

# The Irregular Shelterwood System: Review, Classification, and Potential Application to Forests Affected by Partial Disturbances

Patricia Raymond, Steve Bédard, Vincent Roy, Catherine Larouche, and Stéphane Tremblay

## ABSTRACT

Structurally different from even-aged and balanced uneven-aged stands, irregular stands are an integral part of forested landscapes in northeastern North America. The maintenance or restoration of irregular stand structure may be desirable, especially in areas under ecosystem-based management. This can be achieved at the stand level through the implementation of irregular shelterwood systems. The objectives of this synthesis are to assemble the existing knowledge about the system, clarify the terminology in use, and discuss its place in silviculture in northeastern North America. Irregular shelterwood is compared with other regeneration methods and we propose a classification based on three variants. This silvicultural system is compatible with ecosystem-based management in forest types driven by partial stand mortality and gap dynamics and provides opportunities for maintaining old-growth forest attributes. However, it presents important challenges, especially with regards to planning, growth and yield prediction, and operational application.

**Keywords:** ecosystem-based management, irregular uneven-aged silviculture, multiaged stand, irregular shelterwood variants, regeneration methods

In many North America jurisdictions, the management of public forestlands has gradually shifted from timber production to ecosystem-based management, with a focus on late-successional habitat

(Kohm and Franklin 1997). In a managed territory, applying principles of ecosystem-based management is a way of achieving sustainable forest management objectives (Galindo-Leal and Bunnell 1995). This implies

that silvicultural practices must emulate ecological processes and interactions if composition, structure, and ecosystem function are to be maintained within their limits of natural variability (Kaufmann et al. 1994, Seymour et al. 2002, Gauthier et al. 2008) at multiple spatial and temporal scales (Galindo-Leal and Bunnell 1995). At the stand scale, the growing interest in ecosystem-based management brings into question current silvicultural practices and how they can contribute to maintaining ecological values (Guldin 1996, Puettmann and Ammer 2007).

This article focuses on the silviculture of irregular stands. In American forestry textbooks, even-aged stands are clearly distinguished from uneven-aged stands (Smith et al. 1997, Nyland 2002). Even-aged stands are composed of trees in the same age class, with the oldest and youngest trees differing

Received November 24, 2008; accepted May 20, 2009.

Patricia Raymond ([patricia.raymond@mrnf.gouv.qc.ca](mailto:patricia.raymond@mrnf.gouv.qc.ca)), Steve Bédard ([steve.bedard@mrnf.gouv.qc.ca](mailto:steve.bedard@mrnf.gouv.qc.ca)), Vincent Roy ([vincent.roy@mrnf.gouv.qc.ca](mailto:vincent.roy@mrnf.gouv.qc.ca)), Catherine Larouche ([catherine.larouche@mrnf.gouv.qc.ca](mailto:catherine.larouche@mrnf.gouv.qc.ca)), and Stéphane Tremblay ([stephane.tremblay@mrnf.gouv.qc.ca](mailto:stephane.tremblay@mrnf.gouv.qc.ca)) are research scientists in silviculture, Direction de la recherche forestière, Ministère des Ressources naturelles et de la Faune, Gouvernement du Québec, Québec, Canada. The authors thank Paul Bouliane and Louis Bélanger for being a source of inspiration with the development of the irregular shelterwood system at Forêt Montmorency Experimental Forest (Université Laval) and give special thanks to Jean Noël and Maripierre Jalbert for their help with the figures, Debra Christiansen-Stowe for the linguistic revision, and Lucie Jobin for assistance with the literature review. The authors also thank Daniel Dumais, Jean-Claude Ruel, Yan Boucher, Jean-Pierre Saucier, Robert S. Seymour, and two anonymous reviewers for their helpful comments on earlier versions of this article.

Copyright © 2009 by the Society of American Foresters.

in age by no more than 20% of the rotation length. Uneven-aged stands contain an intimate association of at least three age classes growing in the same area (Smith et al. 1997, Nyland 2002). Although the debate around the binary classification of stand age structure (even-aged versus uneven-aged) has been going on for decades, it has long been acknowledged that intermediate structures exist (Silvy-Leligois 1953). For instance, two-aged stands have two distinctly different ages classes (Smith et al. 1997, Nyland 2002). Furthermore, authors such as Smith et al. (1997) distinguish “balanced” from “irregular” uneven-aged stands. In balanced uneven-aged stands, age classes occupy approximately equal areas that function as self-contained, sustained yield units, whereas irregular uneven-aged stands (hereafter called irregular stands) are unbalanced and do not contain the age-class distribution necessary to produce a constant yield of mature trees at short intervals indefinitely.

In northeastern North America, irregular stands used to be an important landscape component, given the predominance of late-successional forests (Lorimer 1977, Bouchard et al. 2008, Boucher et al. 2009). Irregular stands typically develop as a result of episodic partial stand mortality occurring in the absence of whole stand-replacing disturbances (Fajvan and Seymour 1993, Fraver and White 2005, Bouchard et al. 2006, Bergeron et al. 2007). Various old-growth attributes, cited in Bauhus et al. (2009), can be found in irregular stands: multiple canopy layers, high variation in tree sizes, presence of several cohorts (e.g., group of trees developing after a single disturbance [Helms 1998]), high spatial heterogeneity of tree distribution, irregular gap size and distribution, and high variation in branch systems and crown structure, as well as the presence of advance regeneration. It is generally acknowledged that structurally complex stands provide a wide variety of habitats for animal and plant species (Hansen et al. 1991, McComb et al. 1993).

In Quebec (Canada), several studies have quantified the historical importance of irregular stands at the landscape scale. In the eastern balsam fir (*Abies balsamea* [L.] Mill.)–white birch (*Betula papyrifera* Marsh) bioclimatic subdomain, e.g., irregular stands used to occupy 39% of the virgin forest (Leblanc and Bélanger 2000). The percentage of unmanaged stands presenting an irregular structure in the western and eastern black spruce (*Picea mariana* [Mill.]–moss biocli-

matic subdomains, is 24 and 45%, respectively (Boucher et al. 2003). A historical study, recently conducted at the boundary between the balsam fir–yellow birch (*Betula alleghaniensis* Britton) and sugar maple (*Acer saccharum* Marsh.)–yellow birch bioclimatic domains, showed the predominance of mature stands with an irregular structure in pre-industrial landscapes (Barrette and Bélanger 2007). The importance of irregular stands in natural forests was also recognized elsewhere in northeastern North America (Lorimer 1977, Lorimer and Frelich 1994, Seymour and Kenefic 1998, Lorimer and White 2003).

Given the ecological significance of irregular stands in unmanaged forests, maintaining these structures on a proportion of the area might be desirable, e.g., to meet ecosystem-based objectives. However, current management practices do not always permit the specificity of irregular stands to be maintained. Generally, the aim is to regulate stand structure, which results in a simplification of stand attributes (Franklin et al. 2007). A good example is the generalized use of clearcutting and its variants in coniferous-dominated stands of Canadian boreal and mixedwood forests (Bergeron et al. 1999, Groot 2002). Using even-aged silvicultural systems in irregular stands sacrifices vigorous small merchantable stems and simplifies stand structure (McCarthy and Weetman 2006). This may have an impact on biodiversity (Aplet 1994, Despons et al. 2002). Although balanced uneven-aged silvicultural systems may conserve several irregular stand attributes, especially those related to vertical structure, the maintenance of an irregular structure over the long term is not the objective (Smith et al. 1997, Angers et al. 2005).

Maintaining the structure of irregular stands without converting them to even-aged or balanced uneven-aged stands requires an appropriate silvicultural system. The irregular shelterwood system, defined as a system of successive cuttings with a long or indefinite regeneration period, offers the flexibility of generating spatial and vertical heterogeneity in stands (Matthews 1989). However, in practice, the use of this system is rather limited in North America (Seymour 1992, 1995). While conducting our literature review, we realized that there is sometimes confusion in the terminology used. In this article, we review the existing knowledge about this system, clarify the current terminology, and discuss the potential appli-

cation of irregular shelterwood in northeastern North American silviculture.

## The Irregular Shelterwood System and Its Variants

As early as the 19th century, practicing foresters in several European locations began expressing their displeasure with the scarcity of mixed stands and forest homogenization generated by the use of even-aged systems such as regular shelterwood and clearcutting with planting (Fourchy 1952, Silvy-Leligois 1953, Spurr 1956). They developed new regeneration methods in response to specific local ecological and economical conditions (Puettmann et al. 2008). This development triggered an important switch from managing regeneration at the stand level to more flexible applications adapted to conditions at smaller spatial scales (Puettmann et al. 2008). Gayer first described the concept of the irregular shelterwood method (*Femelschlag*) and recommended that foresters should seek their inspiration from natural stand dynamics when implementing silvicultural prescriptions (Gayer 1880 in Silvy-Leligois 1953). Gayer’s objectives were to promote the establishment of natural regeneration and the creation of mixed species stands. Shelterwood methods share the common objective of establishing regeneration under the overhead or side shelter of forest cover (Matthews 1989). Irregular shelterwood differs from regular shelterwood and its variants in that the forest cover is retained during a long period of time to accommodate special management objectives (Hannah 1988, Nyland 2002). The method was first investigated by von Huber in Bavaria (Spurr 1956). Initially, stand irregularity referred to vertical variation in tree height, but the concept has evolved to include horizontal variation as well (Schütz 2002). The commonality of the first irregular shelterwood systems (Bavarian, Swiss) was to regenerate the stand by harvesting irregularly spaced small groups of trees (Fourchy 1952). Many *Femelschlag* deviated from the initial form, and today *Femelschlag* refers to a variety of silvicultural systems that differ among countries and forest managers (Matthews 1989).

In the scientific literature, descriptions of irregular shelterwood systems vary as well. However, the common objective is to establish, at each entry, a new cohort composed of desirable midtolerant or tolerant tree species, with a longer regeneration period than a

**Table 1. Variants of the irregular shelterwood system.**

Variant	Expanding-gap irregular shelterwood	Continuous cover irregular shelterwood	Extended irregular shelterwood
Other names	Bayerischer Femelschlag Acadian Femelschlag Irregular group shelterwood Bavarian shelterwood Coupe progressive irrégulière par trouées agrandies	Badischer Femelschlag Swiss or Baden shelterwood Coupe progressive irrégulière à couvert permanent	Slow or delayed regeneration Extended shelterwood Coupe progressive irrégulière à régénération lente
Period of regeneration	>20% rotation length	>20% rotation length	>20% rotation length
Harvesting pattern	Group gradually expanded	Free, single tree, and group	Single tree, group, or strip
Final removal	Optional	No	Optional
Arrangement of cohorts	Juxtaposed cohorts New cohort established besides the previous one	Stratified cohorts New cohort established on the same area than the previous one	Two cohorts during >20% of rotation Only one new cohort established during the rotation
Vertical structure	Regular at small scale Single layer	Irregular Multiple layers	Regular or irregular Single or two layers
Horizontal structure	Irregular Mosaic of cohorts	Irregular Mix of cohorts	Variable according to harvesting pattern
References	Fourchy 1952 Spurr 1956 Lanier 1994 Schütz 2002 Saunders and Wagner 2005 Seymour 2005	Fourchy 1952 Spurr 1956	Smith 1986 Hannah 1988 Seymour 1992, 1995 Lanier 1994 Smith et al. 1997 Nyland 2002

regular system (more than 20% of rotation length; Smith 1986, Hannah 1988, Lanier 1994). We propose a classification based on three variants (Table 1). These variants differ in their spatio-temporal applications, which are in line with their specific objectives. The first variant, expanding-gap irregular shelterwood, aims to regenerate new cohorts in groups that are gradually enlarged until the stand is totally removed (Spurr 1956). With this variant, regeneration and harvesting are closely integrated to achieve a spatial order, which brings the stand together into a managed unit (Matthews 1989). In the second variant, continuous cover irregular shelterwood, the sequence of cuttings is applied more freely in space and time, which permits maintenance of a multicohort structure and a continuous forest cover (Fourchy 1952). The silviculturist works more with the material in place and adjusts the frequency and intensity of interventions to the autecology of the species and local site characteristics (Fourchy 1952). The third variant, extended irregular shelterwood, aims to regenerate the whole stand while keeping a more regular structure. Under this variant, two cohorts are maintained for at least 20% of the rotation length, because of a delay of the final removal (Smith 1986, Nyland 2002).

Figure 1 illustrates the sequence of cuttings for each of the three variants in a hypothetical mixed-species irregular stand. Depending on the variant used, the resulting stand may have juxtaposed (expanding-gap)

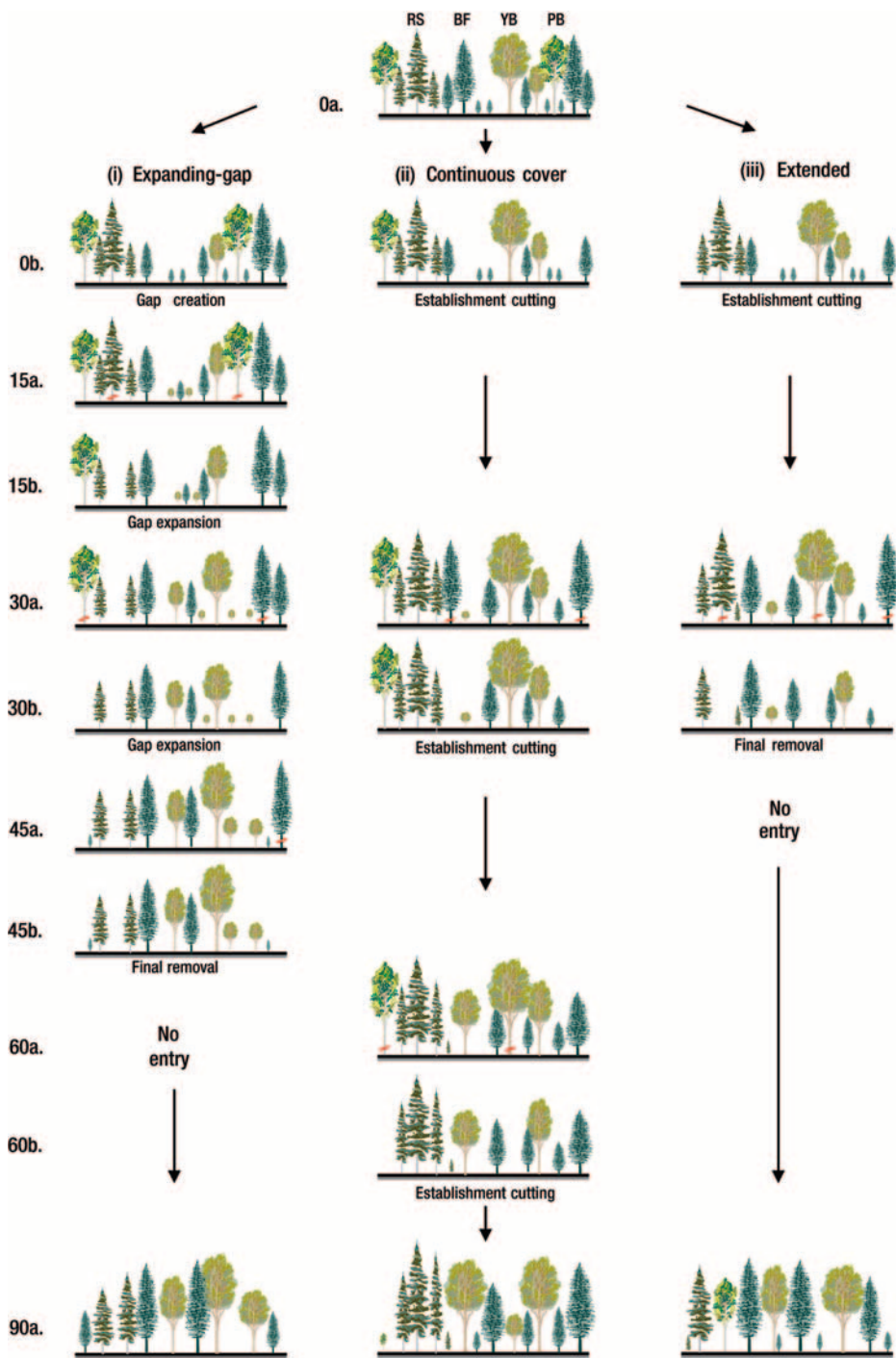
or stratified cohorts (continuous cover and extended) during portions or all of its rotation length and therefore maintains a more or less regular vertical and horizontal structure. All variants may include the retention of legacy trees (Smith 1986, Franklin et al. 2007). The choice of variant should be based on the autecology of desired species, management objectives, and natural stand dynamics. In the example (Figure 1), the choice of variant for a particular stand may be influenced by different reasons. The continuous variant appears to be the most appropriate if there is a need to maintain a continuous forest cover, as is the case for sensitive landscapes, side roads, recreational, and riparian areas. The two others variants may be simpler to apply and economically more advantageous, but they create less heterogeneity in the stand. The expanding-gap variant causes less damage to regeneration because the harvesting sequence is organized in such way that there is usually no return to the regenerating areas (Matthews 1989). The extended variant is the least intensive and is applied similarly to regular shelterwood systems (Nyland 2002). This variant is useful for establishing and protecting a layer of high regeneration over a period of several decades (Seymour 1992).

Silviculturists may opt for the implementation of irregular shelterwood as part of a management plan that is governed by external factors, such as social (e.g., aesthetic, recreational, and social acceptability) or ecological objectives. These objectives may in-

clude conserving specific animal habitats (e.g., woodland caribou [*Rangifer tarandus caribou*]; Daintith et al. 2005, Stone et al. 2008), protecting the regeneration of species sensitive to abiotic damage such as drought and frost (e.g., red spruce [*Picea rubens* Sarg.]; Dumais and Prévost 2007), insect damage (e.g., white pine weevil [*Pissodes strobi* Peck.]; Hannah 1988) and weed competition (e.g., red oak [*Quercus rubra* L.]; Hannah 1988). Of course, while other silvicultural systems may also be appropriate, the objective here is to describe situations when irregular shelterwood could be a relevant tool.

Once irregular shelterwood is identified as a potential tool, a few basic requirements must be verified to ensure that the system is applicable, and then, the general decision key may help to choose a suitable variant (Figure 2). First, desired species must have high or moderate shade tolerances (Schütz 2002). Second, unless enrichment with artificial regeneration is planned, the dominant cover must contain an adequate quantity and favorable distribution of seed trees of the desired species, taking into consideration seed dispersion distances, and the frequency, and abundance of seed crops. Seed trees must be old enough to produce seeds in abundance (Malcolm et al. 2001). Third, the stand must contain sufficient acceptable growing stock and be relatively wind firm to minimize the risk of windthrow during the regeneration period (Malcolm et al. 2001). Finally, age structure, number of cohorts,





**Figure 1.** Example of silvicultural scenarios illustrating three variants of the irregular shelterwood system in a fictive mixed balsam fir–yellow birch stand over a 90-year period. Red bars indicate marked trees. Numbers represent number of years since beginning, a = before cutting, b = after cutting, RS = red spruce, BF = balsam fir, YB = yellow birch, and PB = paper birch.

and the principal structural objective (maintenance or transformation) will be taken into consideration when selecting the most appropriate variant for a given stand (Figure 2).

### Irregular Shelterwood among Other Silvicultural Systems

Because irregular shelterwood has similarities with other systems, what is its real

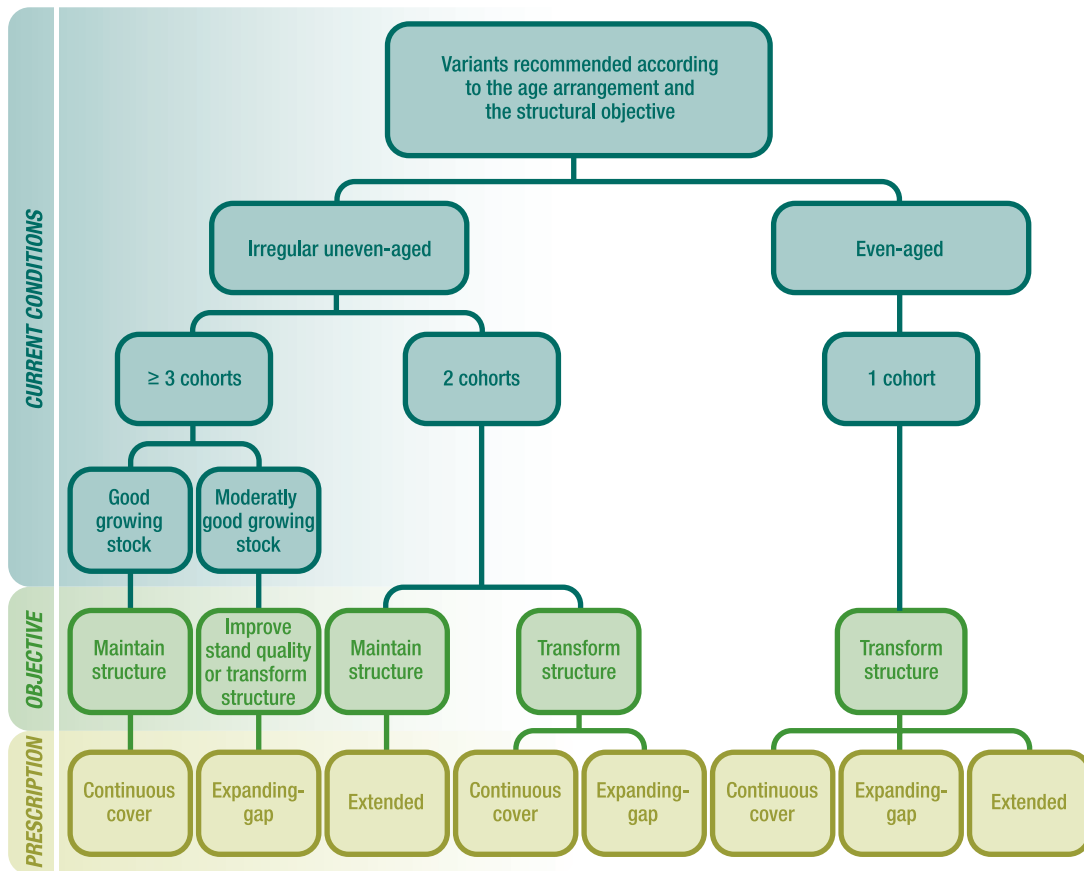
place within the family of regeneration methods? We think that high forest regeneration methods should be classified according to three age structure categories (Table 2). In fact, a range of intermediate age structures exists between even-aged and balanced uneven-aged structures. We propose expansion of the recognized two-aged structure (Smith et al. 1997, Nyland 2002) to a broader “ir-

regular structure” category that better reflects this range (Table 2). The recognition of three categories is necessary because the most defining feature of a silvicultural system is the age structure of a stand (Seymour and Hunter 1999, Nyland 2002). The range of variants associated with an irregular shelterwood system can then be used to manage the array of structures within the irregular category.

Both regular and irregular shelterwood methods have the same objective to induce the establishment of multispecies cohorts by adapting canopy openings to the light requirements of desired species (Smith et al. 1997, Kneeshaw and Bergeron 1998, McCarthy 2001). However, the irregular shelterwood method allows more flexibility for growing mixed stands that are composed of species with different longevities and levels of shade tolerance. This is especially true of the continuous cover variant. The timing of cutting and the selection of harvested trees can be adjusted to the species’ lifespans. Long-lived species such as yellow birch, sugar maple, red spruce, white spruce (*Picea glauca* (Moench Voss), northern white-cedar (*Thuja occidentalis* L.), and white pine (*Pinus strobus* L.) can be maintained in the stand over a longer period of time, while short-lived species like balsam fir and red maple (*Acer rubrum* L.) can be harvested on shorter cutting cycles.

Other principles common to shelterwood methods, such as using the partial cover to ensure a constant seed supply, and sheltering the new cohort from adverse microclimatic conditions and undesirable fast-growing species, are prolonged with the irregular system since the regeneration period is lengthened (Nyland 2002). Overtopped seedlings may also experience slower growth with the irregular method (Smith et al. 1997, Miller et al. 2006, Moores et al. 2007). Shelterwood systems differ from variable retention systems, because the retained trees in the latter do not promote regeneration through shelter (Mitchell and Beese 2002). In variable retention systems, long-term structural diversity is assured by trees that are left standing for at least one rotation without periodic entry in the stand, leading to one regeneration cohort.

The expanding-gap and the continuous cover variants may appear to be similar to selection cutting systems. However, the main difference is that there is no objective to balance the different age classes of the stand by single tree removal or by establish-



**Figure 2.** General decision key for choosing the appropriate variant of irregular shelterwood, according to the age arrangement and the structural objective.

ment of groups on a restricted area or specific spatial arrangement, which is characteristic of selection systems (Fourchy 1952, Matthews 1989). The expanding-gap variant may look similar to group-selection cutting after the first cutting, but it differs thereafter because future cuttings will enlarge the gaps, whereas, the next group-selection cuttings will create new gaps at each entry, thus creating a balanced age-class distribution over the area (Leak 1999, Nyland 2002). In the continuous cover variant, the least rigid of the approaches (Fourchy 1952), the major goal is to obtain stands with the highest production value possible in terms of quality and quantity. Thus, the concept of cutting cycle becomes blurred. Compared with selection methods, the length of cutting cycles and regeneration periods are not fixed, while silvicultural interventions are adjusted to species autecology, site characteristics, and education needs (Fourchy 1952). Therefore, when compared with selection cutting systems, this variant offers greater flexibility (Fourchy 1952, Smith et al. 1997) at the expense of consistency of volume production. Unlike contin-

uous cover irregular shelterwood, the objective of a selection system is to maintain a balanced structure and to achieve a constant periodic yield over cutting cycles. In fact, the idea of balance is an economic concept that allows more straightforward harvest planning and a continuous timber supply (Smith et al. 1997).

### Justification and Potential Application in the Northeast

The renewal of northern hardwood forests is characterized by a small-scale disturbance regime of gap dynamics (Frelich and Lorimer 1991) and selection cutting is a commonly used system in this forest type. Although this system emulates some features of natural dynamics in late-successional stands (Crow et al. 2002, Seymour et al. 2002), it generally creates small openings that are more favorable to shade-tolerant species (Leak and Wilson 1958, Crow and Metzger 1987, Majcen et al. 2005). In the long run, application of single-tree selection cutting can decrease the abundance of mid-tolerant species such as yellow birch (Leak

and Sendak 2002, Neuendorff et al. 2007, Webster and Jensen 2007). Furthermore, windstorms are episodic events that occur in northern hardwood stands (Canham and Loucks 1984, Frelich and Lorimer 1991) and generate additional structural heterogeneity in late-successional forests (Lorimer and Frelich 1994). With the perspective of diversifying silvicultural practices, irregular shelterwood could be an alternative to a regular shelterwood system and might help to increase heterogeneity in these forests. It also offers more possibilities than a group-selection system for promoting the regeneration of less shade-tolerant species.

Stands impoverished by repeated selective (diameter limit) cuttings are common in North America (Prévost et al. 2003, Kenefic et al. 2005). They often contain poor quality trees and regeneration and, because of highly variable harvest intensity, have a rather irregular structure (Robitaille and Boivin 1987, Nyland 2002). These stands are difficult to manage under selection cutting systems because of their poor growing stock (Leak et al. 1987). In stands with a minimum quantity of acceptable growing stock, an irregular

**Table 2. General characteristics of regeneration methods used in natural high forests (after Matthews 1989, Smith et al. 1997, Helms 1998, and Nyland 2002).**

Age arrangement	Stand structure (cohorts)	Regeneration method	Silvicultural objectives and description
Even-aged	Single cohort	Clearcutting	To regenerate the stand with natural seedlings or by planting shortly after complete overstory removal.
		Seed-tree	To regenerate the stand with natural seedlings from widely spaced trees left in the stand until the natural regeneration is established.
		Regular shelterwood	To regenerate the stand under partial shade of mature trees left in the stand by successive fellings until the new cohort of natural regeneration is established. Regeneration period <20% of rotation length.
Irregular uneven-aged	Two cohort	Extended irregular shelterwood	To regenerate the stand and maintain a partial cover for an extended period of time; the stand is composed of an upper and a lower story of trees of seedlings originating from seed, growing in intimate mixture on the same site.
	Irregular multicohort	Expanding-gap irregular shelterwood Continuous cover irregular shelterwood	To regenerate and maintain an unbalanced multiaged stand for a long and indefinite period of time by successive regeneration fellings.
Balanced uneven-aged	Balanced multicohort	Selection cutting	To regenerate and maintain a balanced multiaged stand by removing trees in all size classes either singly or in groups throughout the stand in order to sustain yield of mature trees at short intervals indefinitely.

shelterwood system could be used as a restoration tool instead of even-aged systems such as regular shelterwood. Irregular shelterwood may help to maintain the irregular structure by retaining cohorts of acceptable growing stock, while creating gaps through the removal of the poorest growing stock. Some key elements of mature stands, such as shade-tolerant saplings and seed trees, may be conserved as part of new stands (Smith 1986) to help restore the attributes of irregular stands lost during previous harvests (Fourchy 1952). Regenerated cohorts of desired species can be maintained and site preparation will promote natural regeneration in unproductive openings invaded by undesired vegetation. Also, high-graded, hardwood-dominated stands could be gradually restored with irregular shelterwood and later converted to a selection system.

To our knowledge, only variants of the regular shelterwood system have been documented in northern hardwoods (e.g., Tubbs and Metzger 1969, Ray et al. 1999, Nyland et al. 2000), while effects of irregular shelterwood are still poorly known. However, results from studies in hardwood forests, including group- and patch selection (Leak and Filip 1977, Leak and Gottsaker 1985, Leak 1999) and reserved shelterwood (e.g., Smith et al. 1989, Miller and Schuler 1995, Miller et al. 1997), could be gleaned to im-

plement the three variants of irregular shelterwood in this forest type.

In temperate mixedwood and boreal forests, where balsam fir is abundant, spruce budworm (*Choristoneura fumiferana* [Clem.]) epidemics result not only in whole stand mortality, but in partial mortality as well (Kneeshaw and Bergeron 1999, Bouchard et al. 2007, Kneeshaw et al. 2008). When stands are composed of tree species that are less vulnerable to spruce budworm or other insects, partial mortality may be generated by senescence or windthrow. This was documented for pure black spruce stands by Harper et al. (2002). These types of disturbances could be emulated with an irregular shelterwood system by allowing the establishment of a new cohort after each entry and keeping structural heterogeneity, old-growth attributes, and biodiversity (Gunn and Hagan 2000, Déry and Leblanc 2005). For example, irregular shelterwood could be useful in addressing issues such as red and white spruce rarefaction (Seymour 1992, Barrette and Bélanger 2007, Dumais and Prévost 2007). Moreover, as with other continuous cover systems, irregular shelterwood is well suited to integrated vegetation management strategies focusing on "preventive silviculture" (Roy et al. 2003), especially in forest types prone to severe competition and where the use of herbicides is socially unac-

ceptable or prohibited (e.g., MRN 1994). As with other regeneration methods, site preparation may be required to reduce competition from undesired vegetation and create suitable seedbeds for regeneration of species such as yellow birch, white pine, white spruce, and northern white-cedar (Raymond et al. 2000, Prévost 2008). Finally, where the frequency of irregular stands decreased in boreal and mixedwood forests (e.g., Leblanc and Bélanger 2000), irregular shelterwood may be used for converting stands from even-aged to irregular uneven-aged structures (Spurr 1956, Schütz 2001).

Although irregular shelterwood management (extended variant) is occasionally used by private landowners in North American conifer-dominated stands, there is no consensus on its application or guidelines (Seymour 1992). There are only a few ongoing empirical and controlled trials of irregular shelterwood systems, but literature is scarce on their effects. The expanding-gap variant is currently being studied at Penobscot Experimental Forest (Maine), emulating the 1% natural disturbance frequency that is common in the Acadian forest (Saunders and Wagner 2005, Seymour 2005). In Quebec (Canada), the continuous cover variant has been implemented operationally for more than 10 years in the balsam fir-white birch forest at Forêt Montmorency, as



an alternative to clearcutting in sensitive areas requiring a continuous forest cover (Bouliane and Dubois 2003). To expand our knowledge about the effects of irregular shelterwood in Quebec, le Ministère des Ressources naturelles et de la Faune initiated a comprehensive project across three representative stands of the boreal, temperate mixedwood, and northern hardwood forest zones (MRNF 2009). The goal is to compare the effects of irregular shelterwood with other silvicultural systems with respect to stand structure, quality, yield, composition, and old-growth forest attributes, in a context of ecosystem-based management.

## Challenges of Operational Implementation

Implementing an irregular shelterwood system presents important challenges. Similar to other regeneration methods, advance regeneration may be damaged by cutting (Hannah 1988). Planning and prediction of growth and yield in irregular shelterwood systems is more complex than in even-aged or balanced uneven-aged systems. The main challenges are related to the spatial and temporal arrangements of the cohorts. The harvesting program must be arranged to provide a sustained yield at the forest scale (Matthews 1989, Smith et al. 1997). As for other systems involving partial harvesting, irregular shelterwood has operational difficulties resulting from stand variability and complexity, and it may increase harvesting cost. However, greater individual stem volume, increased lumber yield, and product value may compensate for these higher costs (Ruel et al. 2007). The residual density should be managed to protect the residual canopy trees that may die as a result of the sudden exposure (Nyland 2002) or decrease in quality (e.g., epicormic branches in hardwoods; Godman and Books 1971, Erdmann and Peterson 1972, Trimble and Seegrist 1973). The residual density level must also be controlled to reduce the impact of shading on the development of the desired regeneration (Miller et al. 2006) and to avoid the proliferation of competitive species. There is also an increased risk of windthrow when the residual density is kept low, especially during the conversion of even-aged stands toward irregular ones (Malcolm et al. 2001). Low residual density exposes reserve trees to wind. This element is more important in the presence of species with restricted root systems, particularly on shallow soils and in

windy locations (Ruel 1995). The use of careful logging also plays a role in reducing damage to mature reserve trees and to younger trees during the initial and follow-up cuttings (Nyland 2002).

Moreover, the flexibility of irregular shelterwood may present some risks, because misapplication of the system may result in high grading. To avoid this, quality standards for tree marking and harvesting should be established. When choosing the reserve trees, it is necessary to consider tree vigour, quality for factory lumber, and mortality risk. It is important that the trees remain alive and hold or increase their value during the extended regeneration period (Nyland 2002). Protocols for retention of legacy trees and snags might also be required to address specific biodiversity issues.

## Conclusion

The recent shift in management objectives from timber production to the valorization of multiple forest resources provides opportunities for diversifying silvicultural interventions. Irregular stands were once an important component of our preindustrial landscape. The flexibility of applying the irregular shelterwood system, as illustrated by the three variants described in this article, establishes its potential for achieving ecosystem-based management objectives in several northeastern North American forest types. The irregular shelterwood system may be a valuable tool for maintaining or restoring irregular uneven-aged stands while diversifying silviculture in boreal, mixedwood, and northern hardwood forest zones. However, it is not a panacea and should be used wisely. With such a complex silvicultural system, it is important to define benchmarks to ensure that management objectives are achieved in practice. As with any adaptive management process, it will be essential to adjust practices as we gain more knowledge under North American conditions. The study of this system will require long-term process-based silvicultural research to take into account the complexity of these stands.

## Literature Cited

ANGERS, V.A., C. MESSIER, M. BEAUDET, AND A. LEDUC. 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands of Quebec. *For. Ecol. Manag.* 217:275–293.

APLET, G.H. 1994. Beyond even- vs. uneven-aged management: Toward a cohort-based silviculture. *J. Sustain. For.* 2:423–433.

BARRETTE, M., AND L. BELANGER. 2007. Reconstitution historique du paysage préindustriel de la région écologique des hautes collines du Bas-Saint-Maurice. *Can. J. For. Res.* 37:1147–1160.

BAUHUS, J., K. PUETTMANN, AND C. MESSIER. 2009. Silviculture for old-growth attributes. *For. Ecol. Manag.* 258:525–537.

BERGERON, Y., B. HARVEY, A. LEDUC, AND S. GAUTHIER. 1999. Forest management guidelines based on natural disturbance dynamics: Stand and forest-level considerations. *For. Chron.* 75:49–54.

BERGERON, Y., P. DRAPEAU, S. GAUTHIER, AND N. LECOMTE. 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. *For. Chron.* 83:326–337.

BOUCHARD, M., D.D. KNEESHAW, AND Y. BERGERON. 2006. Tree recruitment pulses and long-term species coexistence in mixed forests of western Québec. *Ecoscience* 13:82–88.

BOUCHARD, M., D.D. KNEESHAW, AND C. MESSIER. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. *Can. J. For. Res.* 37:763–772.

BOUCHARD, M., D. POTHIER, AND S. GAUTHIER. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Canada. *Can. J. For. Res.* 38:1621–1633.

BOUCHER, D., L. DE GRANDPRÉ, AND S. GAUTHIER. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. *For. Chron.* 79:318–328.

BOUCHER, Y., D. ARSENEAULT, L. SIROIS, AND L. BLAIS. 2009. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Lands. Ecol.* 24:171–184.

BOULIANE, P., AND J. DUBOIS. 2003. *Bilan des coupes progressives irrégulières réalisées à la Forêt Montmorency de 1986 à 2002 et établissement d'un dispositif permanent*. Univ. Laval, Dépt. of Sci. Bois Forêt, Québec, Canada. 48 p.

CANHAM, C.D., AND O.L. LOUCKS. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65:803–809.

CROW, T.R., AND F.T. METZGER. 1987. Regeneration under selection cutting. P. 81–94 in *Proc. of a Silvicultural symp. on Managing northern hardwoods*, Nyland, R.D. (ed.). Tech. Publ. 13 (ESF 87-002 and Soc. Am. For. Publ. 87-03), SUNY College of Environmental Science and Forestry, Syracuse, NY. 430 p.

CROW, T.R., D.S. BUCKLEY, E.A. NAUERTZ, AND J.C. ZASADA. 2002. Effects of management on the composition and structure of northern hardwood forests in Upper Michigan. *For. Sci.* 48:129–145.

DAINTITH, N.M., M.J. WATERHOUSE, AND H.M. ARMLEDER. 2005. Seedling response following partial cutting in lodgepole pine forests on caribou winter range in west-central British Columbia. *For. Chron.* 81:409–417.

DÉRY, S., AND M. LEBLANC. 2005. *Lignes directrices pour l'utilisation des pratiques sylvicoles adaptées dans le cadre de la mise en oeuvre de*

- l'objectif 4. Objectifs de mise en valeur des ressources du milieu forestier.* Gouv. Qué., Min. Ress. Nat. Faune, Dir. Env. For. 13 p.
- DESPOITS, M., A. DESROCHERS, L. BÉLANGER, AND J. HUOT. 2002. Structure de sapinières aménagées et anciennes du massif des Laurentides (Québec) et diversité des plantes vasculaires. *Can. J. For. Res.* 32:2077–2093.
- DUMAIS, D., AND M. PRÉVOST. 2007. Management for red spruce conservation in Québec: The importance of some physiological and ecological characteristics—A review. *For. Chron.* 83:378–392.
- ERDMANN, G.G., AND R.M. PETERSON. 1972. *Crown release increases diameter growth and bole sprouting of pole-size yellow birch.* US For. Serv. Res. Note NC-130. 4 p.
- FAJVAN, M.A., AND R.S. SEYMOUR. 1993. Canopy stratification, age structure, and development of multicohort stands of eastern white pine, eastern hemlock and red spruce. *Can. J. For. Res.* 23:1799–1809.
- FOURCHY, P. 1952. En Suisse, quelques aspects de la sylviculture contemporaine. *Rev. For. Fr.* 4:315–341.
- FRANKLIN, J.F., R.J. MITCHELL, AND B.J. PALIK. 2007. *Natural disturbance and stand development principles for ecological forestry.* US For. Serv. Gen. Tech. Rep. NRS-19. 44 p.
- FRAVER, S., AND A.S. WHITE. 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16:597–610.
- FRELICH, L.E., AND C.G. LORIMER. 1991. Natural disturbance regime in hemlock-hardwood forests of the upper Great Lakes region. *Ecol. Monogr.* 61:145–164.
- GALINDO-LEAL, C., AND F.L. BUNNELL. 1995. Ecosystem management: Implications and opportunities of a new paradigm. *For. Chron.* 71: 601–606.
- GAUTHIER, S., M.-A. VAILLANCOURT, A. LEDUC, L. DE GRANDPRÉ, D. KNEESHAW, H. MORIN, P. DRAPEAU, AND Y. BERGERON. 2008. *Aménagement écosystémique en forêt boréale.* Presses Univ. Québec, Québec, Canada. 568 p.
- GODMAN, R.M., AND D.J. BOOKS. 1971. *Influence of stand density on stem quality in pole-size northern hardwoods.* US For. Serv. Res. Pap. NC-54. 7 p.
- GROOT, A. 2002. Is uneven-aged silviculture applicable to peatland black spruce (*Picea mariana*) in Ontario, Canada. *Forestry* 75:437–442.
- GULDIN, J.M. 1996. The role of uneven-aged silviculture in the context of ecosystem management. *West. J. Appl. For.* 11:4–12.
- GUNN, J.S., AND J.M. HAGAN, III. 2000. Woodpecker abundance and tree use in uneven-aged managed, and unmanaged, forest in northern Maine. *For. Ecol. Manag.* 126:1–12.
- HANNAH, P.R. 1988. The shelterwood method in the Northeastern forest types: A literature review. *North. J. Appl. For.* 5:70–77.
- HANSEN, A., T.A. SPIES, F.J. SWANSON, AND J.L. OHMANN. 1991. Conserving biodiversity in managed forests. *Bioscience* 41: 382–392.
- HARPER, K.A., Y. BERGERON, S. GAUTHIER, AND P. DRAPEAU. 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: A landscape scale study. *Silva Fennica* 36:249–263.
- HELMS, J.A. 1998. *The dictionary of forestry.* Society of American Foresters, Bethesda, MD. 210 p.
- KAUFMANN, M.R., R.T. GRAHAM, D.A. BOYCE, JR., W.H. MOIR, L. PERRY, R.T. REYNOLDS, R.L. BASSETT, P. MEHLHOP, C.B. EDMINSTER, W.M. BLOCK, AND P.S. CORN. 1994. *An ecological basis for ecosystem management.* US For. Serv. Gen. Tech. Rep. RM-246. 22 p.
- KENEFIC, L.S., P.E. SENDAK, AND J.C. BRISSETTE. 2005. Comparison of fixed diameter-limit and selection cutting in northern conifers. *North. J. Appl. For.* 22:77–84.
- KOHM, K.A., AND J.F. FRANKLIN. 1997. *Creating a forestry for the 21st century: The science of ecosystem management.* Island Press, Washington, DC. 475 p.
- KNEESHAW, D.D., AND Y. BERGERON. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79:783–794.
- KNEESHAW, D.D., AND Y. BERGERON. 1999. Spatial and temporal patterns of seedling and sapling recruitment within canopy gaps caused by spruce budworm. *Ecoscience* 6:214–222.
- KNEESHAW, D.D., E. LAUZON, A. DE RÖMER, G. REYES, J. BELLE-ISLE, J. MESSIER, AND S. GAUTHIER. 2008. Appliquer les connaissances sur les régimes de perturbations naturelles pour développer une foresterie qui s'inspire de la nature dans le sud de la péninsule gaspésienne. P. 215–240 in *Aménagement écosystémique en forêt boréale*, Gauthier, S., M.-A. Vaillancourt, A. Leduc, L. DeGrandpré, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron (eds.). Presses Univ. Québec, Québec, Canada. 568 p.
- LANIER, L. 1994. *Précis de sylviculture*, 2nd Ed. École Nat. Génie Rural eaux Forêts (EN-GREF), Nancy, France. 477 p.
- LEAK, W.B. 1999. Species composition and structure of a northern hardwood stand after 61 years of group/patch selection. *North. J. Appl. For.* 16:151–153.
- LEAK, W.B., AND R. JR. WILSON. 1958. Regeneration after cutting of old-growth northern hardwoods in New Hampshire. US For. Serv. Northeast. For. Exp. Stn., Pap. no. 103. 8 p.
- LEAK, W.B., AND S.M. FILIP. 1977. Thirty-eight years of group selection in New England northern hardwoods. *J. For.* 75:641–643.
- LEAK, W.B., AND J.H. GOTTSACKER. 1985. New approaches to uneven-aged management in New England. *North. J. Appl. For.* 2:28–31.
- LEAK, W.B., D.S. SOLOMON, AND P.S. DEBALD. 1987. *Silvicultural guide for northern hardwood types in the Northeast (revised).* US For. Serv. Res. Pap. NE-603. 36 p.
- LEAK, W.B., AND P.E. SENDAK. 2002. Changes in species, grade, and structure over 48 years in a managed New England northern hardwood stand. *North. J. Appl. For.* 19:25–27.
- LEBLANC, M., AND L. BÉLANGER. 2000. *La sapinière vierge de la Forêt Montmorency et de sa région: Une forêt boréale distincte.* Gouv. Qué., Min. Ress. Nat., Dir. Rech. For., Mém. Rech. For. 136. 91 p.
- LORIMER, C.G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58:139–148.
- LORIMER, C.G., AND L.E. FRELICH. 1994. Natural disturbance regimes in old-growth northern hardwoods: Implications for restoration efforts. *J. For.* 92:33–38.
- LORIMER, C.G., AND A.S. WHITE. 2003. Scale and frequency of natural disturbances in the northeastern United States: Implications for early successional habitat and regional age distributions. *For. Ecol. Manag.* 185:41–64.
- MAJCNEN, Z., S. BÉDARD, AND S. MEUNIER. 2005. *Accroissement et mortalité quinze ans après la coupe de jardinage dans quatorze érablières du Québec méridional.* Gouv. Qué., Min. Ress. Nat. Faune, Dir. Rech. For., Mém. Rech. For. 148. 39 p.
- MALCOLM, D.C., W.L. MASON, AND G.C. CLARKE. 2001. The transformation of conifer forests in Britain—Regeneration, gap size and silvicultural systems. *For. Ecol. Manag.* 151:7–23.
- MATTHEWS, J.D. 1989. *Silvicultural systems.* Oxford University Press, New York, NY. 284 p.
- MCCARTHY, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Environ. Rev.* 9:1–59.
- MCCARTHY, J.W., AND G. WEETMAN. 2006. Age and size structure of gap-dynamic, old-growth boreal forest stands in Newfoundland. *Silva Fennica* 40:209–230.
- MCCOMB, W.C., T.A. SPIES, AND W.H. EMMINGHAM. 1993. Douglas-fir forests. Managing for timber and mature-forest habitat. *J. For.* 91:31–42.
- MILLER, G.W., AND T.M. SCHULER. 1995. Development and quality of reproduction in two-age central Appalachian hardwoods—10-year results. P. 364–374 in *10th Central hardwood forest conf.*, Gottschalk, K.W., and S.L.C. Fosbroke (eds.). US For. Serv., Northeast For. Exp. Stn., Morgantown, WV. GTR-NE-197.
- MILLER, G.W., J.E. JOHNSON, AND J.E. BAUMGRAS. 1997. Deferment cutting in central Appalachian hardwoods: An update. *For. Landowner* 68:28–31.
- MILLER, G.W., J.N. KOCHENDERFER, AND D.B. FEKEDULEGN. 2006. Influence of individual reserve trees on nearby reproduction in two-aged Appalachian hardwood stands. *For. Ecol. Manag.* 224:241–251.
- MITCHELL, S.J., AND W.J. BEESE. 2002. The retention system: Reconciling variable retention with the principles of silvicultural systems. *For. Chron.* 78:397–403.
- MOORES, A.R., R.S. SEYMOUR, AND L.S. KENEFIC. 2007. Height development of shade-tolerant conifer saplings in multi-aged Acadian forest stands. *Can. J. For. Res.* 37:2715–2723.
- MINISTÈRE DES RESSOURCES NATURELLES (MRN). 1994. *Une stratégie: Aménager pour mieux protéger les forêts.* Gouv. Qué., Min. Ress. Nat., Dir. Prog. For. 197 p.
- MINISTÈRE DES RESSOURCES NATURELLES ET DE LA FAUNE (MRNF). 2009. *Rapport d'activités 2007–2008 et Répertoire des projets de recherche 2008–2009.* Direction de la recherche forestière. Available online at [www.mrnf.gouv](http://www.mrnf.gouv).



- qc.ca/publications/enligne/forets/activites-recherche/projets/description.asp?numero=323; last accessed May 4, 2009.
- NEUENDORFF, J.K., L.M. NAGEL, C.R. WEBSTER, AND M.K. JANOWIAK. 2007. Stand structure and composition in a northern hardwood forest after 40 years of single-tree selection. *North. J. Appl. For.* 24:197–202.
- NYLAND, R.D. 2002. *Silviculture: Concept and applications*, 2nd Ed. McGraw-Hill, New York. 682 p.
- NYLAND, R.D., D.G. RAY, R.D. YANAI, R.D. BRIGGS, L. ZHANG, R.J. CYMBALA, AND M.J. TWERY. 2000. Early cohort development following even-aged reproduction method cuttings in New York northern hardwoods. *Can. J. For. Res.* 30:67–75.
- PRÉVOST, M. 2008. Effect of cutting intensity on microenvironmental conditions and regeneration dynamics in yellow birch-conifer stands. *Can. J. For. Res.* 38:317–330.
- PRÉVOST, M., V. ROY, AND P. RAYMOND. 2003. *Sylviculture et régénération des forêts mixtes du Québec (Canada): Une approche qui respecte la dynamique naturelle des peuplements*. Gouv. Qué., Min. Ress. Nat. Faune Parcs, Dir. Rech. For., Note rech. For. 125. 8 p.
- PUETTMANN, K.J., AND C. AMMER. 2007. Trends in North American and European regeneration research under the ecosystem management paradigm. *Eur. J. For. Res.* 126:1–9.
- PUETTMANN, K.J., K.D. COATES, AND C. MESSIER. 2008. *A critique of silviculture*. Island Press, Washington, DC. 188 p.
- RAY, D.G., R.D. NYLAND, AND R.D. YANAI. 1999. Patterns of cohort development following shelterwood cutting in three Adirondack northern hardwood stands. *For. Ecol. Manag.* 119:1–11.
- RAYMOND, P., J.-C. RUEL, AND M. PINEAU. 2000. Effet d'une coupe d'ensemencement et du milieu de germination sur la régénération des sapinières boréales riches de seconde venue du Québec. *For. Chron.* 76:643–652.
- ROBITAILLE, L., AND J.-L. BOIVIN. 1987. Résultats, après 10 ans, d'une coupe à diamètre minimum d'exploitation dans un peuplement feuillu. *For. Chron.* 63:15–19.
- ROY, V., N. THIFFAULT, AND R. JOBIDON. 2003. *Maîtrise intégrée de la végétation au Québec (Canada): Une alternative efficace aux phytocides chimiques*. Gouv. Qué., Min. Ress. Nat. Faune Parcs, Note rech. For. 123. 7 p.
- RUEL, J.-C. 1995. Understanding windthrow: Silvicultural implications. *For. Chron.* 71:434–445.
- RUEL, J.-C., V. ROY, J.-M. LUSSIER, D. POTHIER, P. MEEK, AND D. FORTIN. 2007. Mise au point d'une sylviculture adaptée à la forêt boréale irrégulière. *For. Chron.* 83:367–374.
- SAUNDERS, M.R., AND R.G. WAGNER. 2005. *Ten-year results of the Forest Ecosystem Research Program—Successes and challenges. Balancing ecosystem values: Innovating experiments for sustainable forestry*. US For. Serv. Gen. Tech. Rep. PNW-GTR-635, Portland, OR. 147–153.
- SCHÜTZ, J.-P. 2001. Opportunities and strategies of transforming regular forests to irregular forests. *For. Ecol. Manag.* 151:87–94.
- SCHÜTZ, J.-P. 2002. Silvicultural tools to develop irregular and diverse forest structures. *Forestry* 75:329–337.
- SEYMOUR, R.S. 1992. The red spruce-balsam fir forest of Maine: Evolution of silvicultural practice in response to stand development patterns and disturbances. P. 217–244 in *The ecology and silviculture of mixed-species forests. A festschrift for David M. Smith*, Kelty, M.J., B.C. Larson, and C.D. Oliver (eds.). Kluwer Publishers, Norwell, MA. 287 p.
- SEYMOUR, R.S. 1995. The Northeastern Region. P. 31–79 in *Regional silviculture of the United States*, 3rd Ed., J.W. Barrett (ed.). Wiley and Sons, New York. 643 p.
- SEYMOUR, R.S. 2005. Integrating disturbance parameters into conventional silvicultural systems: Experience from the Acadian forest of northeastern North America. P. 41–48 in *Balancing ecosystem values: Innovative experiments for sustainable forestry*, Peterson, C.E., and D.A. Maguire (eds.). US For. Serv. Gen. Tech. Rep. PNW-GTR-635. 389 p.
- SEYMOUR, R.S., AND M.L. HUNTER JR. 1999. Principles of ecological forestry. P. 22–61 in *Maintaining biodiversity in forest ecosystems*, Hunter, M.L. Jr. (ed.). Cambridge University Press, Cambridge, UK. 698 p.
- SEYMOUR, R.S., AND L.S. KENEFIC. 1998. Balance and sustainability in multiaged stands: A northern conifer case study. *J. For.* 96:12–17.
- SEYMOUR, R.S., A.S. WHITE, AND P.G. DEMAYNADIER. 2002. Natural disturbance regimes in northeastern North America—Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* 155:357–367.
- SILVY-LELIGOIS, P. 1953. La futaie par bouquets. *Rev. For. Fr.* 5:213–229.
- SMITH, D.M. 1986. *The practice of silviculture*, 8th Ed. John Wiley and Sons, New York. 527 p.
- SMITH, H.C., N.I. LAMSON, AND G.W. MILLER. 1989. An aesthetic alternative to clearcutting? Deferment cutting in eastern hardwoods. *J. For.* 37:14–18.
- SMITH, D.M., B.C. LARSEN, M.J. KELTY, AND P.M.S. ASHTON. 1997. *The practice of silviculture: Applied forest ecology*, 9th Ed. John Wiley and Sons, New York. 537 p.
- SPURR, S.H. 1956. German silvicultural systems. *For. Sci.* 2:75–80.
- STONE, I., J.-P. OUELLET, L. SIROIS, M.-J. ARSENEAU, AND M.-H. ST-LAURENT. 2008. Impacts of silvicultural treatments on arboreal lichen biomass in balsam fir stands on Québec's Gaspé Peninsula: Implications for a relict caribou herd. *For. Ecol. Manag.* 255:2733–2742.
- TRIMBLE, G.R., AND D.W. SEEGRIST. 1973. *Epicornic branching on hardwood trees bordering forest openings*. US For. Serv. Res. Pap. NE-261. 7 p.
- TUBBS, C.H., AND F.T. METZGER. 1969. Regeneration of northern hardwoods under shelterwood cutting. *For. Chron.* 45:333–337.
- WEBSTER, R., AND N.R. JENSEN. 2007. A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Can. J. For. Res.* 37:682–689.