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Using forest stand reconstructions to assess the role of structural continuity for late-successional species

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Abstract

Historical reconstructions of past forest dynamics and stand structures have been used to establish reference conditions for managing present forest ecosystems. In this study we (1) developed and combined a suite of stand reconstruction techniques to describe past stand characteristics, and (2) applied these stand histories to evaluate the relationship between wood-decay fungi and forest continuity. Ten previous selectively logged stands of Norway spruce (*Picea abies* L. Karst.), in the middle boreal zone of southeastern Norway, were studied. We reconstructed stand structures during the 20th century using tree-ring series, growth patterns, age structures, and decay classification and datings of stumps and logs. All stands were selectively logged between 1890 and 1965, with a mean logging interval of 25 years. Harvested volumes (1900–1965) constituted 25–99% of present standing volumes and present volumes were 2.6–21 (median 4) times higher than the lowest estimated historic volumes. Dead wood was categorized into eight decay classes, where one is recently fallen, and eight is almost completely decayed. Six fungus species, assumed to indicate dead-wood continuity, were found on logs in decay classes 2–4, all of which were estimated to be <30 years old. Logs in decay classes 1–4 constituted 85% of logs ≥ 20 cm. Expectedly, fungus abundance increased linearly with increasing number of available logs, but we failed to find a positive correlation between fungi abundance and number of old logs present (decay classes 5–8), when the effect of younger logs (2–4) was accounted for. This finding, together with the stand histories, does not lend support to the hypothesis that a continuous supply of dead wood, at the scale of forest stands, is crucial for the occurrence of the surveyed wood-decay fungi. We propose forest stand reconstructions to hold promise as a tool to assess the role of structural continuity for the occurrence of late-successional and old-growth species. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Coarse woody debris; Decaying logs; Dendroecology; Norway spruce; Old-growth species; Stand reconstruction

1. Introduction

Mimicking natural disturbance regimes has become a widely recognized forest management strategy to assure sustainable ecosystems and to maintain and enhance biodiversity (Hunter, 1990; Swanson and Franklin, 1992; Haila et al., 1994; Angelstam, 1998; Landres et al., 1999). Increasing the amount of undisturbed forest stands and habitat elements associated with old-growth condition is regarded an important part of this management strategy (Liljelund et al., 1992; Esseen et al., 1997; Fries et al., 1997). Primeval old-growth stands are extremely rare in Norway and

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the rest of Scandinavia (Kuusela, 1990), since most of the forested areas were selectively logged until the mid-20th century when clearcutting took over as the main harvesting system. Thus, old-growth features such as decayed coarse woody debris and multilayered stand structures have to be restored from semi-natural selectively logged stands.

The distribution of late-successional species in boreal Scandinavia is limited by habitat characteristics and microenvironment associated with old-growth stands. They may also be constrained by poor dispersal ability, by which they can be said to depend on long-term continuity of certain ecological factors, i.e. a continuous presence of available habitat within the dispersal range of the species. It has been suggested that certain species may serve as indicators of so-called "continuity forest" (Rose, 1976; Peterken and Game, 1984; Bredesen et al., 1997). Such indicator species, mainly cryptogams, have recently been applied in the boreal forest of Scandinavia to identify remnant old-growth stands (Karström, 1992; Bredesen et al., 1997; Norén et al., 1999; Nitare, 2000). To successfully restore old-growth characteristics in managed forest we therefore should know (1) the time required for important habitat features or elements to develop, and (2) whether the species in question are able to colonize newly restored habitats. Answers to these questions can guide prospective forest management for viable populations of old-growth species.

To clarify the dichotomy of habitat versus continuity dependency, historical records like old maps and forest surveys have proven useful (Peterken and Game, 1984; Wulf, 1997; Honnay et al., 1999). However, old maps and surveys with sufficient information to reconstruct forest stand history are, with some exceptions (e.g. Östlund et al., 1997; Linder and Östlund, 1998), rare in boreal Scandinavia. Therefore, alternative methods for studying stand history (Henry and Swan, 1974; Oliver and Stephens, 1977; Lorimer, 1985; Östlund and Linderson, 1995; Fulé et al., 1997) should be applied. These methods have generally been used to describe natural disturbance regimes or forest conditions prior to human influence (Foster et al., 1996). However, they may also be useful when studying the relationship between the occurrence of old-growth species and forest history.

Forest stand reconstructions are in principle simple to perform if it is possible to determine the year of death for each log and stump in the stand, e.g. by dendrochronological crossdating (cf. Fig. 1a). Due to fast decay, crossdating of logs and stumps of Norway spruce has proven difficult beyond the age of 30 years (Dynesius and Jonsson, 1991). To circumvent this problem we combined a suite of reconstruction techniques that enabled us to estimate the year of tree fall or logging.

The objectives of the present study were (1) to develop and combine a suite of stand reconstruction techniques to describe the stand history and past stand characteristics, and (2) to use the stand histories to evaluate the relationship between certain wood-decay fungi and forest continuity. We discuss the benefits and shortcomings of stand reconstruction methods as a tool to assess the role of structural continuity for late-successional species. As a study object we used Norway spruce stands where wood-decay fungi used as indicator species of continuity were found on downed logs. The same approach for stand reconstruction was used to evaluate the historic impact of stand structure on epiphytic lichens in central Norway (Storaunet et al., 2000; Rolstad et al., 2001).

2. Material and methods

2.1. Study area

Study sites were selected within the central part of Nordmarka, a 700 km^2 forested plateau north of Oslo, Norway (59°56′N, 10°44′E). Elevation ranges from 200 to 700 m a.s.l. and the region has a suboceanic climate with mean annual precipitation of 1100 mm and mean annual temperature of 5.5 °C (Tryvannstårnet, 528 m a.s.l.). The region is in the middle boreal vegetation zone (Moen, 1999). Norway spruce (*Picea abies* L. Karst) is the dominating tree species, accounting for more than 95% of the standing volume, and Scots pine (*Pinus sylvestris* L.) and deciduous species constitute the last 5%.

The forest in Nordmarka has been utilized for commercial logging for more than 350 years (Lange, 1966). From 1600 to 1850 charcoal for ironworks, together with firewood and saw-timber, were the most important forest products. After the ironworks shut down in the 1870s, saw-timber, firewood and pulpwood became dominating products.

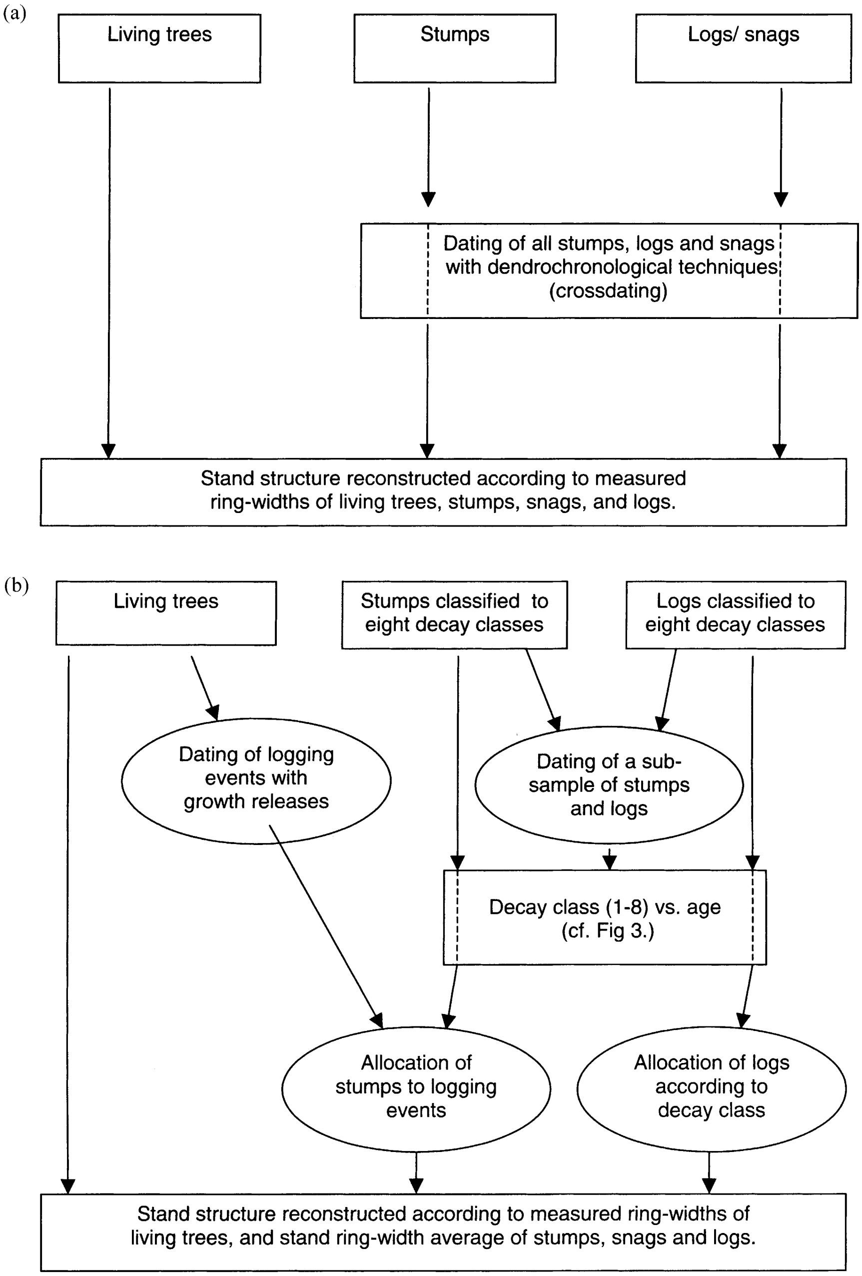


Fig. 1. The principle of stand reconstruction when crossdating of stumps, snags, and logs is: (a) possible, and (b) not possible due to decay.

Although the general trend was a relatively strong pressure on the forest resources, there was spatial and temporal variation in logging activity (Lange, 1966). Selective logging prevailed until the 1940s, when clearcutting took over as the dominating harvesting method. Most of the present mature stands were left unmanaged during the last 30–50 years. Today, mature stands cover ca. 25% of the forested area and downed logs are rare due to previous forestry practice.

2.2. Field sampling procedures

Based on information from the forest owner and forestry maps we searched for mature spruce stands with downed logs. Sample plots were established where we found logs with fruit-bodies of the wood-decay fungus *Phlebia centrifuga* P. Karst. This species is assumed to indicate stands having had a continuous supply of large dead wood (Karström, 1992; Bredesen et al., 1997). It can easily be identified in the field, and it fructifies on relatively recent fallen coarse logs (>20 cm) (Bader et al., 1995; Bredesen et al., 1997).

Ten stands were chosen for further studies as we encountered them. In each stand we designated a circular sample plot with a diameter of 50.5 m (0.2 ha) that included logs with *P. centrifuga*. We surveyed all logs within the plot and searched for five other fungus species assumed to indicate dead-wood continuity (Karström, 1992; Bredesen et al., 1997; Lindblad, 1998): *Phellinus ferrugineofuscus* (Karst.) Bourd. and Galz., *Fomitopsis rosea* (Fr.) Karst., *Phellinus nigrolimitatus* (Rom.) Bourd. and Galz., *Cystostereum murraii* (Berk. and Kurt) Pouz. (not recorded), *Amylocystis lapponica* (Rom.) Singer, and *Leptoporus mollis* (Pers.: Fr.). These species are commonly used as indicator species in biodiversity surveys in Scandinavian forests (see, e.g. Haugset et al., 1996; Norén et al., 1999; Nitare, 2000). All species, except *L. mollis*, are listed as care demanding or vulnerable in the Norwegian Red List (Anon., 1999). Fungus abundance was quantified by recording number of species present on each log, which then was summed over all logs (total fungus records) in the sample plot. This figure is higher than total number of species but lower than total number of fruit-bodies. Because the same fungus individual may produce multiple fruit-bodies on a log, we considered the chosen abundance parameter biologically more meaningful than total number of fruit-bodies.

Most stumps and logs in late decay stages could not be crossdated due to advanced decay. To circumvent this problem we developed a method of reconstructing past stand conditions that involved four steps (cf. Fig. 1b):

1. The diameter, age and growth rate of living trees were reconstructed using measured tree-ring widths.
2. Logging events were determined from growth patterns in living trees.
3. We assessed time since logging or fall for a subsample of logs and stumps in different decay classes (see methods below). These age distributions were used to assign stumps in different decay classes to logging events. Logs were assigned to the year corresponding to the mean age of their decay class.
4. Past stand characteristics were reconstructed by incorporating harvested trees, snags, and logs to the stands.

We recorded the diameter of living trees, logs and snags >10 cm DBH (diameter at breast height, 1.3 m above ground). Living trees were cored with an increment borer at breast height for age determination and radial growth analysis $(n = 981)$. The sample plots were dominated by Norway spruce and only 2% of the sampled trees were Scots pine, birch (*Betula* spp.), aspen (*Populus tremula* L.) and willow (*Salix caprea* L.). The diameter of decayed stumps was measured at the cut surface. Logs and stumps were categorized to eight decay classes (Hofgaard, 1993a) (Table 1). Snags were assigned to the two youngest classes of the decay class system for logs.

To determine the year of fall of a subsample of logs in different decay classes, we used fell scars on living trees and reaction wood in saplings and small trees that were bent over by the falling trees (Dynesius and Jonsson, 1991). Saplings and small trees with scars or suspected reaction wood were cut down, and partial discs were sawn from bigger trees with fell scars. We determined the year of fall for 21 logs in decay classes 2–7. The logging years of a subsample of stumps in different decay classes were determined from growth releases in neighbouring trees. We selected 74 unambiguous cases (9% of the stumps) with only one growth release and only one decay class of stumps adjacent to the living tree.

2.3. Lab procedures and data analysis

Increment cores and discs were shaved with a scalpel to obtain a good surface preparation. Zinc paste was used to make the tree-ring boundaries more visible. Tree-ring widths were measured with an Addo micrometer (precision of 0.01 mm) at 20 or 40×

Table 1
Description of decay classes for logs (Hofgaard, 1993a) and stumps (this study)

Decay class	Description of logs	Description of stumps
1	Recently fallen. Needles and bark still present	Recently cut
2	Solid wood. Needles absent, but twigs and bark still present	Solid wood
3	Wood mostly solid, but infected with rot. Bark beginning to fall off. Only large branches left	Wood mostly solid, but with soft outer surface. Bark beginning to fall off
4	Sapwood soft, bark mostly absent	Sapwood soft. More than 50% of the wood is still solid. All wood has structure
5	Soft wood. Elliptic shape	Soft wood. Less than 50% of the wood is solid, but solid fragments are always present. Often colonized with mosses, lichens and/or dwarf shrubs
6	Soft fragmented wood. Flat elliptic shape	Soft fragmented wood, but parts of the wood have structure. Outline of a stump is still determinable, but deformed. Often colonized with mosses, lichens and/or dwarf shrubs
7	Soft fragmented wood. Log partly hidden	Soft fragmented wood, still rising above the ground, without a core of solid wood, completely overgrown
8	Pulverized wood. Log hidden	Pulverized wood, visible in the litter layer as red woody remains without structure. Outline indeterminable, completely overgrown

magnification. To determine the age of trees when increment cores failed to reach the pith, we estimated the length of the missing radius by matching the curvature of the inner rings to concentric circles drawn on a clear plastic sheet. The mean ring width of the 10 innermost rings was used to estimate the number of rings in the missing radius.

To identify responses to logging events in single trees we examined the radial growth pattern for abrupt and sustained growth increases (Lorimer, 1980, 1985). Norway spruce is a shade-tolerant species and saplings are able to respond to gap openings (Sernander, 1936). For each tree we compared the average tree-ring width over a 10-year period with the average tree-ring width the 10 previous years. We defined a growth release if the increase in radial growth between two successive 10-year periods exceeded 100%. For trees already showing moderate growth before release (>1 mm/year) a 50% increase was applied to define a growth release (Lorimer, 1980). If several consecutive comparisons exceeded the release criteria, the release was dated to the year when the difference was largest (Fajvan and Seymour, 1993). The subsample of stumps was dated according to 100% growth releases in adjacent trees. We added 3 years to account for the time lag usually found in Scandinavia between harvest or windthrow and growth release (Skoklefald, 1967; Bergan, 1971; Dynesius and Jonsson, 1991). To identify logging events within sample plots, we counted the number of trees showing a growth release the following 10-year period. A logging event was defined when growth releases were identified in $\geq 15\%$ of the cored trees.

To assign stumps to logging years we combined the dating of logging events and the age distributions of the different decay classes. We fitted the age distribution of undated stumps to a normal distribution, with distribution statistics obtained from the dated stumps. In cases where two or more logging events occurred within the age range of one decay class, the midpoint year between two logging events was used to allocate the stumps (Fig. 2). Few stumps belonged to decay classes 2, 3, 7 and 8. Hence, the mean ages of stumps in these decay classes were predicted from a linear regression model. The average standard deviation in decay classes 4–6 was used as an estimate for the standard deviation in the other four classes. In three sample plots the age distribution of stumps indicated logging that was not accompanied with evident growth releases. In these cases logging events were defined using a less restrictive criteria or the stumps were assigned to the year that corresponded to the mean age of the decay class. Logs were assigned to the mean year of fall for its corresponding decay class, determined from a

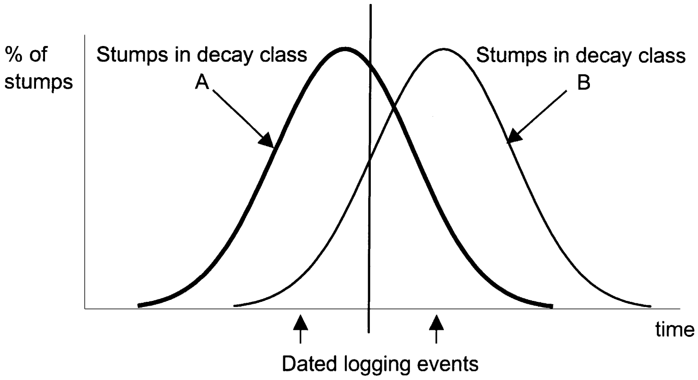


Fig. 2. Illustration showing how stumps were allocated to dated logging events, using estimated age distributions of two decay classes and two logging events. The vertical line at the midpoint between the logging events denotes which stumps that were allocated to the respective logging events.

subsample of 21 logs (cf. Fig. 3). Only a few dated logs were in decay classes 4–8, so the mean fall years of these decay classes were estimated from a linear regression model in the same way as for stumps. We used ANCOVA to test for difference in regression slopes of stump and log age versus decay class (Zar, 1999).

2.4. Reconstruction of past stand characteristics

The DBH of living trees was determined for each year of their lifespan using the tree-ring measurements. The diameters of trees with butt rot were reconstructed using the average ring width from each

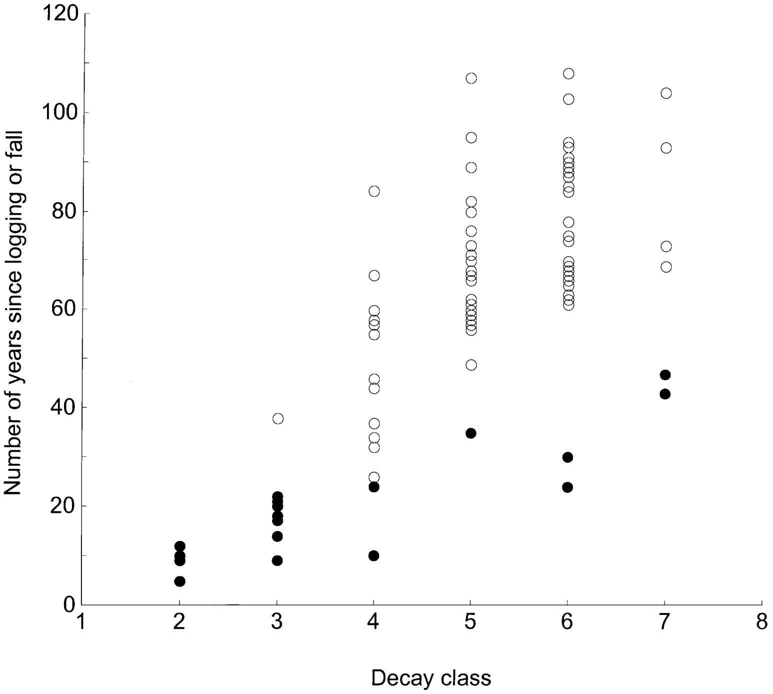


Fig. 3. Number of years since logging of stumps $\geq$20 cm (open circles) and fall of logs $\geq$20 cm (filled circles) according to different decay classes. Decay class 1 is recently cut/fallen and decay class 8 is almost completely decayed. See Table 1 for description of decay classes.

sample plot. The DBH for trees that were stumps at the time of sampling was estimated from a random sample of 113 trees in which we measured both the diameter at stump height (DSH) and at breast height ($\mathrm{DBH} = -0.56 + 0.82\,\mathrm{DSH}$, $r^2 = 0.97$). The diameters and past growth of logs and harvested trees were reconstructed using the average tree-ring width in each sample plot. Bark thickness was estimated using bark functions. The volume of single trees was estimated from volume functions for Norway spruce, and the diameter/height relationship derived from sample trees in each sample plot (Vestjordet, 1967; Fitje and Vestjordet, 1977). The latter is a single-entry volume calculation (see, e.g. Avery and Burkhart, 1994, p. 141), using only the diameter to estimate the volume of single trees at a given diameter/height relationship. The diameter/height relationship was assumed constant throughout the reconstruction period. We estimated diameter distributions and standing volumes at the beginning of each decade, as well as before and after each logging event.

2.5. Sensitivity analysis

We performed two types of sensitivity analysis on factors that could influence the stand reconstruction. First, we tested whether the dating of logging events was robust with respect to the selected criterion, i.e. equal to 15% of the trees showing growth releases within a 10-year period. Applying a 5% criterion and a 5-year period, we checked how this influenced the determination of logging events. The stands were then reconstructed with these additional logging events. Second, we checked the influence of stump and log age assessment, assigning all stumps in each decay class to logging events up to ±30 years (two standard deviations) from the estimated mean age of their decay class. Logs in a given decay class were at the same time assigned to the mean estimated fall year of their neighbouring decay class.

3. Results and discussion

3.1. Age and decay class distribution of stumps and logs

Stumps took more than 100 years to decompose and stump age within each decay class varied considerably (Fig. 3). Most of the stumps (95%) were categorized to decay classes 4–6 ($n = 810$) (Fig. 4). Logs were generally younger than stumps; 85% (logs ≥ 20 cm DBH) belonged to decay classes 1–4 ($n = 140$) (Fig. 4). Within decay classes, logs also appeared to be younger than stumps (comparison of slopes; $F = 6.5$, $p = 0.013$, $n_{\mathrm{stumps}} = 74$, $n_{\mathrm{logs}} = 21$). No stands had all decay classes of logs present, and logs $\geq$20 cm in decay classes 5–8 were rare in all stands (mean = 0.85 logs/0.1 ha) (Fig. 4).

Age estimates of decayed logs vary considerably between study sites in Scandinavia. Logs of intermediate decay classes (4 and 5) averaged 15 years on clearcuts in southern Norway (Næsset, 1999), and 50 years (Hofgaard, 1993b) and 30 years (Jonsson, 2000) in the northern parts of Sweden. Logs decomposed completely in 70 years in the middle part of Sweden (Hytteborn and Packham, 1987), but logs were still visible after 150 years at higher latitudes (Dynesius and Jonsson, 1991; Hofgaard, 1993a). Our age estimate for decay classes 4 and 5 averaged 20 years. Age estimates of decayed stumps are sparse, but our data confirms well with estimates from selectively logged spruce forest in central Norway (Storaunet et al., 2000).

One reason for the different decay rates of logs and stumps in our study is that logs originated during the last 40–50 years, after the selective loggings ceased, and that most stumps originated prior to 1950. This presumably contributed to an overestimation of stump age and an underestimation of log age. This is also proposed as a reason for the low ages of logs found by Næsset (1999). Another explanation for the low age of logs compared to stumps may be differences in the initial condition of the wood when the tree died or was logged. As many as 85% of the logs was broken above root collar level, indicating butt rot before fall. Hence, logs were already decayed when they fell whereas most stumps presumably were fresh. Consequently, the decay rates should be treated with caution as general estimates, but we considered the data sufficient and representative to be used in the stand reconstructions.

3.2. Dating of logging events

The number of logging events identified from growth releases ranged from 2 to 4 during 1890–1965

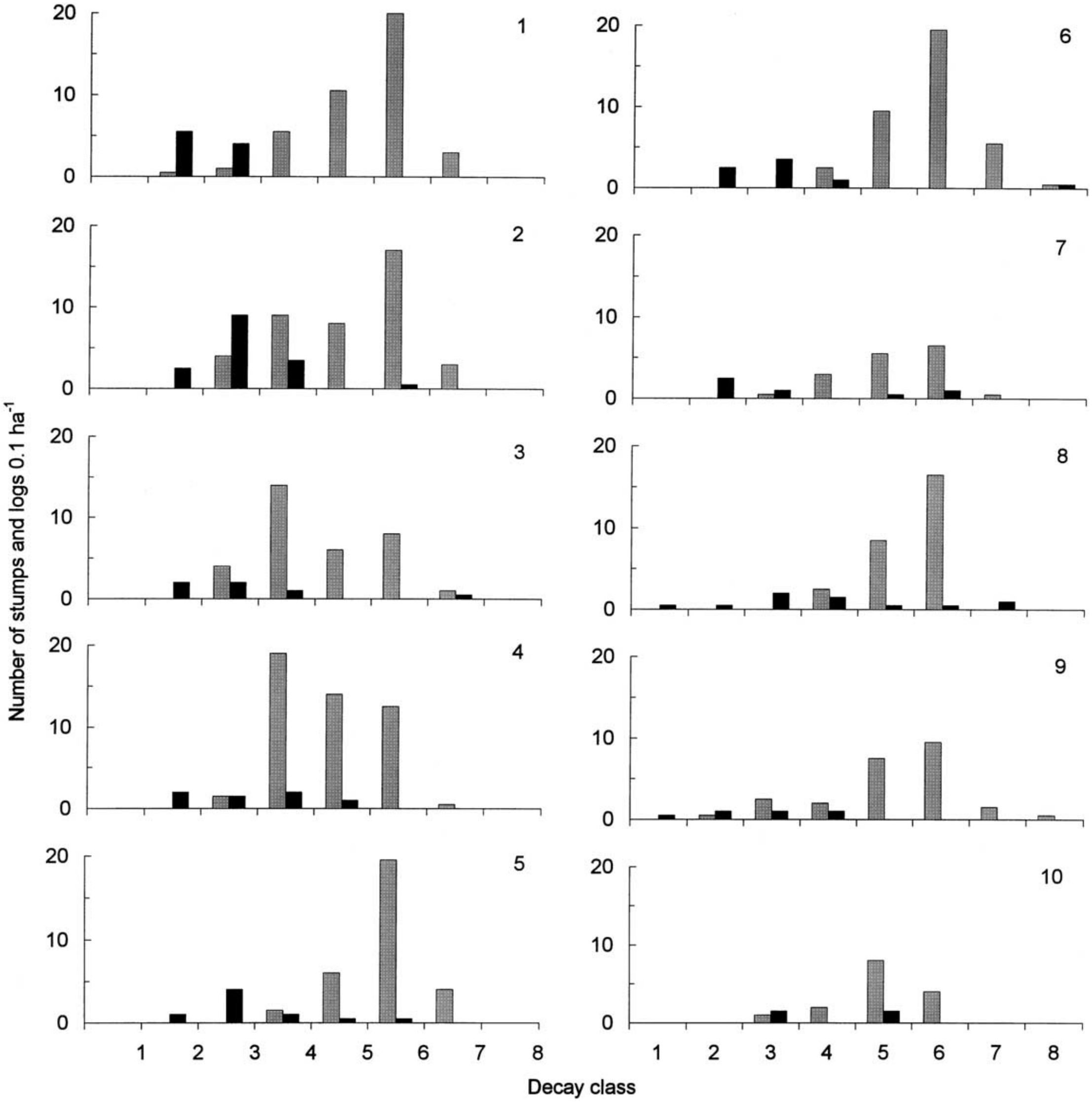


Fig. 4. Decay class distribution of logs ≥20 cm (black bars) and stumps ≥10 cm (shaded bars)/0.1 ha in the 10 sample plots. Decay class 1 is recently cut/fallen and decay class 8 is almost completely decayed. See Table 1 for description of decay classes. Numbers in upper right corner refer to study sites.

(Fig. 5b), and the mean logging interval for all 10 stands was 25 years. The decay class distribution of stumps indicated that growth releases after 1965 were related to treefall after the selective logging ceased. Single dated stumps showed that a few trees were harvested between the identified logging events (Fig. 5b). Growth releases were also found throughout the whole period between 1900 and 1996. However, on an average 68% (range 38–89%) of all growth releases between 1900 and 1970 occurred within the 10-year periods following the defined logging events (Fig. 5b).

The proportion of trees responding with growth release has often been used both to date and to assess the intensity of disturbance events (Lorimer, 1980; Nowacki and Abrams, 1997). In the present study, we restricted the use of growth releases to distinguish and date logging events. As long as stumps and logs are visible, they provide direct evidence of past disturbances. Therefore, we considered dead wood to give better estimates of disturbance intensity over the last 100 years.

3.3. Age-class distribution

Age-class distributions and the tree-ring widths provide information about the forest stand dynamics during the 1800s when other evidence like logs and stumps were lacking or the sample sizes were low. In forest stands 1, 2, 3, 7 and 9, peaks in the age-class distributions (Fig. 5a) and wide tree rings (data not shown) indicated natural disturbance or logging between 1850 and 1900. A large proportion of trees with suppressed growth suggested continuous tree cover in stands 4–6 prior to 1900. However, whereas dead wood (stumps and logs) and growth releases generally provided conclusive evidence of the disturbance history in the 20th century, the age-class

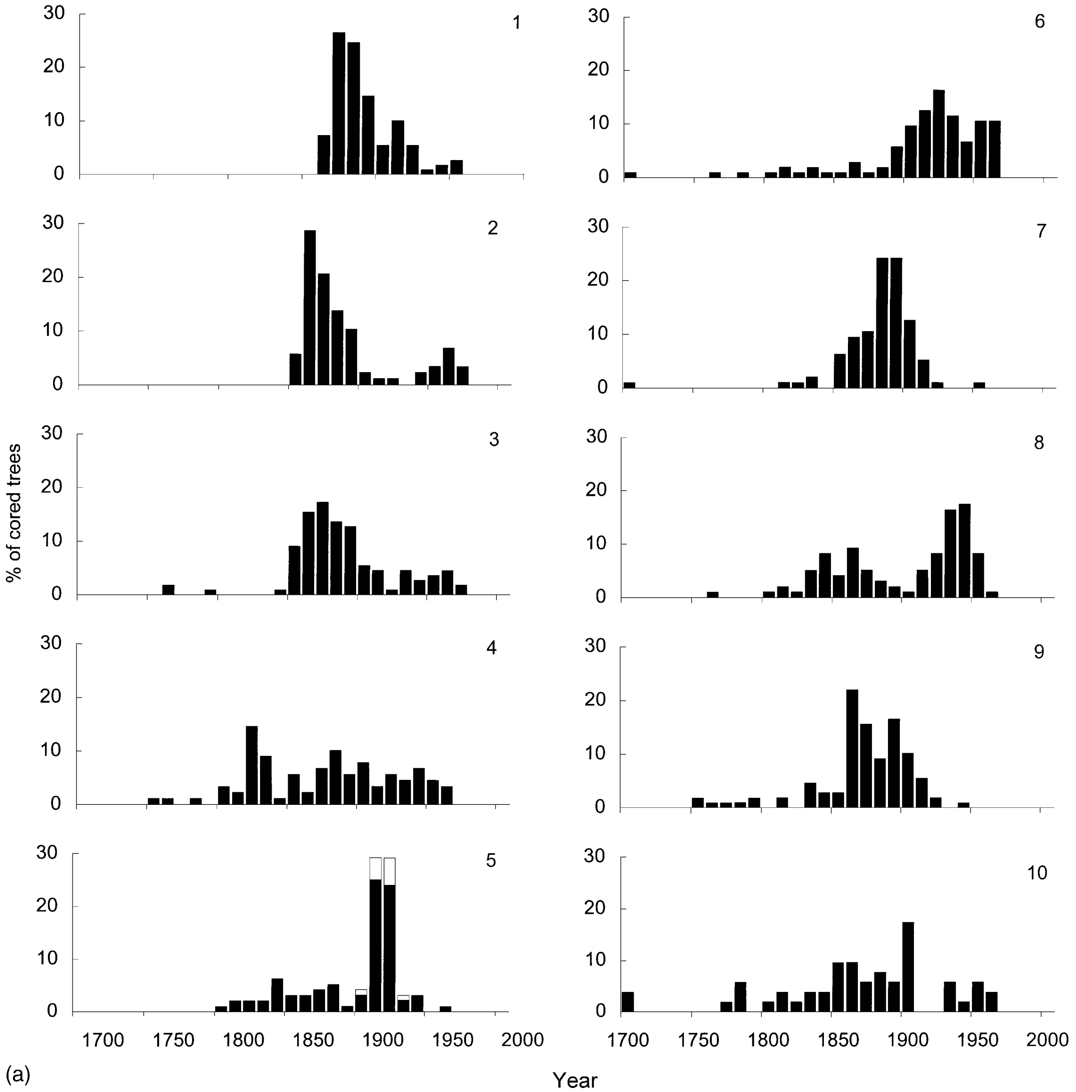


Fig. 5. (a) Age structure of Norway spruce (*P. abies*) (filled bars) and birch (*Betula* spp.) (open bars) in 10-year intervals for trees ≥10 cm (DBH) in the 10 sample plots. Age determination was done at 1.3 m above ground level. Numbers in upper right corner refer to study sites.

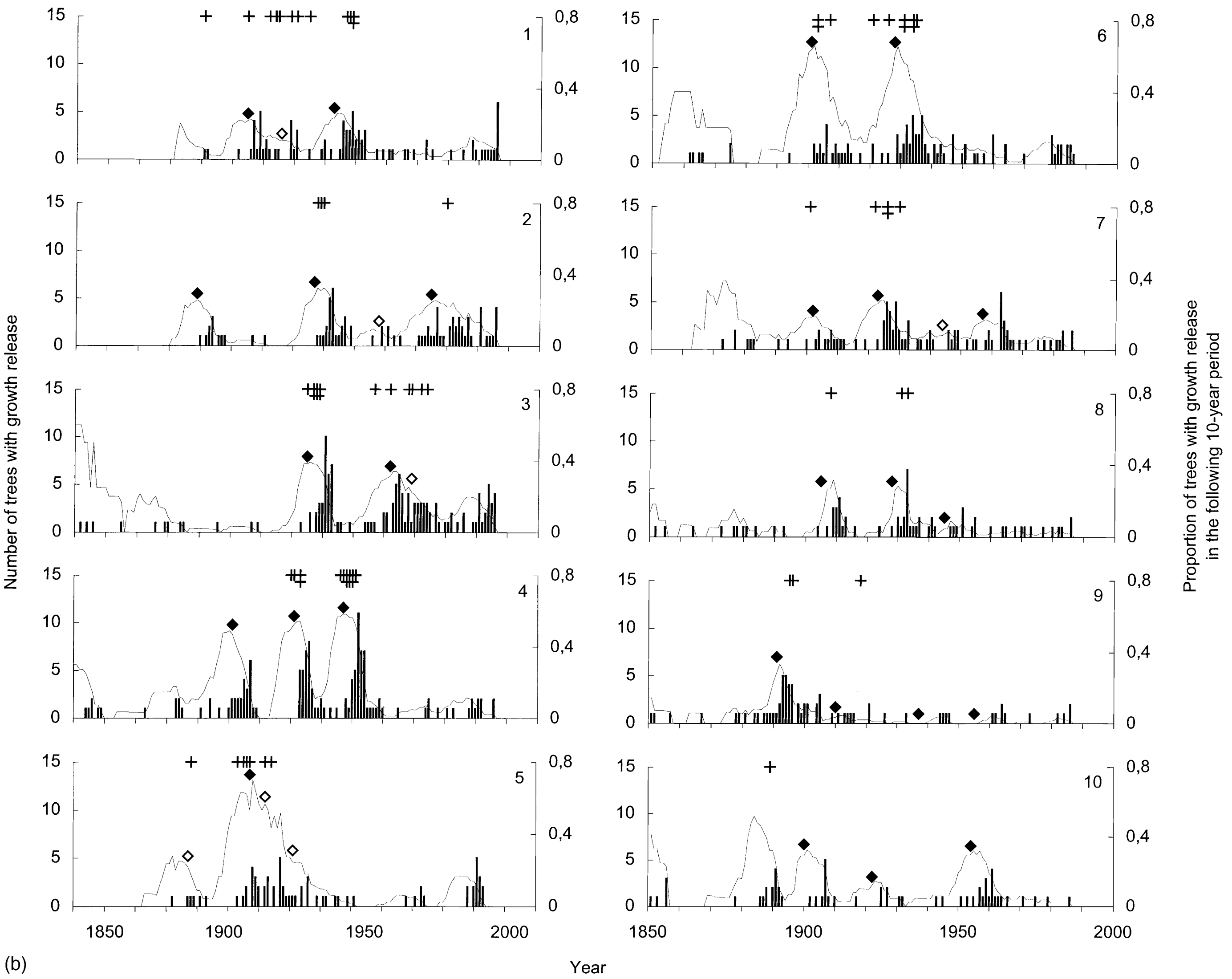


Fig. 5. (b) Number of growth releases per year (bars), and the percentage of living/cored trees with growth release in the following 10-year period (line). Logging events in each stand (filled diamonds) were defined when ≥15% of the cored trees showed growth release. Open diamonds denote logging events when a less restrictive criterion for defining a logging event were used (see text for further details). Crosses denote dated stumps in the sample plot. Numbers in upper right corner refer to study sites.

distributions were rather ambiguous for many stands in this period. Therefore, age-class distributions alone do not provide sufficient evidence to reconstruct reliable records of disturbance events. An unevenaged structure per se does not exclude the possibility that stands may have developed after large-scale disturbances, especially regarding shade-tolerant species (Lorimer, 1985). Evidence from age-class distributions therefore should be used with caution, but it is useful as a supplement to other lines of evidence when reconstructing past stand structures.

3.4. Reconstruction of stand characteristics

Total harvested volume derived from stumps varied from 7 to 26 m^3/0.1 ha, constituting 25–99% of present day standing volume (Fig. 6, Table 2). Single event harvested volume ranged from 1 to 10 m^3/0.1 ha. Present volumes were 2.6–21 (median 4) times higher than the lowest reconstructed volume between 1900 and 1996 (Fig. 6b). The diameter distributions also varied considerably during the 20th century. In particular the number of trees >30 cm DBH increased during the second half of the 20th century (Fig. 6a). The decay class distributions of logs together with the datings strongly suggest that most stands were devoid of coarse woody debris during the first half of the 20th century (Figs. 3 and 4). Two stands were devoid of logs in decay stages 5–8 and none had >2 old logs/0.1 ha.

It was difficult to discern logging events prior to 1900 because of few growth releases. In addition, stumps and logs from this period were decomposed. However, a comparison of present diameter distributions and standing volumes with the ones 100 years ago strongly suggests that the stands had been subject to intensive disturbance or logging prior to 1900. This is supported by historical records showing that the total harvested volume on the forest holding was at a fairly high level throughout the later part of the 19th century (Lange, 1966).

3.5. Sensitivity analysis

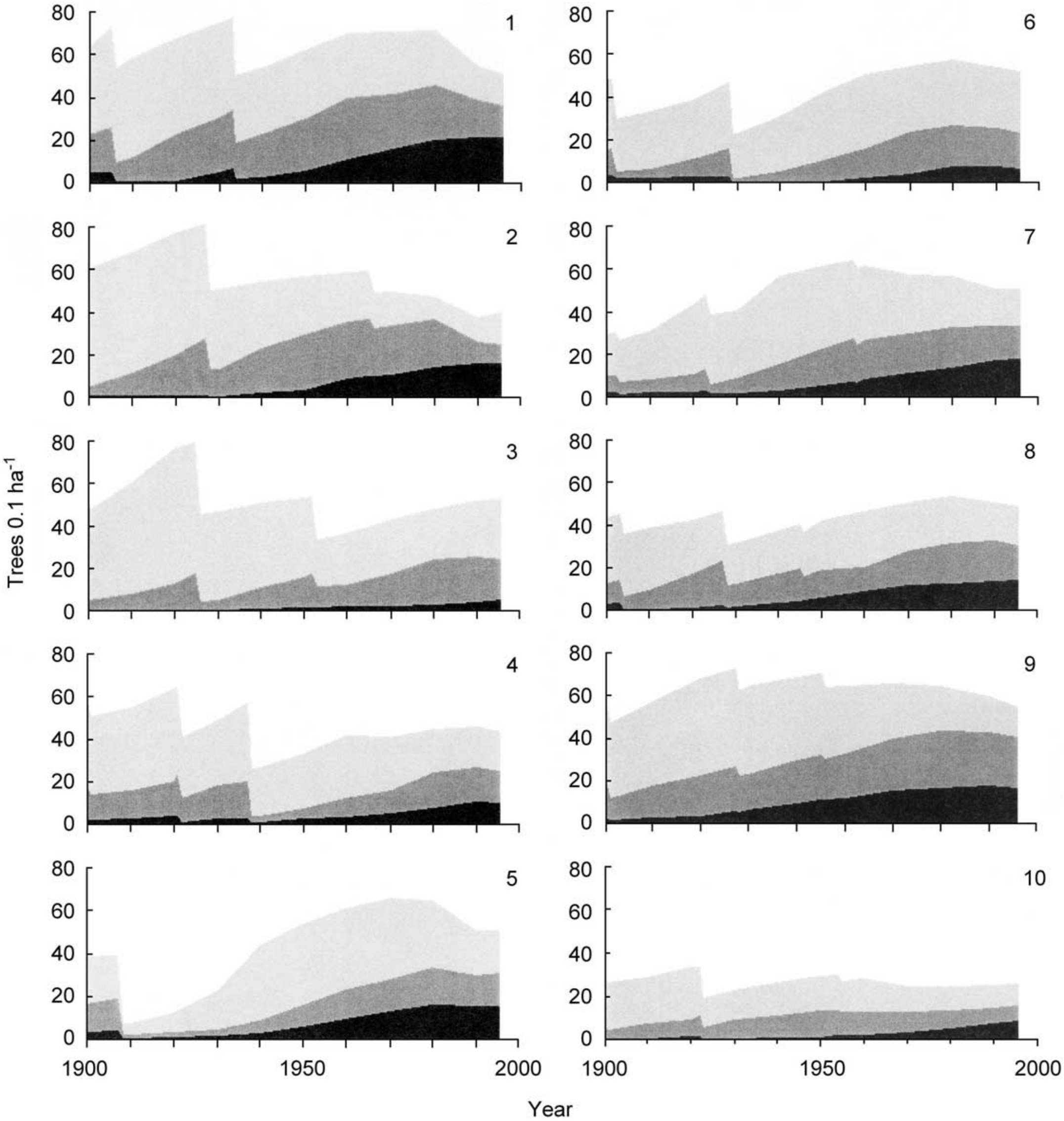
The default criterion for distinguishing a logging event (equal to 15% of the trees with a growth release) was chosen to be a stringent criterion to distinguish major logging events. In most cases the percentage of trees with growth release the following 10-year period was considerably higher than the minimum level of 15% that defined a logging event. On an average, 40% of the remaining trees responded with growth release after logging events (Fig. 5b). When we applied a less restrictive criteria for defining a logging event (5% of trees showing growth release over a 5-year period) the number of logging events increased by one or two at five of the sites. Adding more logging events had minor effect on the reconstructed stand volumes (Fig. 6b). Also, reconstructions done with alternative age estimates of logs and stumps had small effects on the historic volumes, even though the time period of low volumes altered (Fig. 6b).

3.6. Wood-decay fungi

Six fungus species were found out of seven species searched for. All fungi occurred on young logs in decay classes 2–4 with diameter $\geq$20 cm (Tables 3 and 4), and number of fungus records increased linearly with increasing number of available logs ($r^2 = 0.91$, $p < 0.001$, $n = 10$) (Fig. 7a). We tested if the presence of old logs increased the probability of finding fungi on young logs by regressing the residual variation against number of logs in decay classes 5–8 (Fig. 7b). This appeared not to be the case; the correlation coefficient was low and statistically non-significant ($r^2 = 0.15$, $p = 0.26$). Due to low statistical power (75% chance of detecting a correlation coefficient of 0.71 using a significance level of 0.10), we cannot exclude the possibility that old logs had a minor effect on the presence of fungi. We also checked whether number of stumps and historic harvested volume might have influenced the probability of fungi occurrence on young logs (i.e. explained the residual variation after accounting for available logs). In both cases correlation coefficients were low and non-significant ($r = -0.28$, $p = 0.44$, and $r = -0.14$, $p = 0.71$).

Fungi abundance tracked the amount of available young logs. When the effect of available logs was accounted for, presence of old logs, number of stumps, and historic harvested volume failed to explain the residual variation of fungi abundance. All stands had either been devoid of coarse woody debris or the amount of dead wood had been very low from late 1800 up to about 1960. This was shown by the small amounts of logs in decay classes 5–8, originating 40–100 years ago. In addition, peaks in the age-class distributions of several stands between 1850 and 1900 indicated that the stands were in young rejuvenation stages during this period. The stand reconstructions also gave evidence of low standing volumes and few big trees around 1900. Extensive selective logging during 100 years prior to 1960 probably rendered the stands very low or devoid of coarse woody debris.

With certain reservations that the small sample size may have masked minor relationships, we conclude that a continuous supply of dead wood was not crucial for the occurrence of the surveyed wood-decay fungi. Thus, the hypothesis that these fungi



(a)

Fig. 6. (a) Reconstructed number of trees per 0.1 ha for Norway spruce (*P. abies*) in the 10 sample plots between 1900 and 1996 (white: 10–19 cm DBH, gray: 20–29 cm, black: ≥30 cm). Numbers in upper right corner refer to study sites.

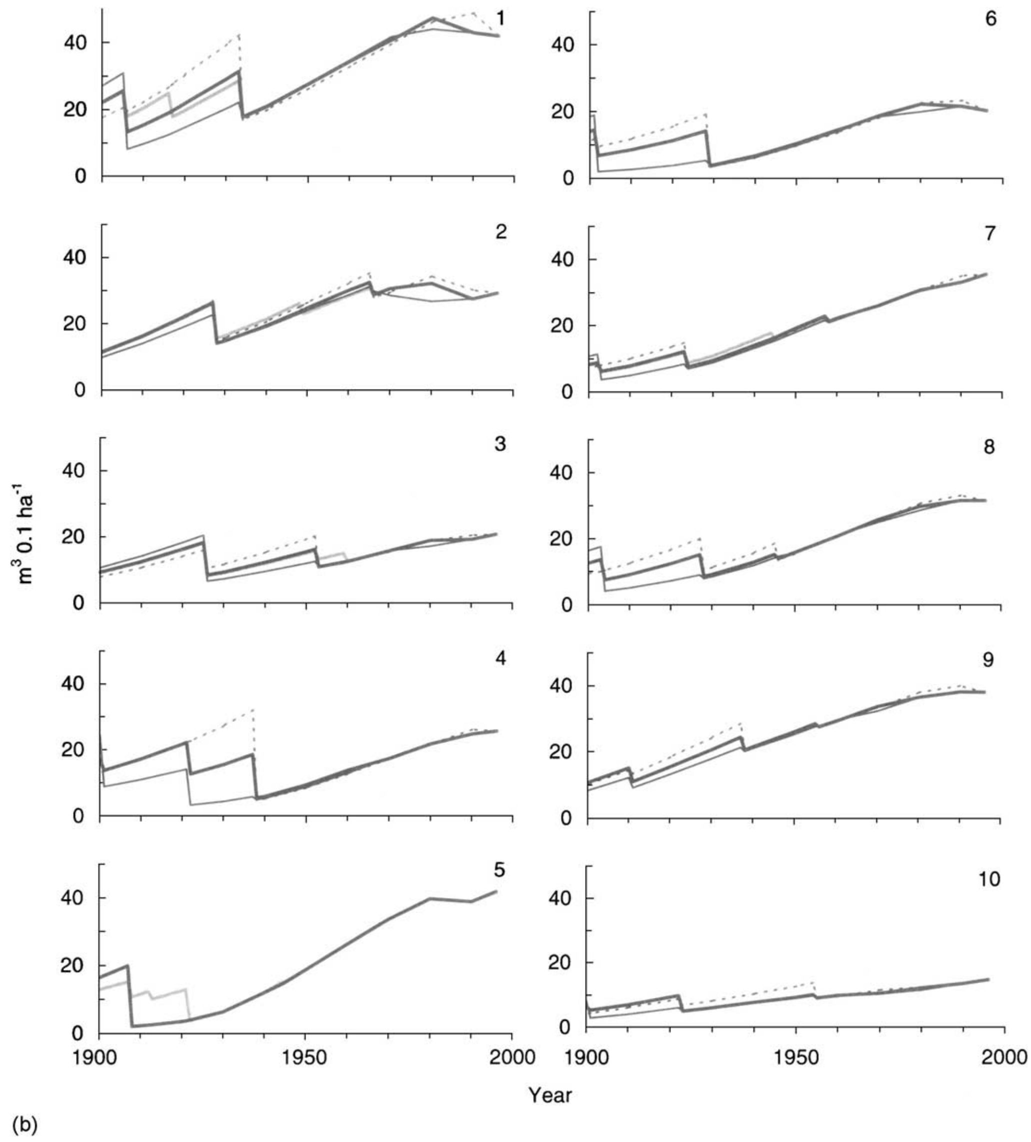


Fig. 6. (b) Reconstructed standing volume for Norway spruce between 1900 and 1996 (m^3/0.1 ha). Thick black line: default reconstruction. Thick gray line: reconstruction with additional logging events. Thin lines: reconstructions when all stumps and logs in each decay class were assigned to logging events at the limits of their age distributions. Numbers in upper right corner refer to study sites (see text for further details).

are continuity-dependent species (Karström, 1992; Bredesen et al., 1997; Lindblad, 1998) is not supported by our results. Apparently, the fungi had either colonized the logs from surrounding stands, or they may have been present at the sites on other substrates than downed logs. One of the surveyed species (*P. ferrugineofuscus*) has been found as wood-decaying fungi in living standing trees with butt rot (Norokorpi, 1979).

3.7. General discussion

Most retrospective dendroecological studies have focused on describing natural disturbance regimes as a

Table 2
Characteristics of the sample plots

Site	Standing volume (1996) m^3/0.1 ha	No. of trees ≥10 cm DBH/0.1 ha	Harvested volume (1900–1996) m^3/0.1 ha	No. of stumps ≥10 cm/0.1 ha	No. of logs ≥20 cm DBH/0.1 ha		Site productivity m^3/ha/year
					Decay classes 1–4	Decay classes 5–8	
1	42	55	26	48	9.5	0.0	7.5
2	29	44	19	52	15.0	0.5	4.8
3	21	56	15	60	5.0	0.5	3.5
4	26	45	26	67	5.5	1.0	5.5
5	42	51	18	35	6.0	1.0	7.5
6	20	53	18	43	7.5	0.5	4.8
7	35	51	9	18	3.5	1.5	9.0
8	32	51	14	31	4.5	2.0	7.5
9	38	56	10	30	3.5	0.0	4.8
10	15	26	7	22	1.5	1.5	2.0

Table 3
Number of logs with species present and total fungus records in the sample plots (0.2 ha)

Site	*P. centrifuga*	*P. ferrugineofuscus*	*P. nigrolimitatus*	*A. lapponica*	*F. rosea*	*L. mollis*	Total fungus records[a]
1	7	2	0	0	0	0	9
2	2	9	0	2	0	0	13
3	2	2	0	0	0	0	4
4	2	1	1	0	0	0	4
5	2	2	0	0	0	0	4
6	2	1	0	0	0	1	3
7	2	1	0	0	1	0	4
8	2	1	1	1	0	0	5
9	1	0	1	0	0	0	2
10	1	0	0	0	0	0	1

[a] Number of species present on each log, summed over all logs.

Table 4
Number of logs by diameter class and decay class with recorded wood-decay fungus species

Species	Diameter class (cm)				Decay class (DBH ≥ 20 cm)				
	10–19	20–29	30–39	≥40	1	2	3	4	5–8
P. centrifuga	0	5	14	4	0	7	15	1	0
P. ferrugineofuscus	0	9	8	2	0	4	15	0	0
P. nigrolimitatus	0	1	2	0	0	0	2	1	0
A. lapponica	0	2	1	0	0	1	2	0	0
F. rosea	0	1	0	0	0	0	1	0	0
L. mollis	0	1	0	0	0	1	0	0	0
No. of available logs	99	92	41	7	3	39	59	22	17

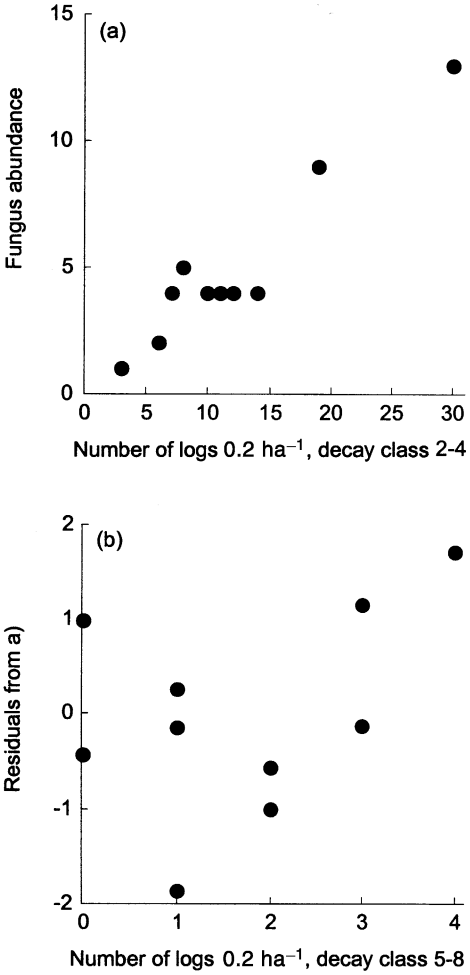


Fig. 7. (a) The relationship between number of logs ≥20 cm/0.2 ha in decay classes 2–4 and fungus abundance ($r^2 = 0.91, p < 0.001$). (b) The relationship between the number of old logs ≥20 cm/0.2 ha (decay classes 5–8) and the residuals from the regression in (a) ($r^2 = 0.15, p = 0.26$).

basic source of information for managing forest ecosystems (Henry and Swan, 1974; Oliver and Stephens, 1977; Lorimer and Frelich, 1989; Payette et al., 1990; Johnson et al., 1994; Östlund and Linderson, 1995; Fulé et al., 1997; Nowacki and Abrams, 1997). Such information can be used to assess anthropogenic change and help managers set goals and contribute to a better understanding of ecological systems (Foster et al., 1996; Landres et al., 1999). In the present study we combined several dendroecological methods and approaches to reconstruct the recent history of selectively logged stands. Our purpose was to provide a tool kit for studying the relationships between forest stand history and species occurrences in forests where historical records are lacking, and where the possibility for crossdating decayed wood is limited to recently fallen or logged trees.

Coarse woody debris is considered to be a limiting factor for several forest species in Scandinavia today, and wood-inhabiting species constitute a large proportion of the red-listed forest species (Berg et al., 1994, 1995; Anon., 1999). Most studies of coarse woody debris and species composition in Scandinavia are based on decay classification of the logs, and several different decay class systems have been applied (Söderström, 1988; Hofgaard, 1993a; Prestø, 1994; Renvall, 1995; Bredesen et al., 1997). Applying a time scale to decay stages of dead wood will provide useful guidance for old-growth restoration. Our datings of logs, along with other studies (Hytteborn and Packham, 1987; Dynesius and Jonsson, 1991; Hofgaard, 1993a; Næsset, 1999; Jonsson, 2000), indicate that the most species-rich intermediate decay stages develop within 20–50 years, depending on microclimate and latitude. The stand history of semi-natural, selectively logged stands with late-successional species can provide valuable information on the effects of proposed silvicultural models to restore old-growth features in managed forest (e.g. Fries et al., 1997).

Recent Scandinavian studies on wood-decay fungi claim that dead wood should be continuously present to ensure viable populations (Bredesen et al., 1997; Lindblad, 1998; Røsok, 1998). However, neither have they tested this hypothesis explicitly by accounting for the effect of substrate quantity and quality per se, nor have they specified the time scale involved. In our study we found six out of seven fungi, assumed to depend on long-term continuity of dead wood. Nevertheless, we found substantial evidence that suitable decay stages of dead wood only had been available during the later part of the 20th century. We therefore agree with Bader et al. (1995) that on a local scale, e.g. within forest stands <1 ha, the occurrence and abundance of wood-decaying fungi mainly seem to be determined by the abundance and quality of dead wood. We propose that the approach presented in this study is used to increase our understanding of the connection between species occurrence and stand history, and that a modified version of the method can be extended to larger spatial scales. The method also provides a tool to evaluate proposed restoration measures by reconstructing past management regimes and stand structures, and evaluate its impact on present habitat characteristics.

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