaped major disturbances for at least the past 150 yr (Caron et al. 2009). This is also consistent with the study by Fraver et al. (2008) in *Picea abies* forests of northern Sweden: stand dynamics were driven by small-scale disturbances, with infrequent moderate-severity disturbances caused most likely by windstorms.

The temporal patterns in late-successional northern boreal *Picea abies* forests were linked with their time since the last stand-replacing disturbance (II). This demonstrates the long-term influence a major disturbance has on forest ecosystem structure and dynamics and the role of autogenic predisposition in determining the patterns of tree mortality. On the other hand, the Pallas-Ylläs results showed that the dynamics in uneven aged stands that have escaped larger disturbances for a long period of time may be driven by relatively stable and continuous background mortality.

Patterns of tree mortality were variable and driven by allogenic disturbance factors in the Dvina-Pinega and North Shore study areas (I, III)

The forests in the North Shore in eastern Canada and in the Dvina-Pinega area in northwestern Russia were both known to have suffered from episodic tree mortality (Nevolin et al. 2005, De Grandpré et al. 2009). The most recent episode in the Dvina-Pinega was due to a combined effect of drought and bark beetles and occurred from 1999 to 2004 (Fig. 3, III). An average of 21% of trees were killed in the stands examined (III). The eastern Canadian study areas were known to have been influenced by episodic tree mortality due to the spruce budworm (Pham et al. 2004, Périgon 2006). However, the episode was too far in the past to be reliably included in the reconstruction of standing-tree mortality, which was limited in time due to the decay and failure of the standing dead trees with time.

In both areas, tree mortality outside of the episodes was continuous (Fig. 3). The average annual tree mortality rates were 0.8%, 0.8%, and 1.2% in the eastern Canadian *Picea mariana*, mixed, and *Abies balsamea* stands, respectively (I). In the Dvina-Pinega area the background mortality rate was 0.5%, as calculated for the period preceding the recent episode of tree mortality (III).

The annual mortality rates were thus higher in the eastern Canadian stands than in both of the uneven aged European study areas in the Pallas-Ylläs (II) and Dvina-Pinega areas (III). At least two possible explanations exist for this. First, as was apparent from the differences between Kazkim and Pallas-Ylläs, tree age can potentially be a major determinant in the probability of tree death in late-successional forests. *Picea abies* is a longer-living species (Sirén 1955, Wallenius et al. 2005) than *Picea mariana* and *Abies balsamea* (Nikolov and Helmisaari 1992). In stands with similarly uneven age structure, the shorter life span of these tree species means a higher turnover rate for the canopy trees than for the *Picea abies* stands. The second factor, independent of age structure, was the influence of the last spruce budworm outbreak in the North Shore. This outbreak probably had long-lasting impacts on the tree mortality rates; some of the trees died slowly due to weakening from the defoliation and from the secondary mortality agents, as well as to gap-expansion processes (Oliver and Larson 1996, Worrall et al. 2005).

The variability in annual tree mortality rates was low in the Dvina-Pinega area prior to the recent episode; this was also the case in the *Picea mariana* stands in the North Shore, whereas the annual variability was more pronounced in the mixed and *Abies balsamea*-dominated stands (Fig. 3). This variability was likely related to the aftereffects of the last spruce budworm outbreak, similar to the higher average mortality rates. Thus, the variability was also lower in the *Picea mariana* stands that were less impacted by the outbreak. These were consistent with the findings of Senecal et al. (2004) that *Picea glauca* in western Quebec suffered from unexplained variability, following the last spruce budworm outbreak.

In the Dvina-Pinega area, the reconstruction of long-term disturbance history in the Dvina-Pinega area depicted a disturbance regime characterized by chronic small-scale events, punctuated with infrequently occurring moderate-severity disturbances (III). In the recent disturbance that led to the death of 21% of the trees in the stands, the spruce bark beetle (*Ips typographus* Wood & Bright) was the visible cause of tree death. However, it was evident that drought conditions had been the underlying factor (III). The stands in the Dvina-Pinega area are predisposed to drought conditions due to the poorly drained soils, which is the result of the low topographic variation and the high content of fine fractions in the soil (Batjes 2005). These types of conditions are known to cause superficial rooting of *Picea abies*, which predisposes the trees to drought stress when the topsoil dries during dry summers (Xu et al. 1997, Puhe 2003). Drought as the underlying cause for the episodic tree mortality was supported by the relationship between tree growth and soil moisture conditions, in which the low soil moisture availability limited tree growth (Aakala and Kuuluvainen, submitted manuscript). Trees with moisture-limited growth are susceptible to drought-mediated mortality during severe droughts (Suarez et al. 2004, McDowell et al. 2008). This interpretation was further supported by the fact that the *I. typographus* found on most of the trees killed commonly requires weakened host trees or abundant breeding material (such as after a wind-throw event, which was not evident in the study area) to build up their populations to epidemic levels (Wermelinger 2004, Raffa et al. 2005, 2008). Drought is commonly such a weakening factor (McDowell et al. 2008). In addition, the most recent episode began directly following the driest summer during the climate data coverage from 1913 to 2007. Correlation analyses further indicated that during the period of available climatic data from 1913 to 2007, both the annual tree mortality rates and growth releases were correlated with soil moisture deficits (III). These findings and the previous accounts of episodic standing-tree mortality in the region imply that the previous moderate-severity disturbances visible in the disturbance chronology were also potentially driven by the occurrence of droughts (III).

The disturbance regime in the Dvina-Pinega stands thus differed from what has commonly been reported from *Picea abies*-dominated boreal forests, in which moderate-severity disturbances are considered to be rare (Gromtsev 2002, Selikhovkin 2005). Even when such disturbances are reported, drought has not been considered as a significant disturbance agent (Syrjänen et al. 1994, Gromtsev 2002, Selikhovkin 2005). An exception is the drought in southern Scandinavia in the mid-1970s that resulted in episodic *Picea abies* mortality (Aronsson et al. 1978, Worrell 1983). Mäkinen et al. (2001) also suggested that a similar mechanism, in which vertical root development was hindered by stony soils, may have contributed to drought-induced damage in *Picea abies* stands in Finland. More often, studies have described gap dynamic forests, with occasional moderate-severity disturbances due to tree senescence and/or wind storms (Jonsson and Dynesius 1993, Kuuluvainen et al. 1998, Fraver et al. 2008).

The spruce budworm outbreaks are well known to influence eastern Canadian stands, but drought and bark beetles can also apparently cause similar tree mortality over large areas in European boreal forests. Although disturbance factors were different, both spruce budworm outbreaks and the drought in the Dvina-Pinega area had similar consequences for deadwood dynamics, since both have resulted in patchy standing-tree mortality. These more or less infrequent moderate-severity disturbances also influence small-scale dynamics in the future, as they influence the availability and susceptibility of living trees to future disturbances. However, the reconstructed patterns of tree mortality in all the study areas also verified that tree mortality occurred continuously, also outside the episodic tree mortality. It seems plausible that this background tree mortality is to a large extent driven by autogenic causes, in which the senescence of the trees plays a major role. This makes background mortality a characteristic process in uneven aged late-successional boreal forests.

Volume of deadwood and their decay stage distributions reflected site productivity and disturbance history (IV, V)

Deadwood volume varied among the study areas and reflected the differences in stand productivity and disturbance histories. The variation in stand-type averages in snag volumes ranged from 6 $m^3 \cdot ha^{-1}$ in Pallas-Ylläs to 41 $m^3 \cdot ha^{-1}$ in the *Abies balsamea* stands of the North Shore (IV, V). The total deadwood volumes (measured in the European study areas) varied from 42 and 44 $m^3 \cdot ha^{-1}$ in Pallas-Ylläs and Kazkim, to 170 $m^3 \cdot ha^{-1}$ in Dvina-Pinega (V). Despite this high variability, the results fit the reported range of variability of deadwood volume in coniferous boreal forests, because the documented absolute volumes have ranged widely, from 19 to 201 $m^3 \cdot ha^{-1}$ (Sippola et al. 1998, Siitonen et al. 2000, Nilsson et al. 2002).

In previous studies of deadwood dynamics, stands with signs of episodic tree mortality have usually not been included. In the absence of such events the differences are therefore considered to reflect mainly site productivity differences (e.g. Sippola et al. 1998, Nilsson et al. 2002, Storaunet et al. 2005). Considering the comparability of forest and deadwood dynamics, the proportion of dead from total woody volume (dead and living) can be a more meaningful measure than absolute volume. This proportion reflected the recent patterns of tree mortality, and was elevated in the Dvina-Pinega area (53%) and in the Kazkim area (38%). In the Pallas-Ylläs stands not impacted by episodic tree mortality, the proportion was 28%. As for the biomass, these volumes represent app. 49%, 37%, and 20% of total biomass in stems in the Dvina-Pinega, Kazkim and Pallas-Ylläs areas, respectively (V). It should be noted that these values contain uncertainties, due to the difficulties in determining the volume of down woody debris in advanced stages of decay, owing to the loss of stem shape (Fraver et al. 2007). Nevertheless, the results from the Pallas-Ylläs study area (without episodic tree mortality in the recent past) were comparable with the results of Krankina and Harmon (1995) that reported the same 20% proportion of dead from total wood volume in southern boreal old-growth forests.

For snags, the proportions of dead out of total standing tree volume were in general higher in the North Shore study areas than in the European study areas. They were 7% in Pallas-Ylläs, 9% in Kazkim, 21% in the Dvina-Pinega, and 15% in *Picea mariana*, 26% in mixed, and 27% in *Abies balsamea*. These values were not directly comparable, because the North Shore values are calculated with large trees only (DBH ≥ 20 cm), which may increase this proportion of dead trees (Nilsson et al. 2002). However, the differences are also indicative of the predominant modes of tree mortality in the areas. In the Pallas-Ylläs and Kazkim stands most standing-tree mortality was due to stem breakage (Lännenpää et al. 2008), and the remnant volume even in recently dead trees is therefore lower than in areas where most trees die standing and fall later on, as has likely occurred in the North Shore area, owing to the last spruce budworm outbreak (Kneeshaw and Bergeron 1998, Vaillancourt et al. 2008). A short time since episodic standing-tree mortality also increases this proportion, as was evidently the case in the Dvina-Pinega stands (V).

Qualitative differences were apparent in the decay class distributions (IV, V). A major determinant was the proximity in time to the last major disturbance, which had a pronounced effect on the decay class distributions in the North Shore, Kazkim, and Dvina-Pinega areas. Similar findings were presented in previous studies with moderate-severity disturbances (Lang 1985, Spies et al. 1988). In the absence of episodic tree mortality, the decay class distribution should over time converge to a steady-state decay class distribution (Kruys et al. 2002, Holeksa et al. 2008). Here the input and output of deadwood in each decay stage are relatively constant, and the decay stage distribution is determined by the class residence time in each decay class. Based on the information on past tree mortality (II), only the Pallas-Ylläs stands may have exhibited a steady-state decay class distribution (V).

Episodic tree mortality events in the past were well visible in relative volumes, as well as in the decay class distributions. Despite the high variability in the deadwood volumes, as well as relative to the total woody volume, deadwood was an important structural component in all the forests studied. Both snags (IV, V) and down woody debris (V) accounted for a considerable proportion of total wood volume and wood biomass.

Snags and down woody debris were persistent ecosystem components (IV, V)

The expected snag residence times were variable (Fig. 4). For *Picea abies* snags in the northern boreal study areas the expected residence times were 21 yr and 27 yr for the Pallas-Ylläs and Kazkim areas. In the middle boreal Dvina-Pinega area this time was considerably shorter, with an expected snag residence time of 12 yr (V). In the eastern Canadian North Shore, the expected residence times for the number of snags were longer, 35–40 yr for *Picea mariana*, and 30–35 yr for *Abies balsamea* (IV).

The expected *Picea abies* snag residence times were within the limits reported previously for the residence times for *Picea* spp. from boreal Canada and Fennoscandia, which have varied from less than 10 years to 34 years (Krankina and Harmon 1995, Lee 1998, Storaunet and Rolstad 2004, Mäkinen et al. 2006). The expected snag residence times were longer in the North Shore. It should be noted that the results were not directly comparable between the North Shore and northern Europe, because snag degradation was not considered in the North Shore. However, the differences probably partially reflect also the causes of tree mortality. Trees killed standing by the spruce budworm may often have their woody material intact and thus remain standing longer, compared with the senescence-related mortality of heartrot-afflicted trees in the northern boreal Europe (Storaunet and Rolstad 2002, Lännenpää et al. 2008). Kneeshaw and Bergeron (1998) noted that 12 yr after the last spruce budworm outbreak in the more southern parts of Quebec, over 80% of budworm-killed trees were still standing. In the North Shore, the 80% proportion of *Abies balsamea* standing was reached at 15-20 yrs after death, so the early part of the decomposition appeared somewhat consistent with these results. However, the long snag residence times in the North Shore may have partially been a methodological artifact due to arbitrarily choosing to increase the time a tree stays in the last decay class 7, because only the least decayed samples from that class were included in the analyses (IV).

For the European study areas the expected residence times were also calculated for down woody debris (V). The expected down woody debris residence times ranged from 20 yr in Dvina-Pinega, to 30 yr in Pallas-Ylläs, and 40 yr in the Kazkim area (V). These residence times were subject to further uncertainty, due to the unknown time the logs had been standing prior to their failure (Storaunet and Rolstad 2002). This was probably a contributing factor for the high variability within the study areas, which was especially apparent in the Kazkim results (V).

Nevertheless, the present results were consistent with those of Kruys et al. (2002) from midnorthern Sweden, where the expected residence time of *Picea abies* down woody debris was 26 yr. The results by Jonsson (2000) are similarly in the same range as the present study results, since *Picea abies* attained a decay class corresponding to the last class in this study on average in 34 yr. However, Storaunet and Rolstad (2002) reported a considerably longer time of 56 yr to reach that stage in Norway. They suggested that such differences may be related to variability in the temporal patterns of deadwood recruitment. In the present study, this effect may explain part of the high variability in the Kazkim results (V): the tree mortality reconstructions showed that very few trees in the Kazkim area died during the period 1970–1977 (II). Thus there were no samples for that period for the decay class dynamics model either. It is possible that this has resulted in fast-decaying trees and the very slow-decaying trees to be included in the sample, and led to high variability in the times since death in the advanced stages of decay.

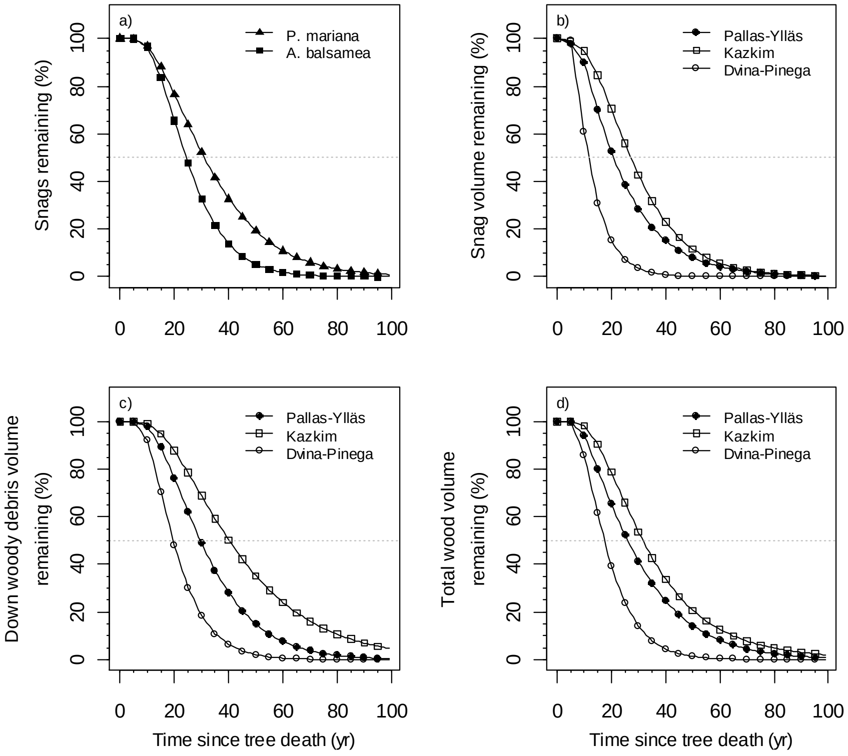

Figure 4. Simulation results of: snag numbers in the North Shore (a), snag volume (b), down woody debris volume (c), and total deadwood volume (d) in the European study areas. Total deadwood volume refers to trees that die standing, and are followed through snag degradation, failure and subsequent decay as down woody debris. The dotted horizontal line represents the 50% of number (a) or volume (b-d) remaining.

The models developed in the present study also facilitated tracking the fate of trees killed standing through snag degradation and failure, and the subsequent decay class transitions as down woody debris. These expected total residence times were 18 yr in Dvina-Pinega, 26 yr in Pallas-Ylläs, and 32 yr in the Kazkim area (V).

During decomposition, snags lost little of their density (V), in agreement with earlier studies (Johnson and Greene 1991, Krankina and Harmon 1995). This is probably related to the simultaneous decrease in the mechanical strength of woody material with decreasing density (Råberg et al. 2005); snags tend to fall prior to major decreases in density. In down woody debris, density losses were more evident, although the decay classes with the lowest densities could not be included in the model for decay class dynamics. This was because they had decomposed beyond a point where cross-dating the year of death was possible, which was required for the model parameters. It was evident that methods other than dendrochronological cross-dating relying on intact tree-ring structure are required for parameter estimation for the most decayed classes and for determining the residence times of biomass and carbon dynamics properly in the models (V).

Decay rates are dependent on climatic differences, mainly through their influence on the biological activity of decomposing organisms. Yatskov et al. (2003) reported a positive relationship between mean annual temperatures and decay rates, when the differing decay resistance of different species was taken into account. The expected residence times for *Picea abies* in the three European study areas followed this tendency, with the most rapid decay in the Dvina-Pinega area with the highest temperatures and slowest in the Kazkim area with the lowest temperatures (V). In addition to what is measured at climate stations, the climatic conditions are also influenced by stand conditions: the microclimatic conditions between the open northern boreal forests, and the middle boreal Dvina-Pinega have probably contributed to the decay rate differences (V). The decay rate differences between *Picea mariana* and *Abies balsamea* are probably influenced by the differing chemical and physical structure of the woody material (Mackensen et al. 2003). However, these differences were likely influenced by the microclimatic differences between the open *Picea mariana* and the closed-canopy *Abies balsamea* stands, similar to the differences among the European study areas, (IV, Campbell and Laroque 2007).

There were no differences among the European study areas in decay-class specific densities in down woody debris, and small differences in snags in the midstages of decay (V). This suggests applicability of the same decay class-specific densities over a range of conditions (cf. Holeksa et al. 2008). This and the differences in decay rates between the study areas and species (IV, V) therefore suggest that the models for decay class dynamics require parameterization for the transition rates in different regions and species, but that the decay class-specific densities may be applicable over wider areas (V).

The models developed facilitate studies on habitat dynamics, as well as biomass and carbon dynamics. The results showed variable decay rates among the study areas and species. This variability highlights the differences in deadwood volumes attributable to differences in site productivity. In lower-productivity stands where wood decay rates were lower, the deadwood in the stands has accumulated over a longer period of time. Despite these differences, deadwood was a long-lasting structural component in all the areas studied. Even in the most rapidly decaying Dvina-Pinega area the expected residence time of a tree killed standing was 18 yr. Deadwood thus forms a persistent carbon storage and habitat structure in late-successional boreal forests.

IMPLICATIONS FOR FOREST ECOLOGY AND MANAGEMENT

Can deadwood volume and quality reach a quasi-equilibrium state in late-successional forests?

In theory, tree mortality and decomposition are balanced in quasi-equilibrium forests, and deadwood volume experiences only minor fluctuations (Bormann and Likens 1979, Janisch and Harmon 2002, Luyssaert et al. 2008). If larger disturbances occur infrequently enough, development of such a state at the stand-scale is theoretically plausible (Shugart 1984), and approximate quasi-equilibrium conditions have been reported from coniferous boreal forests (Hofgaard 1993a, Kuuluvainen et al. 1998, Storaunet 2006). However, their occurrence has also been questioned, mainly due to the long time required for a stand to reach this stage, and the pervasive occurrence of moderate-severity disturbances, as well as fluctuations in abiotic environmental factors (Lang 1985, Spies et al. 1988, Oliver and Larson 1996, Hély et al. 2000, Fraver et al. 2002).

The results from the *Picea abies* stands in the Pallas-Ylläs area suggest that the deadwood pool (II, V, Caron et al. 2009) may attain a quasi-equilibrium state in late-successional boreal forests, with balanced availability of deadwood. This result was in contrast with the model suggested previously for the long-term development of such forests in northern Finland by Sirén (1955). According to Siren's model, forest dynamics are characterized by repeating cycles of even aged stands. In this model, strongly cyclic deadwood volume in late-successional forests would be expected.

However, to some extent similar to what Sirén (1955) proposed, the results from the Kazkim area showed that autogenic development may result in a peak in deadwood volume when the postdisturbance cohort of trees becomes senescent and breaks down. The temporary increase in deadwood volume at this stage is consistent with other models suggested for stand development (Bormann and Likens 1979). At the same time, the high age of 317 yr for the Kazkim stands implies that the quasi-equilibrium stage found in the Pallas-Ylläs area requires a lengthy absence of larger disturbances to develop.

In contrast to the northern boreal *Picea abies* forests, the results from this and previous studies (I, III, Périgon 2006) suggest that in the Dvina-Pinega and the North Shore areas such a quasi-equilibrium state is unlikely to occur, because deadwood volume is highly variable due to the episodic nature of tree deaths. This variability results primarily from the high number of trees killed in the infrequently occurring moderate-severity disturbances, but also from the gap expansion processes following these disturbances that further contribute to increased tree mortality rates (Oliver and Larson 1996, Worrall et al. 2005). Over a longer term, this reduces the number of trees available for subsequent tree mortality (Lang 1985, Berg et al. 2006), before the consequently regenerating trees reach maturity. Thus the volume of deadwood would eventually drop with time when the trees killed in the disturbance decompose. This is further enhanced by the altered susceptibility of the stands to similar disturbances in the future, due to the specificity of many disturbance agents for certain species, tree sizes, or age. For instance, mature stands with a high proportion of *Abies balsamea* are more susceptible to the spruce budworm (Bergeron et al. 1995, MacLean and MacKinnon 1997), and larger trees are more susceptible to droughts (Berg et al. 2006, McDowell et al. 2008). Thus, on the stand scale the volume of deadwood in systems subjected to episodic tree mortality can be expected to fluctuate, with positive temporal autocorrelation following episodic events at short intervals, due to gap expansion, but negative autocorrelation at longer time scales, due to reduction in larger living trees susceptible to tree mortality agents. The dynamics of deadwood in late-successional boreal forests therefore resemble the 'nested bicycle model' of forest dynamics (Worrall et al. 2005), where the background mortality occurs conditional to the moderate-severity disturbances, owing to their influence on the availability and susceptibility of mature trees for tree mortality.

The intensity and longevity of the deadwood pulse in episodic tree mortality is also dependent on site productivity, which was positively correlated with decay rates (IV, V). In the middle boreal Dvina-Pinega, and for *Abies balsamea* in the North Shore with high productivity and rapid decay rates the pulsed pattern is more pronounced, because with similar mortality rates, the pulse of deadwood volume is higher than in a low-productivity stand. This pulse also disappears more rapidly than in systems with lower decay rates.

Due to the predicted changes in climate, development of a future quasi-equilibrium stage also seems unlikely. This was especially apparent in the Dvina-Pinega study area, where climate, stand, and deadwood dynamics were directly linked through the drought-mediated tree mortality (III, Bigler et al. 2007). Over the long-term, the results suggested that the recent episodic tree mortality was at the upper range of variability in terms of disturbance severity, although the tree mortality reconstructions and the disturbance chronology are not directly comparable (III). However, combined with its wide spatial extent, it is possible that the recent episode was outside the range of disturbance variability in the context of the past 200 yr (III). Potential changes in the frequency and severity of future droughts in northwestern Russia (Intergovernmental Panel on Climate Change 2007) may thus lead to increased frequency and severity of future episodes of tree mortality in the Dvina-Pinega area. Somewhat similarly, climate change in the North Shore is expected to lead to more severe and longer-lasting outbreaks of the spruce budworm (Gray 2008). These changes are driven by the direct influence of climate on the spruce budworm demographics. Climate change may also influence the episodic tree mortality through an increase in *Abies balsamea* dominance in the stands (Bergeron et al. 1995, MacLean and MacKinnon 1997), which results from the predicted lengthening of fire cycles, compared with the historical occurrence of forest fires (Bergeron et al. 2004). In addition, recent research has indicated that climatic change has already influenced background tree mortality rates (van Mantgem et al. 2009). If this is the case it would influence deadwood dynamics in all the study areas, due to the common occurrence of background mortality in late-successional boreal forests.

Forest management implications

The results of the present study bear implications regarding deadwood in forest management. First, considering the use of natural deadwood structures as a reference for management objectives (Kuuluvainen 2002), the observed variability in deadwood volume and quality is important. This variability was dependent on the disturbance history of the stands. The range of variability of deadwood volume within the ecosystems subjected to moderate-severity disturbances and the consequent episodic tree deaths is naturally high, but at the same time the constant background mortality of trees ensured the continuous presence of deadwood (I–III). Often in deadwood studies the sampled stands have been selected so that apparent larger disturbances are avoided (Sippola et al. 1998, Nilsson et al. 2002). However, treating deadwood as a static parameter of stand structure is theoretically justified only in quasi-equilibrium systems. At a stand-scale, this requires that forests dynamics are driven by small-scale mortality (gap dynamic forests). This assumption does not hold in forest types where moderate-severity disturbances are common (Lang 1985), such as in the stands studied in the North Shore (De Grandpré et al. 2009) and in the *Picea abies* stands of the Dvina-Pinega area (III). Avoiding episodic events in documenting natural conditions would at first thought lead to neglecting the upper limit of the natural range of variability in deadwood volume. However, due to the decrease in living trees following episodic tree mortality, it may also be that the lower limit of the variability range would remain undocumented.

Second, and from a forest management perspective, a more difficult issue is the quality distribution of deadwood: the continuity of background tree mortality implies continuity in decay stage distribution. This means that the early decay classes with short residence times are continuously formed under natural conditions. However, under low background mortality rates the stand-level volume of deadwood in early decay stages is low (II, IV, V). It has been argued that species specialized for short-lived habitats with low volume have a higher dispersal propensity than species dependent on less ephemeral, and thus also, more abundant substrates under natural conditions (Grove et al. 2002, Jonsson et al. 2005). The stand-level paucity in the intermediate and later stages of decay with longer decay class residence times may thus be more problematic for species dependent on decay stages that are more persistent, and thus in natural conditions more abundant.

Various alternatives for increasing deadwood in production forests have been discussed in the literature, including active deadwood production in association with silvicultural interventions (Penttilä et al. 2004, Jonsson et al. 2005, Lonsdale et al. 2008) and active control of future stem mortality (Harvey and Brais 2007). It is notable that deadwood retained for biodiversity purposes also forms a dynamic carbon storage medium (Bradshaw et al. 2009). However, since continuous input would be needed to maintain the natural decay stage distribution, which would be difficult in production forests, stand-scale approaches would need to be complemented with landscape-scale measures. These include the increase in protection of deadwood-rich areas, and active creation of deadwood in set-aside areas (Jonsson et al. 2005). Targeting the correct areas for active deadwood management is also important, because the landscape structure is a major determinant for stand-scale biodiversity values (Hottola et al. 2009).

CONCLUSIONS

Deadwood is a dynamic component of stand structure in late-successional boreal forests with complex developmental pathways and dynamics. Nevertheless, similarities in the patterns of deadwood dynamics emerged, despite differences in disturbance regimes and tree species autecology within and between eastern Canadian and Northern European study areas.

The results showed that the deadwood volume was dependent not only on site productivity, but also on the stand developmental stage, and the proximity in time to past episodic tree mortality. These factors included the spruce budworm in eastern Canada, and drought in the Dvina-Pinega area in Northern Europe. In the Kazkim area, the role of autogenic disturbance factors as determinants of deadwood volume was still evident in late-successional forests.

Outside the periods of episodic tree mortality, background mortality of trees was continuous. Over time, this resulted in a distribution of deadwood that included all stages of decay. The differences in the decay rates between the regions and tree species influenced the decay stage distributions, in addition to the absolute volume of deadwood. In stands with lower decay rates the accumulation of deadwood in a given decay stage represents a longer time window of tree mortality, thus smoothing some of the differences in deadwood volume due to stand productivity.

In the absence of larger disturbances, late-successional stands may develop into a quasi-equilibrium stage, in which deadwood quantity and quality can be considered as relatively stable components of stand structure. In the boreal forest, the development of such a state requires a considerably long time. For instance, in the Kazkim area the stands were still undergoing successional development at 317 yr after fire. However, in many forest types the quasi-equilibrium stage appears not to exist and is unlikely to develop, because deadwood volume and quality are naturally highly variable due to the occurrence of moderate-severity disturbances. This variability, the continuous input of deadwood through background mortality, and the rates of wood decomposition determine the availability of deadwood as a habitat and carbon storage medium, and make deadwood a highly dynamic resource in coniferous boreal forest ecosystems.

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