Silviculture for old-growth attributes

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ABSTRACT

Silviculture to maintain old-growth forest attributes appears to be an oxymoron since the late developmental phases of forest dynamics, described by the term old-growth, represent forests that have not experienced human intervention or timber removal for a long time. In the past, silvicultural systems applied to old-growth aimed to convert it into simplified, more productive regrowth forests substantially different in structure and composition. Now it is recognised that the maintenance of biodiversity associated with structural and functional complexity of late forest development successional stages cannot rely solely on old-growth forests in reserves. Therefore, in managed forests, silvicultural systems able to develop or maintain old-growth forest attributes are being sought. The degree to which old-growth attributes are maintained or developed is called “old-growthness”. In this paper, we discuss silvicultural approaches that promote or maintain structural attributes of old-growth forests at the forest stand level in (a) current old-growth forests managed for timber production to retain structural elements, (b) current old-growth forests requiring regular, minor disturbances to maintain their structure, and (c) regrowth and secondary forests to restore old-growth structural attributes. While the functions of different elements of forest structure, such as coarse woody debris, large veteran trees, etc., have been described in principle, our knowledge about the quantity and distribution, in time and space, of these elements required to meet certain management objectives is rather limited for most ecosystems. The risks and operational constraints associated with managing for structural attributes create further complexity, which cannot be addressed adequately through the use of traditional silvicultural approaches. Silvicultural systems used in the retention and restoration of old-growthness can, and need, to employ a variety of approaches for managing spatial and temporal structural complexity. We present examples of silvicultural options that have been applied in creative experiments and forestry practice over the last two decades. However, these largely comprise only short-term responses, which are often accompanied by increased risks and disturbance. Much research and monitoring is required still to develop and optimise new silvicultural systems for old-growthness for a wide variety of forest ecosystem types.

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1. Introduction

The global disappearance of primary, natural or unmanaged forests is of major concern (FAO, 2007). Many of these forests are old-growth forests, which provide numerous benefits and habitats unavailable in managed forests (e.g. Lindenmayer and McCarthy, 2002). The forests of Sweden and Finland provide examples of the effect of old-growth disappearance on various aspects of biodiversity. Many of these forests have been managed very intensively over the last 100 years. A comparison of abundance of various insects, birds, mammals, fungi, plants and lichen between intensively managed Swedish and Finnish forests and adjacent natural Russian forests revealed alarmingly a much lower number of species in the managed forests. These differences were attributed partially to the homogenized structure and reduced amounts of snags and woody debris in the even-aged monocultures (Berg et al., 1994; Angelstam, 1996). These, and other studies, suggest that the maintenance of key attributes of natural forests, as found in old-growth forests, is necessary to conserve a wide range of species.

Old-growth forests are a subset of primary forests that develop only under a limited set of circumstances, mostly associated with long periods without major natural disturbances. There are a number of approaches for defining old-growth forests (Wirth et al., 2009). One common approach, adopted in this paper, uses attributes of forest structure and composition, including a wide...
range of tree sizes and the presence of some old trees approaching their maximum longevity (Mosseler et al., 2003) (see also Table 1).

Approaches for maintaining old-growth attributes at stand and landscape scales include setting aside forests for preservation, in which no management takes place. Although highly desirable, in some regions ownership patterns or a high demand for wood products and other forest uses limits the application of this approach (Sarr and Puettmann, 2008). Furthermore, set-aside forests may be prone to natural disturbances (Spies et al., 2006). Areas outside reserves are also important, facilitating gene flow and migration of populations as well as providing complementary habitat (Lindenmayer and Franklin, 2002). It is therefore important to complement set-aside forests with managed forests that also reproduce key attributes of primary and old-growth forests, while, at the same time, addressing other social and economical management goals. This is particularly important in areas where reserves are too small to ensure the occurrence of natural disturbances within their boundaries or to accommodate all developmental stages of forest succession (Kneeshaw and Gauthier, 2003).

Although the primary old-growth forest area is still shrinking in many parts of the world, there are other areas, such as northeastern U.S., Japan and parts of central Europe, where the existing forests are ageing rapidly (Fig. 1) and thus offer new opportunities to increase the area of forest that can fulfill many of the functions and processes typically associated with old-growth (Davis, 1996).

Differences in ecological attributes between old-growth and forests managed for commodity products have been documented in a variety of settings (e.g. Perry and Amaranthus, 1957; Lindenmayer and McCarthy, 2002; Angers et al., 2005; Kenefic and Nyland, 2007). These differences need to be viewed in the context of temporal stand dynamics. Silvicultural practices focussed on wood production commonly result in production cycles of 25–150 years, whereas successional cycles of forests in some regions may continue over several hundred or a thousand years between stand-replacing disturbances (Scherzinger, 1996; Seymour and Hunter, 1999). As a result, managed forests often only cover 10–40% of the potential stand development period, and, consequently, many structural attributes of old forests (see Table 1) are absent or not fully developed in managed forests. In addition, forest harvesting and most other conventional silvicultural interventions do not aim to produce stand character-istics typically found in old-growth (e.g. Moore and Allen, 1999), but rather favour limited structures and tree species based on their economic value, rate of growth and management efficiency.

It is now reasonably well understood that old-growth forests play an important role in harbouring of biodiversity (e.g. Lindenmayer and Franklin, 2002), in terrestrial carbon storage and sometimes sequestration (e.g. Carey et al., 2001) as well as in catchment hydrology (e.g. Vertessy et al., 1996) (see also Wirth et al., 2009). Concerns about their global disappearance have led to major efforts globally to increase the area of old-growth forests in reserves (e.g. USDA/USDI, 1994; DAFF, 2007). To establish such reserves, a definition of old-growth is needed that facilitates mapping and delineation of old-growth in the landscape. Yet the forests fitting one definition can vary widely in their ecological state, disturbance history and physical environments (e.g. Franklin and Spies, 1991). For this reason, the same authors introduced the term “old-growthness” to describe the degree to which forest stands express the various structural and functional attributes associated with old forests, and suggested that structural variability must be considered in our efforts to manage for old-growth (see also Fig. 2). Regrowth or secondary forests, relatively young forests that have regenerated after major disturbances, such as extensive cutting or wildfire (Helms, 1998), also can be highly variable with the same structural features found in old-growth to different degrees (Table 1). Evidence suggests that the occurrence of many, but not all, species typically found in old-growth is linked to specific structural attributes and not to old-growth as such (e.g. Siitonen and Martikainen, 1994; Gibbons and Lindenmayer, 1996; Lonsdale et al., 2008). Thus the strict separation of forested landscapes into old-growth and regrowth forests (Fig. 2) may not represent an optimal species conservation strategy with regard to the provision of habitats in the landscape. Instead, it may be better to manage forests for conservation based on their degree of old-growthness, their local and landscape functions in recognition of the expected opportunities for, and constraints to obtaining desirable levels of old-growthness. However, practically, it could be extremely difficult and costly to evaluate and assign a specific

Table 1

<table>
<thead>
<tr>
<th>Structural attributes commonly associated with different old-growth forests</th>
<th>Examples from different forest types: Angers et al., 2005; Ansley and Battles, 1998; Dyne, 1991; Franklin et al., 2002; Franklin and Van Pelt, 2004; Holt et al., 1999; Kneeshaw and Gauthier, 2003; Meyer et al., 2003; Mosseler et al., 2003; Nilsson et al., 2002; Pollman, 2003; Salas et al., 2006; Siitonen et al., 2000; Tanouchi and Yamamoto, 1995; Tzvetkoy et al., 2003; Tyrell and Crow, 1994.</th>
</tr>
</thead>
<tbody>
<tr>
<td>High number/basal area of large trees</td>
<td>High number/basal area of dead/dying standing trees</td>
</tr>
<tr>
<td>High stand volume or biomass</td>
<td>Large amount/mass of downed CWD</td>
</tr>
<tr>
<td>Large number/basal area of dead/dying standing trees</td>
<td>Wide decay class distribution of logs and/or snags</td>
</tr>
<tr>
<td>High amount/mass of downed CWD</td>
<td>Several canopy layers/vertical variability</td>
</tr>
<tr>
<td>Wide decay class distribution of logs and/or snags</td>
<td>High variation in tree sizes, presence of several cohorts</td>
</tr>
<tr>
<td>Several canopy layers/vertical variability</td>
<td>High spatial heterogeneity of tree distribution/irregular size and distribution of gaps</td>
</tr>
<tr>
<td>High variation in tree sizes, presence of several cohorts</td>
<td>Thick forest floor</td>
</tr>
<tr>
<td>High spatial heterogeneity of tree distribution/irregular size and distribution of gaps</td>
<td>Special attributes (pit and mound relief, presence of epiphytes, presence of cavity-trees, tree hollows)</td>
</tr>
<tr>
<td>Thick forest floor</td>
<td>High variation in branch systems and crown structure/development of secondary crowns</td>
</tr>
<tr>
<td>Special attributes (pit and mound relief, presence of epiphytes, presence of cavity-trees, tree hollows)</td>
<td>Presence of advance regeneration</td>
</tr>
</tbody>
</table>

Fig. 1. The ageing of forests in Germany over the inventory period 1987–2002. Changes are depicted in percent and in absolute area (ha x 1000). Data only for former West-Germany (Source: National Forest Inventory).
degree of old-growthness to each stand. Instead, a third category, partial old-growth or regrowth forests with some level of old-growthness, may be identified between true old-growth and intensively managed regrowth forests, a manageable approach to improve conservation planning (Fig. 2). The degree to which old-growth forests and old-growth structures should be maintained or restored at the landscape level is a complex, political question that requires an assessment of the trade-offs between different landscape values (i.e. Carey, 2003). This issue is outside the scope of this review, which focuses on management at the stand level. For the purpose of this review we have adopted a structure-based approach, and define old-growthness as a general aggregate measure of structural attributes listed in Table 1 for two reasons. Firstly, silvicultural practices modify stand structures and their dynamics directly, and secondly, information about links between stand structures, habitat provision and ecosystem functions is available (e.g. McElhinny et al., 2006).

This review emphasizes conditions for temperate and boreal forests because most studies investigating old-growth forests and their management have been conducted in these two biomes. Despite the large areas of old-growth forests found in the tropics, and their rapid disappearance rates, we have relatively little explicit information about them. Thus, while concepts discussed in this review also apply to tropical forests, specific examples are not provided.

2. Silvicultural approaches to maintain old-growthness

Three complementary approaches to the conservation and maintenance of old-growth forests and old-growthness have been termed reservation, retention, and restoration (Beese et al., 2003; Franklin et al., 1997; Keeton, 2006; Seymour and Hunter, 1999). The reservation of large patches of old-growth forests is an important element of an effective multi-scaled approach to the conservation of biodiversity at the landscape scale (Lindenmayer and Franklin, 2002). In this paper, however, we focus on the retention and restoration of structural attributes at the spatial scale of forest stands. Both are elements of a “coarse filter approach” to conservation, which aims to maintain biodiversity by providing a diversity of structures in stands as well as a diversity of ecosystems and their successional stages across the landscape (Noss, 1987; Hunter, 1991).

Silviculture is the manipulation of forest structures and dynamics to achieve management goals. Consequently, if reservation goals are met through passive management, as is often the case in existing old-growth forests, there is no need to implement silvicultural practices. However, in other settings, silvicultural practices may be beneficial or even necessary to promote old-growthness. These settings can be grouped into three categories: (A) Current old-growth forests, resulting from the long-term absence of large-scale disturbances, and which are under consideration for management for timber production. (B) Current old-growth forests, which are at risk of losing important elements of their structure or of being subject to intensive disturbances that they have not experienced historically. If, for whatever reasons, natural disturbances are unable to reduce this risk, active management may be required to maintain desirable attributes. We term this “cultural old-growth”. (C) Regrowth and secondary forests, which have been managed for other objectives, usually timber production, and are now targeted for the re-development of old-growth attributes.

In these three situations, silvicultural strategies aim at maintaining or increasing old-growth structural attributes in forest stands and hence also in the forested landscape (Fig. 3). Depending on existing forest conditions and economic, social, and political considerations, a combination of these strategies may be most suitable (Sarr and Puettmann, 2008).

3. Silviculture in old-growth forests available for timber production

When existing old-growth forests are to be managed for timber production, they will obviously lose their old-growth status according to most, if not all, definitions. However, to maintain a desirable degree of old-growthness in this situation, two options
exist. In the first option, entire stands are managed using long production cycles, which extend well beyond the ages considered optimal for tree growth. Alternatively, selected trees, or other structural elements are retained in old-growth stands during silvicultural operations, while the rest is managed on shorter production cycles. This scenario is represented by the variable retention approach described by Franklin et al. (1997). We use the term production cycle instead of rotation, since the latter applies strictly to even-aged forests, while the former may be applied to individual trees and thus selection forests.

3.1. Maintenance of old-growth attributes through long production cycles

There are few incentives for managing forests on production cycles that are sufficiently long to include old-growth stages of stand development. For many tree species, the age at which the mean annual increment (MAI) culminates and subsequently declines is quite early relative to the potential maximum age. If landowners are more interested in maximizing the internal rate of return rather than stand growth, production cycles are short. Growing trees or stands to older ages may become economically attractive for species whose mean value increments culminate at an advanced aged. This happens when the decline in productivity after MAI culmination is slow and the market pays a significant size premium, and when the value of timber (on a volume basis) increases with increasing log dimension as often found for high quality hardwoods. On the other hand, recent advances in sawmill and lamination technology have more or less eliminated the size premium for standard quality conifer timber, providing little incentive to produce larger softwoods over longer production cycles. In some settings, landowners may even obtain a lower price for larger logs (e.g. Eschmann et al., 2003). The higher risk of disturbance in long production cycles introduces another concern. For example, as trees age and become taller they become more susceptible to windthrow (Peltola, 2006), more easily water-stressed due to the longer water transport distances between fine-roots and the crown (Ryan and Yoder, 1997), and hence are more susceptible to secondary pathogens such as bark beetles that affect stressed or weakened trees (e.g. Kelsey and Joseph, 2001). Given the uncertainties of future climatic conditions, risk-adverse forest managers will likely shorten production cycles (Kellomäki et al., 2000). An additional factor favouring short rotations is the risk to wood quality, such as discoloration or fungal colonization of stemwood, which increases with age in many tree species (e.g. Knopke, 2003). Therefore extended production cycles are unlikely to be adopted in production forests in the absence of some type of financial compensation from government or private conservation organisations (e.g. Küpker et al., 2005).

However, extended production cycles can have some financial advantages and environmental benefits such as reduced costs for regeneration-related management activities, higher diversity of products or wildlife habitat, hydrological benefits, and increased carbon storage (Curtis, 1997). Also, potential damage from fires may decline with tree age; as tree crowns rise, inter-tree spacing usually increases, and the bark becomes thicker, providing better insulation against damaging temperatures (e.g. Wyant et al., 1986). In some forests, however, the opposite may be the case when fuel ladders develop with age (Spies et al., 2006).

Examples of species and settings that resulted in long production cycles in managed forests include oaks (Quercus) grown for veneer in central Europe, where production cycles may extend to 200–300+ years (Vanselow, 1960). Harvey et al. (2002) present a case for cohort-based stand management with the goal to ensure a proportion of late-successional stands in the southern-boreal forest landscape of Québec. Here, long rotations do not equate to long production cycles for one species, but to the successional pattern of cohort replacement from early to mid and late successional stands that differ in species composition. Through uneven-aged silviculture, the advanced regeneration of shade-tolerant species can be recruited for successively older stands. This cohort-based approach may be more widely applicable in forests undergoing stand-replacing disturbances and distinct successional species replacement.

It is important to realise that extended production cycles, by themselves, can make only a small contribution to increasing the degree of old-growthiness. Only attributes linked to large tree dimension and associated spatial patterning automatically benefit from implementation of long production cycles. The majority of attributes listed in Table 1 require additional management efforts, such as specific retention or restoration prescriptions.

3.2. Retention of old-growth structures

Many foresters recognise the benefits of regeneration methods modelled on natural disturbance dynamics to meet the establishment and early growth requirements of desired tree species. In forests subject to periodic stand-replacing disturbances, and where the target tree species have pioneer characteristics, clearfelling systems have been adopted (e.g. Hickey and Wilkinson, 1999; Bergeron et al., 2001). The application of clearfelling has been very successful in the regeneration of selected tree species. However, over time it has been recognised that forest structure and associated functions and processes differ in many ways between naturally disturbed and clearfelled forests (Lindenmayer and McCarthy, 2002; Pedlar et al., 2002). Even intensive natural disturbances leave behind dead or living structural elements, termed “legacies” (Franklin et al., 1985). The role of these legacies, or residual structures, for conservation of biological diversity and the recovery of ecosystem functioning following disturbance is well recognized (Jonsson et al., 2005; Vanha-Majamaa et al., 2007). Many studies have documented the relationships between the occurrence and abundance of such structural attributes and the occurrence, abundance and diversity of different taxonomic groups (Lindenmayer and Franklin, 2002). Differences in stand structures following natural or silvicultural disturbances have been documented for both stand-replacing disturbances and small scale, gap-phased disturbances (e.g. Coates and Burton, 1997; Spies and Franklin, 1989). For example, the implementation of uneven-aged selection systems has led to a substantial lack of old-growth attributes (Keddy, 1992; Coates, 1995; Coates and Burton, 1998). Furthermore, the size distribution and spatial arrangement of gaps is more uniform in selectively logged stands (Puettmann et al., 2008). However, simple changes in management practices may counteract these trends. For example, reducing the degree of tree utilisation can increase the abundance of CWD in selection or other silvicultural systems to levels higher than in unmanaged forests. While these inputs are often only temporary, in forests with CWD decomposi- tion times substantially exceeding the interval between harvests, such periodic inputs could sustain abundant downed wood continuously (e.g. Doyon et al., 2005; Goodburn and Lorimer, 1998).

The structural simplification of selection forests demonstrates that retention of structural attributes should be considered in treatment prescriptions for uneven-aged silvicultural systems where appropriate. However, in this context the term “retention” implies that an attribute that would be removed under conventional management is deliberately retained for conservation purposes. This is fitting for most structural attributes retained in a modified clearfelling system, such as variable retention harvested. The term is less appropriate for selection systems. In these
systems, standard operations leave much of the stand behind. In these settings the term retention should be limited to structural attributes, such as dead trees, habitat trees, or non-vigorous and low quality trees, which would be removed under conventional uneven-age management. Modified prescriptions to maintain undisturbed stand patches or an intact understorey may be more appropriately called “restricted selection”. In addition to retained structural attributes, the spatial and size distribution of gaps is important for emulating patterns created by natural disturbances (e.g. Coates and Burton, 1997).

The retention of structural elements at the time of harvesting is based on two assumptions: 1) retained structures help maintain a higher level of biodiversity and ecosystem functioning on site than that attained without them, at least in the short term; and 2) retained structures facilitate the rapid recovery of biodiversity and ecosystem functioning (also called “life-boat hypothesis”).

The structural elements that can be retained (Tables 1 and 2) range in spatial scale from individual trees to large patches of vegetation. The list of structural attributes characterising old-growth conditions is remarkably similar across many different forest types. However, owing to the lack of a common inventory protocol, these attributes have been quantified differently in each study, making it extremely difficult to aggregate the information.

The benefits of retaining selected structural attributes have been demonstrated in numerous studies, especially in the context of the first assumption. Recent reviews (e.g. Lindenmayer and Franklin, 2002; Rosenvald and Löhmus, 2008) concluded that these two assumptions are met in most situations. However, a detailed review of the large body of literature on effects of retention is beyond the scope of this paper. The following studies provide examples of the benefits of retention on birds and understorey (Merrill et al., 1998; Beese and Bryant, 1999), canopy lichens (Coxson and Stevenson, 2005), aerial insects (Deans et al., 2004), ground-layer bryophytes (Dovčiak et al., 2006), small terrestrial mammals (Gitzen et al., 2007) and saproxylic beetles (Jonsell and Weslien, 2003). Since the retention of structural attributes has not been practised for very long, short-term responses (assumption 1) are documented better than the long-term responses (assumption 2). In relation to the second assumption, short-term studies can only document the presence of propagules and sexually mature organisms in retained structures, and few studies have investigated the recolonisation of harvested areas originating from retained vegetation patches (e.g. Fisher and Bradbury, 2006; Tabor et al., 2007).

For management purposes, it is particularly important to learn how ecosystems respond to varying degrees of structural attributes retained and to different spatial arrangements of these attributes (Table 2). This scientific information is available only for few ecosystems and, even then, only to a limited extent (Lindenmayer and Franklin, 2002). The ecological effects and

Table 2
Silvicultural considerations regarding the retention of structural attributes.

<table>
<thead>
<tr>
<th>Structural attribute to be retained</th>
<th>Desired density</th>
<th>Preferred spatial arrangement</th>
<th>Stability and dynamics</th>
<th>Risks and undesirable effects</th>
<th>Other management considerations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live and habitat trees</td>
<td>Depends on habitat requirements of species that use trees and on spatial extent of desirable (e.g. seed dispersal) and undesirable (regrowth suppression) effects</td>
<td>Dispersed to meet ecosystem functions over entire area (seeds, water table, habitat)</td>
<td>Depends on windthrow risk (exposure, tree parameters, soil type)</td>
<td>Exposed and stressed trees may become breeding sites for secondary pathogens such as bark or jewel beetles</td>
<td>Retention of individual trees more hazardous than aggregates during harvesting and site preparation</td>
</tr>
<tr>
<td>Standing dead trees</td>
<td>Depends on habitat requirements of species that use them, but see risks</td>
<td>Dispersed to serve as habitat for saproxylic organisms</td>
<td>Low windthrow risk, high risk of burning. Durability depends on decay resistance</td>
<td>Safety concern near roads, tracks and other frequented places</td>
<td>CWD on the ground</td>
</tr>
<tr>
<td>CWD on the ground</td>
<td>Same as above</td>
<td>Dispersed distribution preferred for many organisms with very low mobility and small home ranges</td>
<td>Persistence depends on decay resistance of species and log dimensions. Recruitment from snags and live trees required to maintain pool</td>
<td>Fresh logs as breeding ground for pathogens (e.g. bark beetles)</td>
<td>Large CWD as obstacle for machine based operations. Placement should take extraction system into account</td>
</tr>
<tr>
<td>Patches with undisturbed vegetation incl. advance regeneration</td>
<td>Depends on size and functions. As source of propagules, dispersal distances should be considered. Edge effects into patches should be minimised</td>
<td>Dispersed retention not possible</td>
<td>Stability depends on size, edge effects, and exposure to wind and fire. Some disturbance within patches is not incompatible with retention goals</td>
<td>Same risks as for above attributes. Patches may harbour browsing animals that affect regeneration</td>
<td>Large patches are operationally easier than many small ones, in particular, where fire is required for site preparation</td>
</tr>
</tbody>
</table>

The desired attributes, their spatial arrangement, stability and associated risks will depend on forest type, disturbance regime and retention objectives. The desired density of structural attributes also always depends on the level of acceptable production losses.
tradeoffs of varying degrees of retained structures are being assessed in several experiments, for example, by the Ecosystem Management Emulating Natural Disturbances (EMEND) project in Alberta (Spence and Volney, 1999). Results from EMEND confirm that different minimum retention levels are needed for different organisms (Gandhi et al., 2004).

In the evaluation of spatial patterning of retention structures, the comparison of dispersed versus aggregated retention has received some attention (Franklin et al., 1997, 1999). A listing of advantages and disadvantages of these two approaches in relation to various retention goals shows that neither approach provides a consistently better achievement (Franklin et al., 1997). Consequently, these authors generally recommend a combination of dispersed and aggregated retention (“variable retention”).

Silvicultural prescriptions are specific solutions to a specific set of circumstances and management objectives (Smith, 1962). Thus, retention prescriptions that become part of a silvicultural system need to fit with this constraint. Important considerations for incorporating the retention of structural attributes into silvicultural systems include the desired density and distribution of retained structures, their stability/longevity and how the spatial arrangement may influence the risks associated with specific retention practices and the effects on forestry operations (Table 2).

The desired density of retained structural attributes, as listed in Table 2, depends, to a large degree, on the specific species, species groups or the processes of concern. For example, to maintain saproxylic insects, the density and distribution of CWD of preferred and required wood characteristics is important (e.g. hardwood vs. softwood, or specific species). In addition, the proportion of CWD in the various decay classes, and the range and distribution of log dimensions may be important for providing continuity of habitat in space and time for species with different mobility (Grove, 2002). Thus, in the absence of better information, varying retention densities in both space and time may be the best approach for maintaining processes, and providing habitats for a wide range of organisms.

Although a topic of much study, we do not yet understand fully how various organisms or ecosystem functions respond to various amounts and arrangements of CWD (Harmon, 2002). However, even if good information on ecological responses were available, the question of what constitutes satisfactory amounts and distributions of retention attributes is still largely subjective, based on factors such as acceptable economic impact, conservation status of species affected, and associated risks.

Similarly, as a result of the fairly recent interest in variable retention, knowledge about the stability and long-term dynamics of retained structural elements is limited. The susceptibility of standing structural attributes to uprooting, snapping or otherwise succumbing to the influences of wind, fire, dieback and pathogens is, in many situations, likely to be higher than in an intact forest (Bladon et al., 2008). Information about the post-harvest dynamics of these structures is, in many situations, likely to be higher than in an intact forest status of species affected, and associated risks.

D’Amato, 2002), competitive effects of overstorey trees in vegetation outside their crown projection area (Puettmann and White, 2001; Rose and Muir, 1997). However, the magnitude of growth reduction appears to be highly variable and depends on a range of factors such as size and vigour of retained trees, shade tolerance of the establishment understorey, site resource availability, and spatial patterns of retained trees. Reductions appear larger on sites with low productivity, probably due to the combined effects of shading and root competition. Where retained trees suppress vegetation outside their crown projection area (Puetzmann and Damato, 2002), competitive effects of overstorey trees in aggregated retention most likely will be less than in dispersed retention, particularly when shade-intolerant species dominate the recruitment layer (e.g. Palik et al., 1997).

Retained trees that become stressed due to sudden exposure after harvesting are likely to be more susceptible to secondary pathogens. Furthermore, some damaging insects may benefit from the warmer microclimate after harvesting and the provision of fresh breeding and foraging material in abundant CWD. This may be particularly problematic for coniferous forests, where bark beetles are important pest species. Factors, such as whether insect populations are at endemic levels or how many damaged trees are available for insects, can determine the size of bark beetle or pine shoot borer (Tomicus sp.) populations in a restoration area with retained trees and CWD (Eriksson et al., 2006; Martikainen et al., 2006). Under favourable conditions, the damage from insects and diseases after retention harvests does not necessarily exceed that
under conventional silvicultural systems. However, in regions with warmer climates than in the boreal forest example above, insect populations may become more responsive and be of greater concern. It may therefore be advisable to retain trees and CWD of species that are less susceptible to insect damage (Vanhala-Majamaa and Jalonen, 2001), or to use fire to lower the suitability of CWD as breeding material (Eriksson et al., 2006).

The density and spatial arrangement of retained structures have a variety of other implications for forestry operations and ecosystem development (Table 2; see also Franklin et al., 1997; Beese et al., 2003). Given the complexity of factors and their potential interactions, it is not surprising that many large-scale, operational-size experiments are currently being conducted to investigate the effects of different retention strategies on ecological, economic and social forest values (e.g. Coates et al., 1997; Abbott et al., 1999; Spence and Volney, 1999; Brown et al., 2001; Brais et al., 2004; Poage and Anderson, 2007). The degree to which results from these experiments are specific to their local forest types or the extent to which they can be extrapolated, is a question of great importance, since these research efforts are concentrated in temperate and boreal regions and similar studies are lacking in the tropical and subtropical forests.

4. “Cultural old-growth” forests

In several definitions, old-growth forests have been characterised by a long-term absence of intensive disturbance. However, in some old-growth forests, regular minor disturbances are required to maintain old-growthness or to stabilise forest structure (Kauffmann et al., 2007). Well-known examples of this type of forest include the ponderosa pine forests in western North America (see Kauffmann et al., 2007 for more examples). While stand-replacing fires are rare, these forests were subject to frequent (3–38 years) low intensity fires in the pre-European era. Native Americans likely had a major influence on this fire regime to encourage development and fruiting of plants, to increase the abundance of selected species while discouraging others, and to facilitate hunting (Hessburg and Agee, 2003). Other opinions suggest that Native American burns only supplemented or substituted for natural lightning fires in these fire-prone environments (Baker, 2002). However, the fire-regimes changed substantially in many places with the landscape changes subsequent to the arrival of European settlers (Hessburg and Agee, 2003). Through a reduction in fire-frequency, mainly due to grazing and fire suppression, a number of ecosystem characteristics changed. Specifically, forest floor depth and fuel loads increased, as did tree densities, particularly of shade-tolerant and fire sensitive conifers such as Douglas fir and true firs (e.g. Covington et al., 1997). These changes led to reduced soil moisture and understorey vegetation diversity, and to increased mortality of old trees (Binkley et al., 2007).

As a result of the increased amounts of fuel, continuous canopy and fuel ladders, high intensity crown fires are likely to be stand-replacing events. Restoration efforts, which include the removal of trees and ground fuel through thinning and controlled burning, maintain open stand structures that prevent or reduce the likelihood of high-intensity fires (Covington et al., 1997). Where the maintenance of old-growth structures is dependent on active management of disturbance regimes, as in the example above, we might speak of “cultural old-growth”. In addition to the maintenance of disturbance regimes that have shaped these forests, additional restoration management may be necessary, as outlined below.

5. Restoring old-growth attributes in regrowth and secondary forests

Much of the forested area previously covered by old-growth in temperate, Mediterranean and subtropical regions has been converted to regrowth or secondary managed forests with substantially different structures and, in many cases, different species compositions as well (Sands, 2005).

A change in management objectives towards encouraging development of old-growth structures requires a shift in management approaches and practices. In stands where management was highly intensive and successful at homogenizing composition and structure, this shift requires a longer time period for successful “transformation” or “conversion” (Kend and Gaheue, 2001; Kuuluvainen et al., 2002). In many parts of Finland, for example, aspen has been removed almost completely, and considerable effort is required to bring large aspen trees back (Vanhala-Majamaa et al., 2007). However, stands in which management was not aimed at, or was unsuccessful at homogenizing composition and structures may have many of the desired structural attributes already, and thus require less restoration effort (Newton and Cole, 1987).

From a landscape perspective, restoration can be used to complement conservation efforts (Fig. 1) by reserves to enhance habitat quality and quantity, (2) in multiple-use forests between small and fragmented reserves to complement habitat and improve connectivity, and (3) to create buffer zones between reserved and intensively managed forest areas (Kuuluvainen et al., 2002).

Restoration practices mainly aim to increase structural complexity of forest stands (see McElhinny et al., 2005, for a definition of structural complexity). This may be achieved through the management of density and tree regeneration (Kend and Gaheue, 2001; O’Hara, 2002; Choi et al., 2007; Davis et al., 2007). While these two aspects are part of “traditional” silvicultural practices, the new suite of restoration objectives provides unique challenges. For example, while traditional silvicultural systems are designed to optimize conditions for regenerating seedlings, overstorey densities specified in restoration treatments may be driven by wildlife habitat objectives, which are suboptimal for regeneration (Puettmann and Ammer, 2007). Furthermore, silvicultural restoration prescriptions need to address a variety of other components of stand structure and composition, such as canopy and crown structures as well as understorey vegetation typically found in old-growth (Table 1) (Franklin et al., 1981; Davis, 1996).

The list of structural components found in old-growth forests (Table 1) does not provide information about their relative importance, which is likely to vary among different stand types, ownerships and regions (Mansourian et al., 2005). Developing a hierarchy of priorities for the desired structural and composition components (Table 1) will help to resolve potential conflicts. In regions in which present old-growth can be used as a blueprint for management efforts, structure and composition targets can be quantified in detail (e.g. Cissel et al., 2006; Bergeron et al., 2001). In areas where old-growth is absent or limited, desired future conditions may need to be more generic (Zerbe, 2002; Mansourian et al., 2005). Specific structure and composition goals can be derived either from historical evidence, or an understanding of habitat requirement of selected species or taxonomic groups (e.g., Conner and Rudolph, 1991; Thompson et al., 2003). The latter can be regarded a fine-filter approach to conservation (Hunter, 1991) in contrast to broader goals of management for structural complexity.

A specific list of attributes considered essential or desirable goals for management (Table 1) together with an inventory of current conditions provides an information base for assessing which strategies are best suited to achieve the goals (e.g. Schmidt et al., 2001). Besides ecological constraints, concerns about costs, social acceptability and short-term negative impacts of necessary practices are important, and may influence the decision whether to use a passive, reserve-based approach towards increasing old-growth, or an active management approach. Kuuluvainen et al. (2002) provide some good examples of active management
approaches for increasing old-growth attributes relatively quickly. The potential benefits of an active management approach rely on two basic assumptions (see also Keeton, 2006):

1. Active management can accelerate the development of old-growth structural attributes in forest stands (Fig. 3).
2. Active restoration of old-growth structures offers additional advantages over passive (non-manipulative/unguided) restoration, including higher predictability and reduced risks, and a higher level of provision of goods and services, such as timber.

Initial approaches to restoration suggested adopting “traditional” uneven-aged silvicultural practices (Benecke, 1996; Emmingham, 1998). However, structural goals and associated constraints and conditions in managing for old-growth are quite different from the conditions that have led to the development of current silvicultural systems (Puettmann et al., 2008; for examples about the impact of such differences see Kenefic and Nyland, 2007). Traditional silvicultural systems were developed for efficient timber production in intensively managed, homogenized forests (Puettmann et al., 2008). In contrast, restoration goals for old-growth typically focus on increasing structural complexity (Keeton, 2006). Because of the limited scientific information currently available to guide our efforts, various research programs were initiated in the 1990s to investigate whether management could accelerate the development of old-growth structural components, and also the potential benefits of an active restoration approach (e.g. Poage and Anderson, 2007; Seymour et al., 2006; Kuehne and Puettmann, 2006). Most of these studies are relatively recent and information about many aspects, especially long-term responses, is still rare. The following section reviews our current understanding of the two above-mentioned assumptions for a variety of stand components.

If a few, large trees are a desirable characteristic of future stands, the average tree response, which is often documented in thinning studies, is not a useful measure. The largest trees in a stand appear to be influenced less by the overall competitive conditions in the stand or by their local neighbourhood (D’Amato and Puettmann, 2004; Simonin et al., 2006). Consequently, thinning intensities around these trees need to be higher than in “standard” thinning prescriptions to achieve a substantial growth response (Davis et al., 2007).

Criteria for tree retention need to acknowledge desirable future species compositions and structure. Typically, managed stands comprise a limited set of crop tree species. However, even managed plantations often contain a few trees of non-crop species, which usually have regenerated naturally (e.g. Keenan et al., 1997; Davis et al., 2007). These trees may have little economic value and therefore are discriminated against in release or thinning treatments as potential competitors (Waldstad and Kuch, 1987; Mason and Milne, 1999). However, they become of greater interest as residual trees in restoration treatments to increase the diversity of species and structural conditions in the stand. These less desirable tree species, if left during thinning operations can make a significant contribution to the seedling bank and thus on future development of a stand towards the composition of old forests (Keeton and Franklin, 2005; Kuehne and Puettmann, 2008). Practices required to ensure the survival of ecologically important midstorey species could include removal of overtopping trees, even potential crop trees (e.g. Welden et al., 1991).

Similarly, selection of cut-and-leave trees may be altered to provide for a variety of crown structures. For example, forked trees, or trees with cavities or diseased or damaged tops may provide unique habitat features, but typically are marked for removal because of their low value (Kenefic and Nyland, 2007). Another argument for their retention is that the economic benefit of selling such (non-crop) trees is often relatively small. Restoration activities also may aim at actively preventing the mortality of cavity trees during management activities (Conner et al., 1991; Bull et al., 2004; Kenefic and Nyland, 2007). Mortality of cavity trees is typically higher than that of healthy trees (Conner et al., 1991), and decisions about thinning densities should consider leaving extra trees, which are designated as potential future cavity trees (e.g. Cissel et al., 2006).

While it has been shown that the development of many tree attributes can be accelerated through management activities (e.g. Choi et al., 2007), information about the influence of restoration activities on other attributes is lacking. For example, development of certain crown structures, such as dead branches, has been documented in old forests, but not in response to thinning in mature or old forests (Ishii and McDowell, 2002; Ishii and Kadotani, 2006). The experiences from thinning studies in young stands, when crowns consist largely of small or semi-permanent branches may not be transferable.

In a variety of ecosystems, the species diversity and biomass of understorey vegetation has been shown to increase after thinning or partial cuts (West and Osler, 1995; Bailey and Tappeiner, 1998; Bauhus et al., 2001). Several studies showed that the degree of thinning related positively to the increase in understorey vegetation diversity and biomass (Harrington and Edwards, 1999; Battles et al., 2001; Elliot and Knoepp, 2005). The initial response of understorey vegetation appears to be a combination of a response to the harvesting disturbance and changes in the availability of resources such as light and water. Moreover, the interplay between these factors may lead to a decline in understorey cover (Thomas et al., 1999; Davis and Puettmann, in press). For example, shrubs injured in logging operations are unable to exploit increased resource levels until they recover from damage (Kraft et al., 2004; Davis and Puettmann, in press). Unfavourable microclimatic conditions, such as lower humidity, are probably also responsible for the initial decline of mosses after thinning (Davis and Puettmann, in press). On the other hand, herbaceous species increase in diversity and abundance quickly, but over time will be repressed by regrowth of overstorey trees and shrubs (Beaudet et al., 2004; Davis and Puettmann, in press).

Initially thinning appears to alter species composition towards early successional species (Griffis et al., 2001), a trend contrary to that found in unmanaged old-growth forests (Keenan et al., 1997; Schoonmaker and McKee, 1988). However, after longer periods without larger disturbances, understorey species composition in thinned stands becomes more similar to old-growth than in unthinned stands (Bailey and Tappeiner, 1998; Lindh and Muir, 2004). This is probably due to the recovery of the overstorey cover after thinning (Davis et al., 2007; Maas-Hebner et al., 2005), which has been shown to reach overstorey cover levels (He and Barclay, 2000) and leaf areas (Bailey and Tappeiner, 1998) similar to unthinned and old-growth stands within two to three decades. The resulting reduction in light levels (Beaudet et al., 2004) and below-ground resources (Riegel et al., 1995) in conjunction with plant interactions among understory plants, such as competitive and facilitative processes (Thomas et al., 1999; Delagrange et al., 2006) are most likely responsible for the shift in species composition.

Restoration efforts to influence the understorey, in many cases will influence tree regeneration as well. For example, advanced regeneration is important for future dynamics of forest ecosystems as it facilitates an increase in species diversity and hence quality of different canopy layers (Mesquita, 2000; Murphy et al., 1999). The establishment of a vigorous tree understorey provides an important functional component for resiliency and adaptability of such ecosystems as advanced regeneration can usually respond quickly to overstorey mortality or removal.
Fully stocked, homogenous stands can be manipulated easily to increase structural and environmental variability within a stand. Even in the absence of specific planning, inherent stand variability and logistic constraints are likely to create some spatial heterogeneity following thinning (Berger et al., 2004). In restoration treatments, structural variability can be generated if criteria other than spacing are used in prescriptions. For example, management based on tree size, e.g. diameter-limit cuts or target diameter harvesting, leads to increasing small-scale spatial variability (Angers et al., 2005). Prescriptions also can include a wide range of residual tree-to-tree distances or gaps, and leave unthinned islands (Cissel et al., 2006). The latter may be regarded as aggregated retention in the thinning phase. However, gaps, small openings or evenly spaced canopies may close relatively quickly by lateral branch expansion and vertical growth of mid and understory trees such that these openings are only a temporary feature (van der Meer and Bongers, 1996; Spiechta et al., 2005).

Most managed forests contain lower CWD levels than old, unmanaged forests (e.g. Morganti and Kansas, 2003; Ekbohm et al., 2006). The recognition of the importance of CWD has led to a range of active and passive approaches to increase the woody detritus pool in managed forests (see Table 3), although, in most cases, it is very difficult to determine the quantity and distribution of CWD required to achieve certain management objectives (Harmon, 2002). Active approaches comprise girdling or poisoning to create standing dead trees, and felling and pulling to create CWD on the ground (e.g. Keeton, 2006). In addition, leaving more slash, including trees, after harvesting as well as burning to kill some live trees are means to increase CWD at the time of harvesting (e.g. Vanha-Majamaa et al., 2007). However, in continuous-cover forestry and restoration practice, active creation of CWD is likely to be restricted to special situations, for example where there is an immediate need to provide habitat for threatened organisms (e.g. Filip et al., 2004) or where, in the absence of woodpeckers, such as in Australia, cavities take a very long time to develop (Gibbons and Lindenmayer, 2002).

Passive approaches to increase CWD can rely on density-dependent (competition driven) and density-independent mortality. Density-dependent mortality as a result of self-thinning is particularly high in young even-aged stands or groups. Ferguson and Archibald (2002) showed that the basal area of dead standing trees was closely related to the amount of live tree basal area in fire-origin boreal forests of northwestern Ontario. Thus, what might be a suitable practice to promote late-successional understory (see above) is also suitable for the passive creation of dead wood (e.g. Vanderwel et al., 2006). However, a large proportion of this material may be small in size, and therefore unsuitable for particular types of saproxylic organisms.

Density-independent mortality, which may be between 1 and 2% per annum in mature and old stands (Van Mantgem and Stephenson, 2007; Lewis et al., 2004) ensures a constant supply of dead wood. If individual or groups of dying or dead trees are not salvaged, even after disturbances, or salvaging is reduced, the input of CWD could be increased considerably. Bouget and Duelli (2004) argue that, even in continuous forests with the risk of bark beetle infestation, windthrow gaps can be managed in an adaptive way that allows the retention of freshly created CWD islands.

By modeling CWD dynamics in Norway spruce stands, Ranius et al. (2003) demonstrated that the risk of losing sufficient quantities of CWD in the different decay classes is high, if insufficient live trees that can die over the course of a production cycle are retained. How much CWD persists over the course of a production cycle depends on the initial and continued input of dead trees and the decomposition rate of standing and downed CWD. To ensure a continual CWD input, it is important to retain live trees in a way that avoids high mortality rates soon after harvesting disturbance. Thus the maintenance of CWD is closely linked to the quantity and distribution of retained live trees (Table 2). The decomposition rate of CWD depends on a range of factors, including species-specific decay resistance, time until snag fall, stem size, climatic variables and the decomposer community (Mackensen et al., 2003; Ranius et al., 2003), all of which may need to be considered in an approach to maintain or increase dead wood. Lonsdale et al. (2008) have listed a number of examples where the application of best management practices has resulted in increased CWD levels. In addition, restoration practices aimed at creating CWD must be aware of possible conflicts with management of wildfire risk, insect pests and forest disease outbreaks. Lonsdale et al. (2008) discuss further issues related to dead wood management.

Just like any silvicultural treatment, constraints and risks of restoration treatments need to be evaluated carefully. Many restoration treatments are associated with substantial costs, which may prevent their widespread application, particularly on private land. Combining such treatments with harvesting operations that provide revenue and some form of compensation may be necessary for implementation (Keegan et al., 2002). Furthermore, restoration treatments may lead to increased risk of disturbance, at least in the short term (e.g. Cremer et al., 1982). This is generally undesirable in forests also managed for timber production. For example, sudden canopy openings caused by intensive thinning or gap creation may lead to higher windthrow rates until trees stabilize through altered taper or crown dimensions (Mitchell, 2000; Achim et al., 2005). The potential for higher intensity fires may increase as understorey and midstorey vegetation layers and downed wood provide higher fuel loads (Aage, 1993).

To assess long-term development of stand structure and composition in response to alternative restoration options, increasingly silviculturalists are using simulation models. Because of the higher predictability of tree development, most efforts focus on tree growth and mortality, with notable exceptions. Early attempts relied on standard growth and yield prediction models.
(e.g. Birch and Johnson, 1992). Alternatively, ecologically gap models (Busing and Garman, 2002) or individual tree models provide more flexibility to simulate a variety of treatments (Choi et al., 2007). Most individual tree models have the limitation that they assume regular tree spacing. However, the recent development of spatially explicit models (e.g. SORTIE-ND: Coates et al., 2003), which may even include stochastic elements (e.g. LANDIS-II: Mladenoff, 2004), provide an opportunity to represent spatially variable treatments both within and among stands.

In summary, the development of many structural and composition components of old-growth stands can be accelerated through silvicultural interventions. However, the dynamics of the responses differ between ecosystems and initial conditions (e.g. Choi et al., 2007), and the timing and direction of the response of various structural components are not necessarily coupled. Some responses to restoration are very dynamic, e.g. increase in species diversity in understory vegetation. Furthermore, structural components that are related to tree size can be manipulated efficiently through density management. However, secondary responses, e.g. wildlife populations or lichen communities, require much longer time periods to develop (Batty et al., 2003). The stand development stage, when the ecosystem is still or most responsive to restoration treatments, varies for the different structural attributes (Puettmann and Berger, 2006). To complicate things further, opposite response trends may occur. For example, advanced regeneration may develop into a dense midstorey layer that limits the development of the shrub and herb understory. The complexity of interacting factors suggests that restoration should not be prescribed homogenously or at the stand level. Instead, decisions about priorities, timing, and what proportion of stands should provide what old-growth attributes of structure or composition may be necessary for efficient restoration efforts. Lastly, it is important to note that restoration treatments not only have to deal with logistical constraints and social acceptability, but they also need to deal with temporarily increased risks of disturbances.

6. Conclusions and outlook

Silviculture for old-growth attributes should not be considered as an oddity by foresters since the special ecological services that old-growth provides are becoming increasingly valued by society due to their rarity. Since silviculture is aimed at manipulating forest stands to achieve human objectives, managing for old-growthness is merely a new objective to add to the long list of the current ones. One of the main differences with previous objectives is that managing for old-growthness does not normally provide direct benefits to the landholder, but rather an indirect benefit to society as a whole. Consequently, in order to make silvicultural practices for old-growthness an attractive option, society as a whole would need to place a financial value on old-growthness. This is already occurring in some areas and countries, where government programs compensate private owners for foregoing harvesting, or for harvesting forests in unconventional ways. Similarly, certification could be considered as a kind of market incentive for maintaining old-growthness on some part of the managed landscape. While it may be feasible technically to retain and restore complex forest structures, silviculturists are also challenged to make these strategies work economically.

Here, we reviewed silvicultural approaches for old-growthness at the forest stand level. However, stand-level silvicultural strategies of course are influenced by the landscape or regional setting. Thus there are many other questions that need to be addressed at a larger scale to optimise silvicultural approaches. In this context we need to ask how much and where old-growthness should be maintained or developed preferably in the landscape, since the probability of disturbance changes with ecosystem type and landscape setting (Keeton and Franklin, 2004; Wirth et al., 2009). It will also be easier to implement complex structures in some parts of the landscape than in others (e.g. steep slopes).

An outstanding research question for managing for old-growthness concerns the quantity, spatial arrangement and temporal dynamics of forest structural attributes required to meet various management objectives.

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References

Abbott, R.S., White, J.D., Woodard, B.L., 1999. The benefits and challenges of large-scale silvicultural experiments: perspectives from forest managers on the Demonstration of Ecosystem Management Options (DEMO) study. Northw. Sci. 73, 118–125 (Special Issue).


Pinus strobus L. stands in Ontario.


menced plant-Douglas-fir seedlings in variable retention forestry sites on
resources availability and seedling responses in a longleaf pine ecosystem. Can. J.
Res. 27, 1458–1464.
relation to disturbance and forests type in boreal Canada. Forest Ecol. Manage.
58, 185–197.
1501–1511.
Res. 27, 1458–1464.
relation to disturbance and forests type in boreal Canada. Forest Ecol. Manage.
58, 185–197.
1501–1511.
Res. 27, 1458–1464.
relation to disturbance and forests type in boreal Canada. Forest Ecol. Manage.
58, 185–197.
1501–1511.
Res. 27, 1458–1464.