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SURVIVAL AND GROWTH OF UNDER-PLANTED TREES: A META-ANALYSIS ACROSS FOUR BIOMES

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Abstract. The transformation of natural forest regeneration processes by human activities has created the need to develop and implement new models of forest management. Alternative silvicultural systems such as variable retention harvest, partial and patch cuts, and older forest management practices such as under-planting, are used in many forests around the world, particularly in North American oak stands, the boreal and coastal temperate rain forests of Canada and the United States, and in many degraded tropical regions of Asia and the Americas. Specific objectives are pursued in each of these biomes, but some are common to most regions, such as preservation of cover and structure and their associated benefits for natural or artificial regeneration due to moderation of the microclimate, development of optimal light and competition conditions, and reduced predation by herbivores. Shelterwoods are often presented as an alternative to clear-cutting to improve the survival of planted trees. A meta-analysis of published results with randomization tests was performed to test the relationship between overstory density and planted seedling growth and survival. Multiple comparisons were also used to reveal optimal levels of overstory density, if they exist. A majority of studies show that survival and growth improve as stand density decreases to an intermediate level, below which they either drop or stabilize. This level seems optimal in most conditions, as it is also more apt to fulfill other objectives imposed on today's forest activities, such as the conservation of forest processes and structures, and the reconstruction of degraded stands through the accelerated return of mid- to late-successional species.

Key words: alternative silvicultural systems; ANOVA-like multiple regressions; enrichment planting; forest regeneration; meta-analysis; overstory density; permutation test; seedling height growth; seedling survival; shelterwood; under-planting.

Introduction

The interruption or changes in forest regeneration processes induced by human activities is prevalent in many places around the world (Kozlowski 2002). Many stands show regeneration problems even several decades after harvesting or agricultural abandonment. These problems range from the simple lack of regeneration to a shift to species composition that is less desirable economically and ecologically. In response, we have seen during the last decades the emergence of ecosystem management and alternative techniques such as variable retention harvest, patch or partial cutting, and the recycling of older practices such as under-planting in shelterwoods, two-storied or mixed stands, and continuous cover forestry.

This new forestry is presented as a valuable alternative to forestry practices that have, in many places, not been able to fulfill their dual role of providing developing economies with a much-needed resource and ensuring adequate regeneration for a sustainable harvest (Rowe 1992, Greene et al. 2002, Mitchell et al. 2004). These silvicultural approaches are used in biomes as different as tropical or boreal forests, and deciduous or coastal temperate forests (Fig. 1). They share the common objective of the preservation of forest cover and structure and their associated benefits for natural or artificial regeneration. Silvicultural practices such as two-storied and uneven-aged stand structures are proposed to achieve structural objectives, as well as those of timber production and aesthetics (Brandeis et al. 2001). They are a response to situations where the natural recovery of forest composition is compromised or too slow and unpredictable to provide the forest products and services required by increasing population growth (Tappeiner et al. 1997, Kozlowski 2002).

Transformations of natural landscapes by human activities have profound implications for future resource management (Bouchard and Domon 1997, Kozlowski 2002), and current demands on the world's forests for social, environmental, and economic benefits require new approaches and rapid implementation of relevant results (Harrington 1999, Burley 2004). Forest plantations now have the potential to provide wood and non-woody products, as well as to promote the conservation of natural forests (Food and Agriculture Organization of the United Nations 2001).

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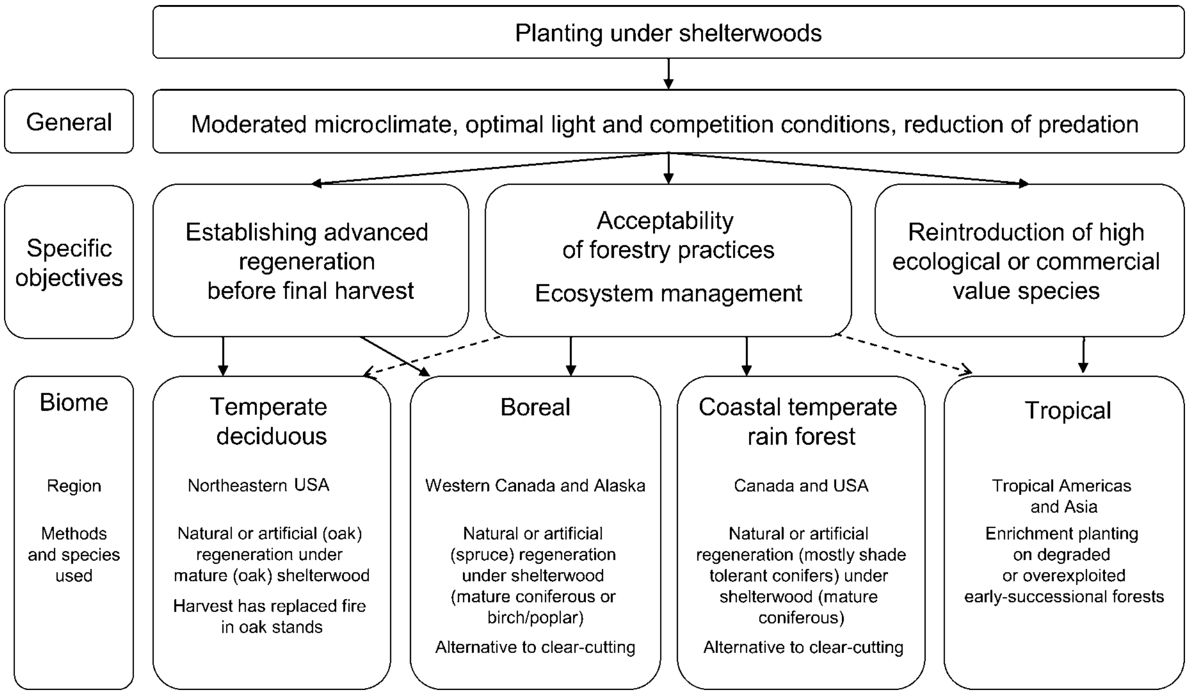

FIG. 1. Planting under shelterwoods: general and specific objectives for the different biomes covered in this paper.

Shelterwoods: common and specific objectives

Although "shelterwood" can refer to a specific silvicultural technique used particularly in northeastern U.S. oak forests (regeneration cut followed by overstory removal, see Johnson et al. [1986]), the term is also used to describe the residual forest cover under which natural or artificial regeneration is managed after a partial cut (Sauvageau 1995, Ashton and Peters 1999, Langvall and Orlander 2001); the latter is used in the present work. The alternative silvicultural systems share the common features of producing an environment, the shelterwood, that is favorable to tree regeneration (Fig. 1). Many subscribe to the general concepts of ecosystem management and continuous cover forestry, as a response to criticisms of forest overexploitation, monocultures, and clear-cuts in particular (Rowe 1992, Kenk and Guehne 2001, Rojo and Orois 2005). The methods associated with these concepts have the potential to achieve the objectives of sustainable development described in the Rio/Helsinki accords and of the certification of forest products (Pommerening and Murphy 2004), although these objectives of acceptability of forest practices are explicitly stated only in the boreal and coastal temperate forest literature (Fig. 1) (Lieffers et al. 1996, Barg and Edmonds 1999, Greene et al. 2002).

Shelterwoods are used in the boreal and American oak forests to establish regeneration before overstory removal by commercial harvesting (e.g., Brose et al. 1999, Spetich et al. 2002, Zaczek 2002). Regeneration of white spruce (*Picea glauca* [Moench] Voss) by the management of naturally occurring or planted seedlings following clear-cutting often proves difficult and expensive (Youngblood and Zasada 1991, Lieffers et al. 1996, Stewart et al. 2000), and is increasingly challenged in the boreal forest for aesthetic reasons, real or perceived environmental damage, and its variable efficiency at establishing the next cohort of conifers. Fire, naturally associated with the oak forests of northeastern America, is now controlled and has been replaced by the harvest of mature stands as the major perturbation (Lorimer et al. 1994, Buckley et al. 1998). Traditional, single-cut harvesting, however, has proven ineffective in ensuring adequate regeneration of oak stands, which are often replaced by less desirable species after harvesting. The proposed solutions involve a preparation cut to create a shelterwood under which natural or artificial regeneration can establish prior to the removal of the residual overstory (Fig. 1; Johnson 1984, Loftis 1990).

Enrichment planting can be used under a thinned overstory where the objective is the introduction of valuable species in degraded forests. It may be useful in areas where natural regeneration is insufficient, for reintroducing species that have disappeared following overexploitation, or to establish forest species that are inappropriate in open plantations. It may include planting of species of commercial or local value, using different approaches such as under, gap, or strip planting. Such is often the case with overexploited, early-successional, tropical forests of Asia and Central and South America, in stands no longer offering the possibility of a harvest in the mid-term, and where

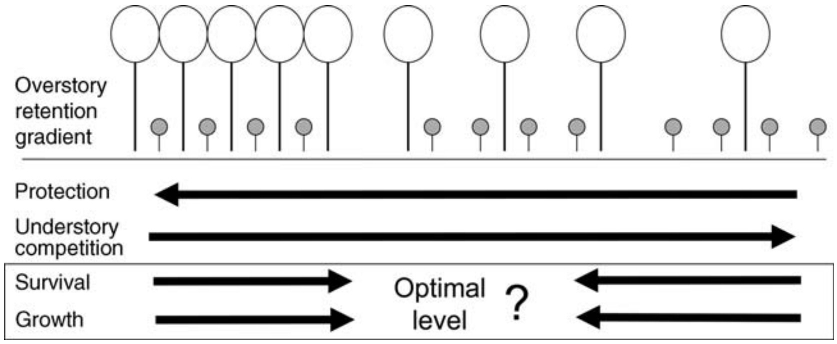

FIG. 2. Diagram model of the effect of overstory density on several factors, based on assumptions found in the literature. The residual density of the overstory decreases from left (unmanaged forest or dense shelterwood) to right (light shelterwood or clear-cut). The effect on the factors is shown by increasing or decreasing arrows.

ecological restoration is an objective (Fig. 1; Aide et al. 2000, Ashton et al. 2001, Martinez-Garza and Howe 2003). Rehabilitation of non-productive stands or former natural ecosystems using enrichment planting is also used in the southern United States for the restoration of bottomland hardwood forests (Gardiner et al. 2004), and in the eastern United States to restore the once important chestnut (*Castanea dentata* Marsh. [Borkh.]) (McCament and McCarthy 2005). It is also used for the conversion of even-aged plantation monocultures into mixed or two-storied stands and generally more complex systems (Truax et al. 2000, Kenk and Guehne 2001, Parker et al. 2001).

Under-planting is generally better accepted because it combines an artificial approach (planting) with the management of the existing natural stand (the shelterwood). It allows for the maintenance of a vegetation structure composed of different layers and complex assemblages of plants of various sizes and functions, and as a result retains a forest character (e.g., Lahde et al. 1999, Pommerening 2002, Drever and Lertzman 2003). Maintaining a forest structure may contribute to conserving biodiversity and ecosystem functions in managed stands (McComb et al. 1993, Hansen et al. 1995). Accelerated development of mature forest characteristics can be facilitated by moderate thinning or partial harvesting to favor the establishment of natural or artificial regeneration (McComb et al. 1993, DeBell et al. 1997).

Several advantages of a forested environment, such as a shelterwood, are stated in the literature for the developing natural or artificial regeneration and are schematized in Fig. 2 as a function of residual density. The forested environment, as opposed to a clear-cut or very thin density retention, would improve the survival of planted trees by protecting them from excessive evapotranspiration, wind and temperature extremes, and associated damage (e.g., Langvall and Lofvenius 2002, Agestam et al. 2003, Pommerening and Murphy 2004; Fig. 2). Predation, particularly by deer in temperate forests, could be reduced by the retention of cover (Buckley et al. 1998, Agestam et al. 2003). Competition by herbaceous plants and understory shrubs should also be reduced (e.g., Lieffers and Stadt 1994, Truax et al. 2000, Carnevalea and Montagnini 2002; Fig. 2), which would allow an effective establishment of the planted trees and their positive reaction to an eventual opening of the residual stand (Johnson 1984, Gordon et al. 1995, Buckley et al. 1998). Height growth and trunk shape should be improved by the preservation of a vertical structure (Schütz 2001, Pommerening and Murphy 2004). These alleged advantages of a shelterwood are not always documented by formal experimental testing in the literature, and when they are, results are not always conclusive.

The shelterwood method essentially seeks to create a compromise in the light environment, to reduce competition by decreasing available light, while still ensuring a sufficient quantity for tree regeneration establishment (Lieffers and Stadt 1994). A wide range of light conditions can be induced by a gradient of tree retention (Drever and Lertzman 2003), and will impact differently on several factors. While many studies discuss some or all of these issues, conservation and succession usually remain as concepts, and are not subjected to experimentation. Some studies do present data on protection (from extremes in temperature, frost, wind, etc.; e.g., Barg and Edmonds 1999, Man and Lieffers 1999, Langvall and Orlander 2001), and predation (e.g., Gordon et al. 1995, Buckley et al. 1998, Truax et al. 2000). The bulk of papers presenting results from field trials, however, are concerned with growth (mostly height growth) and survival of under-planted trees. Survival and growth are what practitioners are looking for from forest management, but they can also be used as indicators of the success of the shelterwood technique to protect the planted trees from climate extremes, predation, and understory competition, and to improve future stand composition and productivity.

Survival and growth as indicators of the success of the under-planting approach

Because of the potential for generalization from these two indicators and their relative accessibility in the literature, we chose published results of survival and height growth for the basis of this investigation of the success of the under-planting technique. The conservation of residual forest cover by thinning prior to under-planting has been suggested as a method of improving the survival of planted trees. It is often simply proposed as an alternative to clear-cuts, in which survival would be reduced, especially in boreal ecosystems (Man and Lieffers 1999, Langvall and Orlander 2001), but it is rarely discussed as a function of the whole range of residual densities (Fig. 2).

Annual increments that are below the potential of the species planted are often deemed satisfactory, as the emphasis is put on the successful establishment of planted trees and their capability, at the appropriate time, to respond positively to the opening created by the overstory removal or successive partial releases (Johnson 1984, Spetich et al. 2002). Nevertheless, researchers and forest practitioners tend to predict better growth under a managed partial overstory than in a clear-cut; best growth is predicted where an optimal compromise is reached between controlling competition and allowing enough resources (mostly light) to reach the planted trees (Lieffers and Stadt 1994, Buckley et al. 1998, Truax et al. 2000; Fig. 2). A considerable body of data from under-planting trials is available, but only rarely do any of the published studies cover the whole range of overstory densities, from a fully stocked unmanaged stand to zero residual overstory, that would be necessary to fully demonstrate the effect of the methods involved. This demonstration is facilitated by the use of already published data of survival and growth in a meta-analysis, a powerful tool which allowed us to bring together data from several studies conducted under a wide range of overstory densities, and to reveal patterns that are not obvious when single studies are examined (Goldberg et al. 1999, Gómez-Aparicio et al. 2004). By testing survival and growth of under-planted seedlings for five classes of overstory densities in four documented biomes, we used meta-analysis to answer the following questions: (1) Is there a significant relationship between overstory density and survival or growth of artificial regeneration?, and (2) If significant, can an optimal density of residual overstory be identified? If the partial retention of forest cover is found optimal, that would lend support to alternative forestry practices targeting the preservation of forest cover and structure.

Methods

A common basis for comparison was needed to complete the meta-analysis. Residual density levels, either applied or recommended, are often defined using basal area, canopy cover, line opening width (in the case of strip or line planting), or even stocking, a qualitative expression of the adequacy of tree cover on an area, in terms of crown closure, number of trees, basal area, or volume, in relation to a pre-established norm (Haddon 1988). This can make the interpretation and comparison of thinning prescriptions very difficult (Dey and Parker 1996). We constructed an overstory density index from canopy opening values, stocking values, the ratio of opening width to neighboring trees or original canopy height, or available light values, using the cases where two or more of these measurements were given (Kim et al. 1996, Buckley et al. 1998, Man and Lieffers 1999, Parker et al. 2001, Peña-Claros et al. 2002, Drever and Lertzman 2003, Maas-Hebner 2005). We also used our own data of light and canopy openness (Paquette et al., *in press*). Special care was used in cases for which measurements did not match, for example when light was measured some years after the silvicultural treatment was applied (e.g., Drever and Lertzman 2003), giving enough time for at least some vegetation layers to partly recover (Paquette et al., *in press*). We then combined these data to create the overstory density index presented in Table 1. This index allows for a classification of the literature according to results obtained in terms of survival and height growth in relation to overstory density (Table 2).

Five classes of overstory density were used in close association with the literature. We begin with trials conducted under uncut (UC), unmanaged closed canopies, often referred to as "control" treatments. This is followed by three contrasting levels of shelterwood densities for which trials were conducted in most biomes. These levels are arbitrary but they were chosen because they represented the range of conditions used in the literature while still offering as much contrast as possible. Studies presenting results for several levels mostly used contrasting levels that fell within those used here. We complete this index with trials conducted in clear-cuts (CC), which is also a point of comparison often used in under-planting literature.

We then reviewed all recent papers reporting growth or survival data for planted trees under shelterwoods around the globe. Data in sufficient numbers could be collected for only four biomes: the temperate deciduous forest of the northeastern United States, where mostly red oaks (*Quercus rubra* L.) are used; the boreal forest of western Canada and Alaska, using white spruce; the tropical Americas and Asia, using several species of economic or ecological value; and the coastal temperate rain forest of British Columbia, Canada, and Oregon, USA, using mostly the typical conifers of these forests (Table 2). We included results from peer-reviewed articles in which survival or growth could be calculated and overstory densities used were given or could be calculated. We found no evidence of paper bias according to journal quality, such as measured by an "impact factor" (i.e., *Journal Citation Reports*; Murtaugh 2002). After careful review, 24 papers presented usable data and were retained for the meta-analysis of survival and growth of under-planted trees according to the overstory density level used. Many of these studies presented results for several species, overstory densities,

TABLE 1. Overstory density index developed according to four descriptive variables used in the literature.

Overstory density	Available light (%)	Stocking (% of original basal area)	Canopy cover (%)	Opening width : canopy height
Uncut "control" (UC)	~0	100	~100	0
Dense shelterwood (Dsw)	<25	>60	>75	<0.25
Intermediate shelterwood (Isw)	25–50	40–60	50–75	0.25–0.40
Light shelterwood (Lsw)	>50	<40	<50	0.40–2
Clear-cut (CC)	~100	~0	~0	>2

or sites; a total of 191 entries of survival results and 165 entries for growth were recorded (Table 2).

Some measure of "effect size" is ordinarily used in meta-analysis where, for example, the absolute or relative difference between "control" and "treatment" are presented (Osenberg et al. 1999). We do not have a clear "treatment effect" here, but rather a range of overstory conditions under which trials were conducted, sometimes comparing results between levels, sometimes between one shelterwood and some "control," uncut forest, or, at the other end of the gradient, a clear-cut, or even simply reporting results for one shelterwood treatment. Raw data of growth and survival were therefore used to compare results between overstory density levels.

Published results varied in time span from plantation establishment, which could be a problem in meta-analysis (Goldberg et al. 1999, Osenberg et al. 1999). All efforts were made to recover initial heights and calculate yearly height increments using the following equation (for example, from histograms, when annual height increments were not published per se) so that experiments could be compared on a common basis:

$$\text{Annual height increment} = \frac{\text{Total height} - \text{Initial height}}{\text{Number of years}}. \quad (1)$$

The difference in time is more challenging for published results of survival, because mortality is often reported to be concentrated almost exclusively in the first year or first few years after plantation (Tworkoski et al. 1986, Cogliastro et al. 1990, 1993), which would tend to suggest the use of an overall mortality (at the end of the experiment). However, other studies reporting detailed survival data (per year or even month), especially in the tropical biome, present rather regular, continuous patterns of mortality for the duration of the study (Ramos and del Amo 1992), or reported annual rates directly (Peña-Claros et al. 2002), lending support to the use of a yearly survival rate. In Table 2, we report survival as a final rate at the end of the study, and the number of years during which the study was conducted. For the meta-analysis we used both forms of survival rates, which will be discussed further. The annual rate of survival is obtained from final rates from the following equation, which is easily reversed to obtain final rates from annual data:

$$\text{Annual survival rate} = \text{final survival rate}^{(1/\text{number of years})}. \quad (2)$$

As a general rule, one entry is made in Table 2 for each independent observation. For studies reporting results of multiple manipulations, experiments were considered independent observations if (1) they involved different species, or (2) different (independent) levels of overstory density, or (3) different sites were used (Englund et al. 1999). Replicates within the same site are not considered independent observations (an average is then used). Only results for planted trees are used; direct seeding or natural regeneration trials are excluded because their growth and survival cannot be compared with planted seedlings in the first years. When different planting stocks of the same species were used, an average was made. Treatments of fertilization and/or post-planting competition control using herbicides are excluded, but studies using herbicides for stand preparation before planting are included. Open field trials are not included since they are different from clear-cuts. However, some treatments not intended as clear-cuts, for example some "green tree retention" or "patch-cut" trials, were included in that category because they had almost no canopy cover left or openings that were greater than twice the height of the neighboring forest (Table 1). In the case of studies where the reduction of the stand density was incremental, we retained the most pertinent level, defined as the level at which planted trees made the greater part of their recorded growth. When animal browsing or other mechanical damage was measured and significant, only damage-free seedlings were retained here.

STATISTICAL ANALYSIS

Although a weighted analysis would have been preferable (weighing of each entry by the inverse of its sampling variance; Gurevitch and Hedges 1999), only some papers gave any measure of growth variance (including error bars on histograms). This is often the case in ecology, but should not preclude the use of meta-analysis given the importance of the body of literature (Goldberg et al. 1999, Gurevitch and Hedges 1999). Variances are almost never given for survival data since it is an absolute value, unless replications of treatments are used (with blocks for example). Unweighted randomization tests (Goldberg et al. 1999, Gurevitch and Hedges 1999) were therefore done on published

TABLE 2. Published results of under-planting trials for four different biomes; survival and growth increment are classified per overstory density used (according to Table 1).

Biome/source	No. overstory treatments	No. sites	No. years		Species planted
			Survival	Growth	
Temperate deciduous					
Johnson (1984)	3	1	5	5	*Quercus rubra*
Lorimer et al. (1994)	2	2	5	5	*Quercus rubra*
Gordon et al. (1995)	1	1	6	4	*Quercus rubra*
Dey and Parker (1997)	2	1	2	2	*Quercus rubra*
Tworkoski et al. (1986)	2‡	1	3§	3§	*Quercus rubra* *Quercus alba* *Pinus strobus*
Truax et al. (2000)	1	4‖	8	2¶	*Quercus rubra* *Quercus macrocarpa* *Fraxinus pennsylvanica* *Fraxinus americana*
Buckley et al. (1998)	4	2	2	1	*Quercus rubra*
Larrick et al. (2003)	3	1	4	4	*Quercus rubra*
Bardon et al. (1999)	1	2	5	5	*Quercus rubra*
Parker et al. (2001)	5	1	5	5	*Fraxinus americana* *Quercus rubra* *Pinus strobus*
Teclaw and Isebrands (1993)	3	1	3	3	*Quercus rubra*
Mean					*All*
Boreal					
Stewart et al. (2000)	4	1#	4	3	*Picea glauca*
Man and Lieffers (1999)	4	1	3	3	*Picea glauca*
Youngblood and Zasada (1991)	3	3	3	3, 5††	*Picea glauca*
Mean					*Picea glauca*
Tropical					
Montagnini et al. (1997)	1	4	4–7	4–7	*Cordia trichotoma* *Enterolobium contortisiliquum* *Bastardiopsis densiflora* *Ocotea puberula* *Euterpe edulis* *Peltophorum dubium* *Balfourodendron riedelianum* *Parapiptadenia rigida* *Nectandra lanceolata* *Didymopanax morototoni* *Jacaranda micrantha*
Peña-Claros et al. (2002)	5	1	4	4	*Bertholletia excelsa*
Ådjers et al. (1995)	4	1	2	2	*Shorea johorensis* *Shorea leprosula* *Shorea parvifolia*
Ramos and del Amo (1992)	3	1	6.7	6.2	*Cordia alliodora* *Swietenia macrophylla* *Brosimum alicastrum*
Ådjers et al. (1997)	2	1	3	3	*Durio zibethinus*
Ådjers et al. (1996)	1	1	3	3	*Shorea johorensis* *Shorea leprosula* *Shorea parvifolia* *Shorea faguetiana* *Shorea fallax* *Shorea polyandra* *Hopea sangal* *Dipterocarpus cornutus* *Dipterocarpus kunstleri* *Shorea ovalis*
Mean					*All*
Coastal temperate					
Helgerson (1990)	2	1	5	5	*Pseudotsuga menziesii*
Brandeis et al. (2001)	4	1	4	4	*Pseudotsuga menziesii* *Abies grandis* *Thuja plicata* *Tsuga heterophylla*

TABLE 2. Extended.

Survival (%)†					Annual height increment (cm)				
UC	Dsw	Isw	Lsw	CC	UC	Dsw	Isw	Lsw	CC
	84		84	84		6		13	18
26, 28	94, 93				0, 0	7, 3			
		83					9		
89		99			2		10		
90		89			2		17		
94		87			3		10		
100		97			29		43		
	98, 92, 85	25				28, 23, 18	20		
	100, 90, 90	87				23, 20, 15	43		
	95, 95, 45	97				13, 10, 1	35		
	97, 87, 65	68				13, 18, 1	33		
99, 99		100, 100	99, 99	98, 98	4, 5		4, 5	4, 4	10, 7
76		76		76	2		7		20
		73, 72					7, 5		
95	98,98,95,95	97			2	4, 8, 0, 1	9		
50	90, 72, 75, 80	85			1	5, 8, 4, 6	20		
77	87, 90, 90, 90	95			4	8, 11, 8, 11	16		
		98	95	95			10	13	10
77	*88*	*85*	*94*	*90*	*5*	*10*	*17*	*9*	*13*
96		98, 98,98			6		7, 5, 6		
78		92	91	87	5		10	10	8
			98, 98, 96	99, 98, 96				8, 8, 8	6, 8, 11
87		*97*	*96*	*95*	*6*		*7*	*9*	*8*
		70, 67, 95, 61					35, 30, 59, 39		
		80					86		
		63, 50, 95					149, 97, 66		
		47, 40, 75					47, 29, 34		
		27					37		
		30					59		
		47, 100					18, 29		
		40					17		
		63					64		
		35					19		
		94					27		
62	91, 95	89	95		13	63,69	108	111	
45		58	45, 35		22		59	60, 36	
70		85	75, 78		23		50	72, 58	
40		78	50, 53		21		60	70, 78	
	18	50	45			32	34	137	
	18	56	25			40	38	65	
	35	45	3			10	16	12	
			83	55				60	64
			56					127	
			67					114	
			48					89	
			55					54	
			67					51	
			24					64	
			78					84	
			6					28	
			38					34	
			41					63	
54	*51*	*63*	*51*	*55*	*20*	*43*	*50*	*70*	*64*
78	98				5	19			
	10	20, 37	37						
	50	70, 88	95						
	72	77, 94	95						
	12	40, 45	50						

TABLE 2. Continued.

Biome/source	No. overstory treatments	No. sites	No. years		Species planted
			Survival	Growth	
Maas-Hebner et al. (2005)	4	1‡‡	4, 8§§	8	*Tsuga heterophylla* *Picea sitchensis* *Pseudotsuga menziesii* *Abies grandis* *Thuja plicata* *Alnus rubra* *Acer macrophyllum*
Mitchell et al. (2004)	4	1	7	7	*Abies amabilis* *Tsuga heterophylla*
Mean					*All*

Note: Key to abbreviations: UC, uncut; Dsw, dense shelterwood; Isw, intermediate density shelterwood; Lsw; light density shelterwood; and CC, clear-cut.

† Most often reported survival (at the end of the study).

‡ A third treatment was available but could not be used here since the release was applied three years after the trees were planted (see *Methods*).

§ The trees were under-planted three years prior to treatment; only the three species listed are used.

|| Six sites were used, but two of them were old fields (not clear-cuts; see *Methods*).

¶ Trees were under-planted three years prior to treatment, and then a shelterwood was applied for two more years, after which the trees were completely released; only the years under shelterwood are used for growth (mortality occurred within the first years).

Six sites were used, but only means were published.

†† Results are given for third and fifth years; an average of these two results was used here.

‡‡ Three sites were used, but only means were published.

§§ Survival under the "no thin" treatment (UC) was given after four years (eight years are used elsewhere).

|| || Due to the high mortality of trees planted under the "no thin" treatment (UC), growth data were not presented.

¶¶ Severe browsing by elk prevented the authors from testing for a treatment effect on *Acer macrophyllum.*

results to test for a significant relationship between survival or growth and overstory density, within each biome. This is a simple one-way ANOVA problem that can be reformulated as a multiple regression analysis once the classification criterion is recoded with dummy variables (one dummy for each of the five classes of Table 1) (ter Braak and Looman 1987, Legendre and Legendre 1998). The ANOVA-like multiple regressions were computed with the R software (R Development Core Team 2005) using the "rda" and the "anova.cca/permutest.cca" functions of the "vegan" package (J. Oksanen, R. Kindt, P. Legendre, and R. B. O'Hara, *unpublished program* [forthcoming as version 1.7-91 of the vegan package available on the R-project web site]),[2] using 99 999 permutations (plus one for the original data) of the raw data (Anderson and Legendre 1999). This allowed for the computation of a pseudo-F statistic (the ratio of constrained to unconstrained inertia from a redundancy analysis) and corresponding probability with one degree of freedom for both the model and the residuals.

Within each biome, only those density classes with two or more entries were used for the analysis. More randomization tests were then computed where significant relationships were found to further test for differences between classes of overstory density. These a posteriori multiple comparisons were performed by recoding the datasets so as to contrast density levels (sum of contrast coefficients equals to zero). The computation is the same as the above multiple regressions, and is repeated for all possible pair-wise comparisons within a biome. A multiple comparisons table was then constructed using the appropriate Dunn-Sidak corrected alpha levels found with the following equation (Sidak 1967), where α is the global type I error (0.05) and c is the number of possible comparisons:

$$P_{\text{corrected}} = 1 - (1 - \alpha)^{1/c}. \quad (3)$$

Both the a posteriori approach for all possible comparisons and the Dunn-Sidak correction are considered conservative.

RESULTS AND DISCUSSION

Survival

Overall survival (at the end of the experiments) of under-planted trees did not show a significant relationship with overstory density levels in most biomes (except coastal temperate) (Table 3). This could be due to much variation in study durations (Table 2) that could preclude the use of this response variable for the analysis of otherwise comparable studies. Annual survival rates, on the other hand, are free from this variation and offer the possibility of comparing such results on a common basis (one year). Significant relationships are then detected for all biomes except the boreal forest (Table 3). Although differences seem small (in absolute values), the survival rates are annual, and mortality differences will compound over the years and could become

[2] ⟨http://cran.r-project.org⟩

TABLE 2. Continued. Extended.

Survival (%)†					Annual height increment (cm)				
UC	Dsw	Isw	Lsw	CC	UC	Dsw	Isw	Lsw	CC
5	94	94	94		‖ ‖	61	61	61	
0	90	90	90		‖ ‖	44	44	44	
0	87	87	87		‖ ‖	38	38	38	
0	94	94	94		‖ ‖	34	34	34	
35	90	90	90		‖ ‖	13	13	13	
0	94	94	94		‖ ‖	90	90	90	
1	64	64	64		‖ ‖	¶¶	¶¶	¶¶	
			82	90, 93, 94				10	15, 15, 14
			82	87, 92, 93				18	25, 26, 26
15	*71*	*72*	*81*	*92*	*5*	*43*	*47*	*39*	*20*

important, as is the case here. Within-group variances are also very small, and differences can be effectively detected (Table 3). In the temperate deciduous forest of northeastern America, survival seems constant throughout the range except in the deepest shade (uncut, or control trials) where it drops to 93%, but a trend is not easily identified because only two opposite levels of shelterwood (dense and light) give results significantly different than those from an uncut forest (UC; Fig. 3).

In tropical forests, the maximum annual survival of planted trees is reached with an intermediate shelterwood and it is significant (Fig. 3). The greatest increase in annual survival was found to be between the uncut forest and the dense overstory (Table 3). The gain is smaller from dense to intermediate densities, and drops under a light shelterwood or clear-cut (this last level was not included in the statistical analysis because only one observation was available; Table 2). Tropical survival data are more variable and show lower survival rates than in other biomes (Table 3), probably because of the greater number of species and poor knowledge of their light requirements (e.g., Ådjers et al. 1995, Davidson et al. 2002).

In this biome many authors presented results for several species, the survival rates of which were sometimes very different, even nil (in such cases that species was not retained for assembling Table 2). It is interesting to note that Montagnini et al. (1997) report results for 11 species, none of which could be found in an earlier review by Weaver (1987) of 160 species used in enrichment planting trials in tropical America alone (only three genera were common to both papers). In the present review, out of the 15 species reported for the tropical Americas (Table 2), only five are included in Weaver's review, three of which had previous success in enrichment planting (*C. alliodora, D. morototoni,* and *S. macrophylla*). All species used in Asia are *Dipterocarpaceae* with only one exception (*D. zibethinus,* Bombacaceae). Although Dipterocarps are a major source of prime wood in tropical Asia, little is known about their silviculture and light requirements which cover a wide range of shade tolerance (Ådjers et al. 1996, Tuomela et al. 1996).

A significant increase in survival (both overall and annual) is detected in the coastal temperate rain forest biome between the unmanaged forest and the dense shelterwood (Fig. 3). Survival then rises slowly all the way to the clear-cut but no significant differences could be detected between these classes, even after re-running the analysis without the entries for the uncut level (which could have masked other, smaller, differences between the remaining levels). The largest gain by far, and the only significant one, is again observed with only a small reduction in density (between an uncut forest and a dense shelterwood) already insuring adequate survival of under-planted trees (Fig. 3).

No overstory density effect on planted tree survival could be detected in the few papers available for boreal forests. Other results from direct seeding (Youngblood and Zasada 1991) and natural regeneration trials (Wurtz and Zasada 2001), found no effect of overstory density on survival. Scarification, on the other hand, which reduces understory competition, is generally recognized as an effective method of promoting the establishment and survival of naturally regenerated or direct seedings of spruce (Stewart et al. 2000). More research is needed, therefore, to identify optimal residual density for reducing understory competition and promoting seedling survival in that biome. Lieffers and Stadt (1994) successfully achieved understory competition reduction and optimal spruce growth with an intermediate shelterwood, but they counted on natural regeneration and did not provide survival results.

It could be argued that the overall survival reported in many studies mostly occurred in the early years of establishment and could be artificially reduced with the use of annual data in the case of studies that were run over several years. This could be a serious problem if studies largely different in time span were reported under different overstory levels (short studies at one end of the range and longer ones at the other end, for example). This is not the case here, and several studies present results over two or more overstory levels (with the same duration; Table 2). Also it seems that contrary to survival in traditional open field plantations, mortality under a partial overstory occurs over a longer time

TABLE 3. Means (and SE) of survival rates and annual height increment for different overstory densities in four documented biomes and meta-analysis statistical results.

Biome/overstory density	Overall survival (%)	Annual survival† (%)	Annual increment (cm)
Temperate deciduous			
Uncut	77 (7.9)	93 (2.4)	5 (2.3)
Dense	88 (2.3)	98 (0.42)	10 (1.5)
Intermediate	85 (4.3)	97 (0.92)	17 (3.1)
Light	94 (3.5)	98 (0.48)	9 (5.2)
Clear-cut	90 (4.4)	97 (1.1)	13 (2.5)
Results	$N = 66$; $P = 0.2901$	$N = 66$; $P = 0.0368$	$N = 66$; $P = 0.0169$
Boreal			
Uncut	87 (9.0)	96 (3.5)	6 (0.7)
Dense			
Intermediate	97 (1.5)	99 (0.50)	7 (1.1)
Light	96 (1.7)	99 (0.50)	9 (0.5)
Clear-cut	95 (2.7)	98 (1.1)	8 (1.0)
Results	$N = 14$; $P = 0.2303$	$N = 14$; $P = 0.4210$	$N = 14$; $P = 0.2390$
Tropical			
Uncut	54 (7.1)	75 (6.0)	20 (2.3)
Dense	51 (17)	87 (4.6)	43 (10.7)
Intermediate	63 (4.3)	91 (1.2)	50 (6.2)
Light	51 (5.3)	77 (3.1)	70 (7.0)
Clear-cut	*55*	*82*	*64*
Results	$N = 56$; $P = 0.3515$	$N = 56$; $P = 0.0012$	$N = 56$; $P = 0.0146$
Coastal temperate			
Uncut	15 (10)	31 (14)	*5*
Dense	71 (9.1)	90 (4.6)	43 (9.9)
Intermediate	72 (6.5)	92 (2.6)	47 (11)
Light	81 (5.2)	96 (1.9)	39 (16)
Clear-cut	92 (1.1)	99 (0.17)	20 (2.5)
Results	$N = 54$; $P < 0.0001$	$N = 54$; $P < 0.0001$	$N = 27$; $P = 0.2397$

Notes: Analysis results are based on 99 999 permutations (plus original data). N = number of entries used for statistical analysis; only those overstory densities, within a biome, with two or more entries are used (values in italics are excluded).
† See *Methods* for survival equations.

period, many studies still reporting significant losses after more than five years, which would support the use of annual survival rates.

Survival of planted trees generally increases with decreasing stand density, but this is significant only between the uncut control trials and any level of shelterwood, after which no gain is observed. Reduced survival with further thinning of the overstory is only observed in the tropical biome. However, several studies have measured less favorable microclimates in clear-cuts under many forest types (Man and Lieffers 1999, Langvall and Orlander 2001, Langvall and Lofvenius 2002). Only Ramos and del Amo (1992) and Buckley et al. (1998) have succeeded in showing a decrease in survival (accompanied by an increased growth of the surviving trees) with a major reduction of the stand's density. Agestam et al. (2003), studying beech seedlings (*Fagus sylvatica* L.), have measured greater damage to plants after a clear-cut, particularly by frost, but also better growth. Explanations considered for this phenomenon mostly concern climate, the extreme effects of which would be moderated by a shelterwood, even when sparse (Barg and Edmonds 1999, Man and Lieffers 1999, Langvall and Lofvenius 2002, Agestam et al. 2003, Pommerening and Murphy 2004).

Growth

There is a definite progression and significant relationship of annual height increments with decreasing stand density in the deciduous and tropical biomes for the first levels of density (Table 3). As with survival, the greatest absolute gains in growth are observed with only a small thinning to the dense level. The a posteriori tests performed on the temperate deciduous biome results, although conservative and already showing significant differences (Fig. 3), may not be very relevant because the somewhat predictable results from the uncut trials could mask the more important differences between thinning densities. We tested that by contrasting the intermediate shelterwood, which demonstrated maximum growth, against the dense and light shelterwoods and the clear-cut together, with a significant result ($P = 0.0124$). Growth is at a maximum in the temperate deciduous forest under intermediate shelterwoods and is significantly reduced with further thinning of the stand. Most studies report results for red oak, which is moderately shade tolerant (Sander 1990) and intolerant of understory competition as demonstrated by Smidt and Puettmann (1998). The intermediate level of overstory density, where maximum growth is observed, offers a good compromise and corresponds to the model of Buckley et al. (1998), where optimal growth should be

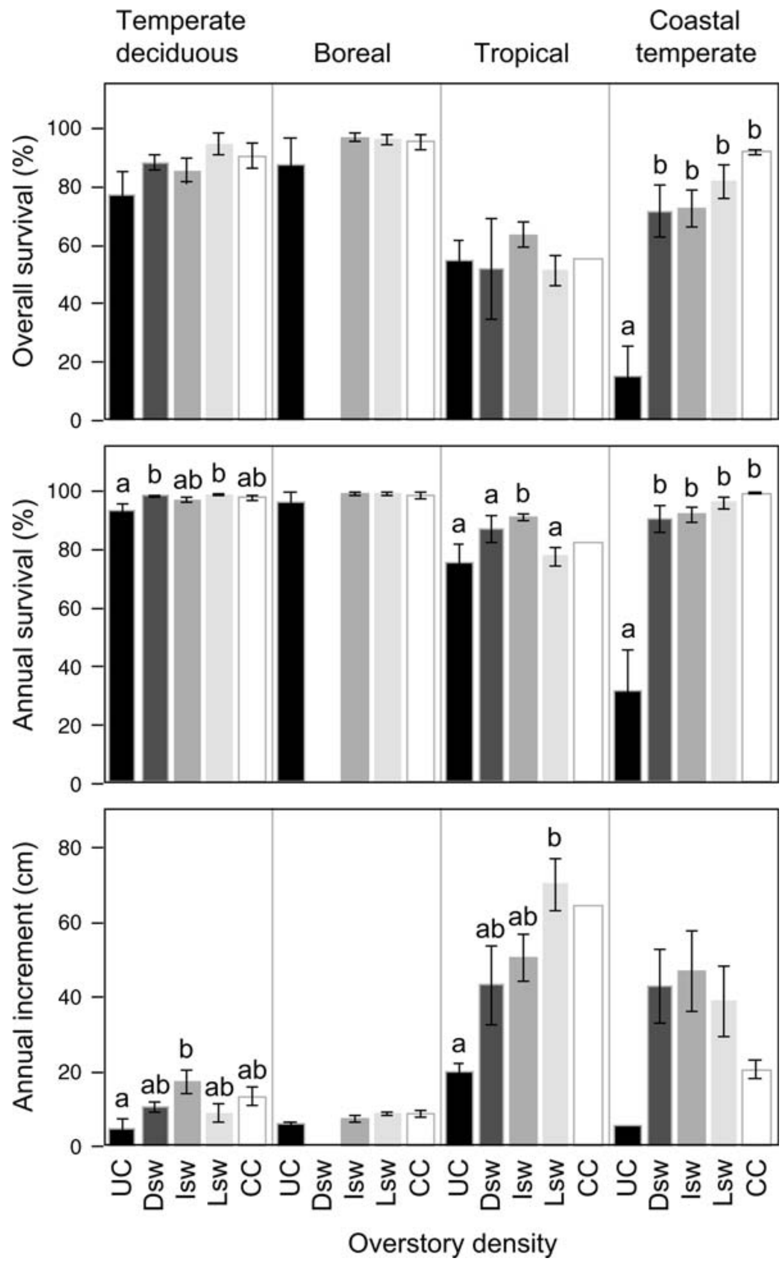

FIG. 3. Survival rates and annual height increment (mean ± SE) for each overstory density within four documented biomes. Key to abbreviations: UC, uncut; Dsw, dense shelterwood; Isw, intermediate density shelterwood; Lsw; light density shelterwood; and CC, clear-cut. Results of multiple comparison analyses are given (means not sharing the same letter are different) for a global type I error of 0.05 (critical Dunn-Sidak corrected values are 0.0051 and 0.0085 for comparisons of five or four levels, respectively). Multiple comparison tests were computed only on significant relationships (Table 3); all classes are otherwise considered equal.

obtained at an intermediate level of overstory density. The growth values reported for the deciduous forest are not very high, however, and are below the minimum levels suggested by Johnson (1984) for ensuring the establishment of red oak in shelterwoods. It could be that height growth is decreased but diameter growth increased in lower density stands and clear-cuts, which is actually one of the alleged benefits of under-planting. Better height growth for red oak is often reported in open fields on former farm land when weed control (chemical, mechanical, or physical barrier) is applied (Cogliastro et al. 1990, 2003, Lambert et al. 1994), but a comparison with a clear-cut is inappropriate and these results were not included here.

In the tropical biome, the maximum growth is reached with light shelterwoods (Fig. 3; only one entry was made under the clear-cut category and it was not included in the analysis). The height increments are higher, as expected, but results are again highly variable (Table 2), probably for the same reasons as for survival (a great number of species used and poor knowledge of their ecology). In the tropical biome, growth does increase with decreasing stand density, but the greatest gains are acquired with only a small thinning from uncut, control forests (20 cm) to a dense shelterwood (40 cm; Table 3). Ådjers et al. (1995) do not report any additional gain in growth when cut strips exceed two meters in width in a three meter high young tropical stand. Although some efforts are being made to better understand the species requirements for tropical reforestation purposes (see Davidson et al. 2002), this knowledge is incomplete. Weaver (1987) found that only about 15% of the 160 species reviewed for enrichment planting purposes had any success.

In the boreal biome, no significant relationship could be detected between growth and density, but the maximum absolute height growth is reached with a light shelterwood (Table 3). Reported growth of planted white spruce is generally small, as is expected from this biome. Partial cuts are often proposed as alternatives to clear-cuts in the boreal forest to control understory competition and maintain mixed species composition to mimic natural stand dynamics (Lieffers and Stadt 1994, Greene et al. 2002). According to Lieffers and Stadt (1994), acceptable leader growth of 9–25 cm for mid-tolerant white spruce can be obtained at light levels between 15% and 40% transmission, and no differences in height growth are noted between seedlings growing at 40% and those in open, clear-cut sites.

Four levels of density had sufficient data for the analysis in the coastal temperate biome, but no density effect could be detected (Table 3). The decrease in height growth in clear-cuts is not significant, and all results from that level came from a single study (Mitchell et al. 2004) in which the light shelterwood treatment actually produced lower growth than in the other more open treatments presented, including a clear-cut. Only one study reported results under an unmanaged overstory (it was not included in the analysis); at 5 cm of annual height growth, it is very much lower than the average. Because most or all trees died under the control (uncut) treatment in the study by Maas-Hebner et al. (2005), height growth of the few survivors was not reported and could not be used here, though it was probably very low and would have confirmed the trend we observed, which is a highly probable, significantly reduced growth under uncut stands. Brandeis et al (2001) reported growth increments in volume, and these data could not be included in the statistical analysis either, but they showed a gradual increase for all four species with the thinning of the stand (from dense to light shelterwoods).

As with other biomes, the greatest gains in growth were obtained at relatively dense levels of overstory. All conifer species used in this biome are considered shade tolerant or even very tolerant (except *P. menziesii*, sometimes described as intermediate). But several studies on natural regeneration found that these species generally grew best under full or nearly full light (reviewed in Brandeis et al. 2001). Few data are available for planted seedlings, although they are used in great numbers, and the few results reviewed here do not concur with natural regeneration trials, as both growth and survival were not improved significantly with further decreases in the stand density past a dense shelterwood. This points to a probable "planting shock" experienced by conifer seedlings in clear-cuts due to increased understory competition, unfavorable micro-climate, and the newly planted seedling's inability to compete in the year or years immediately following plantation (Man and Lieffers 1999, Maundrell and Hawkins 2004). Although naturally regenerated conifers can perform well in clear-cuts and under other light density management such as patch cut or green tree retention, some partial shade is needed to protect the planted seedlings initially and allow them to get established before the final cut or additional reductions of the residual overstory.

Conclusion

Under-planting activities have proven to be effective methods of artificial regeneration in many forested habitats around the globe. In temperate deciduous forests, tropical forests, and coastal temperate rain forests, increased survival of under-planted trees is ensured by only a moderate thinning of the stand to a dense or intermediate density. Survival is stable or improves slightly with further decreases in overstory density, except in the tropical biome, the only one where a significant decrease in survival rate is observed at lighter densities, pointing to an optimum intermediate level. Growth follows a similar pattern in most biomes, with a sharp increase with only a moderate thinning to a dense shelterwood. Growth keeps improving slightly with further thinning of the stand to a light shelterwood in tropical forests. The growth of under-planted trees is significantly reduced in the temperate deciduous biome under shelterwoods thinned beyond an intermediate density, pointing again to an intermediate density for this biome.

In general, the greatest gains in survival and growth are achieved before or at an intermediate level of shelterwood and stabilize or decrease under thinner stands. Under thinner shelterwoods and clear-cuts, protection from climatic stresses such as frost and wind, as well as from predation, is diminished, while under-growth competition is higher. An intermediate level of overstory density seems to be a good compromise in most cases, where resources and protection are balanced. Forest managers should note that any level of shelterwood is temporary, and light levels will decline as the stand recovers. This will occur at varying rates, fastest in tropical biomes and slowest in boreal biomes. In most cases, regular maintenance is strongly suggested, at intervals that vary according to biome and species under-planted. The keys to sustained growth are an optimal intensity of the initial thinning to ensure successful establishment, and the correct timing of the subsequent interventions.

In the biomes surveyed, light shelterwoods and clear-cuts present no definite advantages in growth or survival over denser conditions, which are often better accepted and apt to fulfill the other objectives now imposed on forest management, such as the conservation of structure and processes in a forested landscape. Our analysis suggests an optimal thinning density for the growth and survival of under-planted seedlings. However, further research is needed to demonstrate whether sustainable management objectives can also be achieved through thinning and under-planting.

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Literature Cited

Ådjers, G., S. Hadengganan, J. Kuusipalo, K. Nuryanto, and L. Vesa. 1995. Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction and maintenance method of planting line on selected *Shorea* species. Forest Ecology and Management **73**:259–270.

Ådjers, G., J. Kuusipalo, S. Hadengganan, K. Nuryanto, and L. Vesa. 1996. Performance of ten dipterocarp species in restocking logged-over forest areas subjected to shifting cultivation. Journal of Tropical Forest Science **9**:151–160.

Ådjers, G., J. Kuusipalo, S. Nduka, and A. Otsamo. 1997. Planting *Durio zibethinus* in abandoned shifting cultivation areas: results three years after planting. Journal of Tropical Forest Science **9**:315–320.

Agestam, E., P. M. Ekö, U. Nilsson, and N. T. Welander. 2003. The effects of shelterwood density and site preparation on natural regeneration of *Fagus sylvatica* in southern Sweden. Forest Ecology and Management **176**:61–73.

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology **8**:328–338.

Anderson, M. J., and P. Legendre. 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. Journal of Statistical Computation and Simulation **62**:271–303.

Ashton, M. S., C. V. S. Gunatilleke, B. M. P. Singhakumara, and I. A. U. N. Gunatilleke. 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. Forest Ecology and Management **154**:409–430.

Ashton, M. S., and C. M. Peters. 1999. Even-aged silviculture in tropical rainforests of Asia: lessons learned and myths perpetuated. Journal of Forestry **97**:14–19.

Bardon, R. E., D. W. Countryman, and R. B. Hall. 1999. Tree shelters reduced growth and survival of underplanted red oak seedlings in southern Iowa. Northern Journal of Applied Forestry **16**:103–107.

Barg, A. K., and R. L. Edmonds. 1999. Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. Canadian Journal of Forest Research **29**:705–713.

Bouchard, A., and G. Domon. 1997. The transformations of the natural landscapes of the Haut-Saint-Laurent (Québec) and their implications on future resource management. Landscape and Urban Planning **37**:99–107.

Brandeis, T. J., M. Newton, and E. C. Cole. 2001. Underplanted conifer seedling survival and growth in thinned Douglas-fir stands. Canadian Journal of Forest Research **31**:302–312.

Brose, P., D. Van Lear, and R. Cooper. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. Forest Ecology and Management **113**:125–141.

Buckley, D. S., T. L. Sharik, and J. G. Isebrands. 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. Ecology **79**:65–78.

Burley, J. 2004. The restoration of research. Forest Ecology and Management **201**:83–88.

Carnevalea, N. J., and F. Montagnini. 2002. Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. Forest Ecology and Management **163**:217–227.

Cogliastro, A., D. Gagnon, and A. Bouchard. 1993. Effet des sites et des traitements sylvicoles sur la croissance, l'allocation en biomasse et l'utilisation de l'azote de semis de quatre espèces feuillues en plantation dans le sud-ouest du Québec. Canadian Journal of Forest Research **23**:199–209.

Cogliastro, A., D. Gagnon, D. Coderre, and P. Bhéreur. 1990. Response of seven hardwood tree species to herbicide, rototilling, and legume cover at two southern Quebec plantation sites. Canadian Journal of Forest Research **20**:1172–1182.

Cogliastro, A., D. Gagnon, S. Daigle, and A. Bouchard. 2003. Improving hardwood afforestation success: an analysis of the effects of soil properties in southwestern Quebec. Forest Ecology and Management **177**:347–359.

Davidson, R., Y. Mauffette, and D. Gagnon. 2002. Light requirements of seedlings: a method for selecting tropical trees for plantation forestry. Basic and Applied Ecology **3**:209–220.

DeBell, D. S., R. O. Curtis, C. A. Harrington, and J. C. Tappeiner. 1997. Shaping stand development through silvicultural practices. Pages 141–149 *in* K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C., USA.

Dey, D. C., and W. C. Parker. 1996. Regeneration of red oak (*Quercus rubra* L.) using shelterwood systems: ecophysiology, silviculture and management recommendations. Forest research information paper #126. Ontario Forest Research Institute, Sault-Sainte-Marie, Ontario, Canada.

Dey, D. C., and W. C. Parker. 1997. Overstory density affects field performance of underplanted red oak (*Quercus rubra* L.) in Ontario. Northern Journal of Applied Forestry **14**:120–125.

Drever, C. R., and K. P. Lertzman. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research **33**:137–146.

Englund, G., O. Sarnelle, and S. D. Cooper. 1999. The importance of data-selection criteria: meta-analyses of stream predation experiments. Ecology **80**:1132–1141.

Food and Agriculture Organization of the United Nations. 2001. Global forest resources assessment 2000: main report. FAO forestry paper 140. Food and Agriculture Organization of the United Nations, Rome, Italy.

Gardiner, E. S., J. A. Stanturf, and C. J. Schweitzer. 2004. An afforestation system for restoring bottomland hardwood forests: Biomass accumulation of Nuttall oak seedlings interplanted beneath eastern cottonwood. Restoration Ecology **12**:525–532.

Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. Ecology **80**:1118–1131.

Gómez-Aparicio, L., R. Zamora, J. M. Gómez, J. A. Hódar, J. Castro, and E. Barazaa. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications **14**:1128–1138.

Gordon, A. M., J. A. Simpson, and P. A. Williams. 1995. Six-year response of red oak seedlings planted under a shelterwood in central Ontario. Canadian Journal of Forest Research **25**:603–613.

Greene, D. F., D. D. Kneeshaw, C. Messier, V. Lieffers, D. Cormier, R. Doucet, K. D. Coates, A. Groot, G. Grover, and C. Calogeropoulos. 2002. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). Forestry Chronicle **78**:281–295.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142–1149.

Haddon, B. D., editor. 1988. Forest inventory terms in Canada. Third edition. Canadian Forest Inventory Committee, Forestry Canada, Ottawa, Canada.

Hansen, A. J., W. C. McComb, R. Vega, M. G. Raphael, and M. Hunter. 1995. Bird habitat relationships in natural and managed forests in the west Cascades of Oregon. Ecological Applications **5**:555–569.

Harrington, C. A. 1999. Forests planted for ecosystem restoration or conservation. New Forests **17**:175–190.

Helgerson, O. T. 1990. Response of underplanted Douglas-fir to herbicide injection of sclerophyll hardwoods in Southwest Oregon. Western Journal of Applied Forestry **5**:86–89.

Johnson, P. S. 1984. Responses of planted northern red oak to three overstory treatments. Canadian Journal of Forest Research **14**:536–542.

Johnson, P. S., C. D. Dale, and K. R. Davidson. 1986. Planting northern red oak in the Missouri Ozarks: a prescription. Northern Journal of Applied Forestry **3**:66–68.

Kenk, G., and S. Guehne. 2001. Management of transformation in central Europe. Forest Ecology and Management **151**:107–119.

Kim, C., T. L. Sharik, M. F. Jurgensen, R. E. Dickson, and D. S. Buckley. 1996. Effects of nitrogen availability on northern red oak seedling growth in oak and pine stands in northern lower Michigan. Canadian Journal of Forest Research **26**: 1103–1111.

Kozlowski, T. T. 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. Canadian Journal of Forest Research **158**:195–221.

Lahde, E., O. Laiho, and Y. Norokorpi. 1999. Diversity-oriented silviculture in the Boreal Zone of Europe. Forest Ecology and Management **118**:223–243.

Lambert, F., B. Truax, D. Gagnon, and N. Chevrier. 1994. Growth and N nutrition, monitored by enzyme assays, in a hardwood plantation: effects of mulching materials and glyphosate application. Forest Ecology and Management **70**: 231–244.

Langvall, O., and M. O. Lofvenius. 2002. Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. Forest Ecology and Management **168**:149–161.

Langvall, O., and G. Orlander. 2001. Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Canadian Journal of Forest Research **31**:155–164.

Larrick, D. S., T. W. Bowersox, G. L. Storm, and W. M. Tzilkowski. 2003. Artificial oak regeneration in historic woodlots at Gettysburg national military park. Northern Journal of Applied Forestry **20**:131–136.

Legendre, L., and P. Legendre. 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam, The Netherlands.

Lieffers, V. J., R. B. Macmillan, D. MacPherson, K. Branter, and J. D. Stewart. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. Forestry Chronicle **72**:286–292.

Lieffers, V. J., and K. J. Stadt. 1994. Growth of understorey *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light. Canadian Journal of Forest Research **24**:1193–1198.

Loftis, D. L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. Forest Science **36**:917–929.

Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology **82**: 227–237.

Maas-Hebner, K. G., W. H. Emmingham, D. J. Larson, and S. S. Chan. 2005. Establishment and growth of native hardwood and conifer seedlings underplanted in thinned Douglas-fir stands. Forest Ecology and Management **208**:331–345.

Man, R., and V. Lieffers. 1999. Effects of shelterwood and site preparation on microclimate and establishment of white spruce seedlings in a boreal mixedwood forest. Forestry Chronicle **75**:837–844.

Martinez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology **40**:423–429.

Maundrell, C., and C. Hawkins. 2004. Use of an aspen overstory to control understory herbaceous species, bluejoint grass (*Calamagrostis canadensis*), and fireweed (*Epilobium angustifolium*). Northern Journal of Applied Forestry **21**:74–79.

McCament, C. L., and B. C. McCarthy. 2005. Two-year response of American chestnut (*Castanea dentata*) seedlings to shelterwood harvesting and fire in a mixed-oak forest ecosystem. Canadian Journal of Forest Research **35**:740–749.

McComb, W., T. Spies, and W. Emmingham. 1993. Douglas-fir forests: managing for timber and wildlife habitats. Journal of Forestry **91**:31–42.

Mitchell, A. K., B. G. Dunsworth, J. T. Arnott, R. Koppenaal, R. Benton, G. Goodmanson, T. Bown, and J. Sandford. 2004. Growth limitation of planted conifers regenerating under montane alternative silviculture systems (MASS): seven-year results. Forestry Chronicle **80**:241–250.

Montagnini, F., B. Eibl, L. Grance, D. Maiocco, and D. Nozzi. 1997. Enrichment planting in overexploited subtropical forests of the Paranaense region of Misiones, Argentina. Forest Ecology and Management **99**:237–246.

Murtaugh, P. A. 2002. Journal quality, effect size, and publication bias in meta-analysis. Ecology **83**:1162–1166.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: Goals, metrics, and models. Ecology **80**:1105–1117.

Paquette, A., A. Bouchard, and A. Cogliastro. 2006. Successful under-planting of red oak and black cherry in early-successional deciduous shelter woods of North America. Annals of Forest Science, *in press*.

Parker, W. C., K. A. Elliott, D. C. Dey, E. Boysen, and S. G. Newmaster. 2001. Managing succession in conifer plantations: converting young red pine (*Pinus resinosa* Ait.) plantations to native forest types by thinning and underplanting. Forestry Chronicle **77**:721–734.

Peña-Claros, M., R. G. A. Boot, J. Dorado-Lora, and A. Zonta. 2002. Enrichment planting of *Bertholletia excelsa* in secondary forest in the Bolivian Amazon: effect of cutting line width on survival, growth and crown traits. Forest Ecology and Management **161**:159–168.

Pommerening, A. 2002. Approaches to quantifying forest structures. Forestry **75**:305–324.

Pommerening, A., and S. T. Murphy. 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry **77**:27–44.

R Development Core Team. 2005. R: a language and environment for statistical computing, version 2.2.0. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, J. M., and S. del Amo. 1992. Enrichment planting in a tropical secondary forest in Veracruz, Mexico. Forest Ecology and Management **54**:289–304.

Rojo, J. M. T., and S. S. Orois. 2005. A decision support system for optimizing the conversion of rotation forest stands to continuous cover forest stands. Forest Ecology and Management **207**:109–120.

Rowe, J. S. 1992. The ecosystem approach to forested land management. Forestry Chronicle **68**:222–224.

Sander, I. L. 1990. Red oak (*Quercus rubra* L.). Pages 727–733 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Volume 2: hardwoods. USDA Forest Service, Washington, D.C., USA.

Sauvageau, F. 1995. Silvicultural terms in Canada. Second (revised) edition. Canadian Forest Service, Natural Resources Canada, Ottawa, Ontario, Canada.

Schütz, J.-P. 2001. Opportunities and strategies of transforming regular forests to irregular forests. Forest Ecology and Management **151**:87–94.

Sidak, Z. 1967. Rectangular confidence regions for the means of multivariate normal distributions. Journal of the American Statistical Association **62**:626–633.

Smidt, M. F., and K. J. Puettmann. 1998. Overstory and understory competition affect underplanted eastern white pine. Forest Ecology and Management **105**:137–150.

Spetich, M. A., D. C. Dey, P. S. Johnson, and D. L. Graney. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. Forest Science **48**:504–517.

Stewart, J. D., S. M. Landhäusser, K. J. Stadt, and V. J. Lieffers. 2000. Regeneration of white spruce under aspen canopies: Seeding, planting, and site preparation. Western Journal of Applied Forestry **15**:177–182.

Tappeiner, J. C., D. Lavender, J. Walstad, R. O. Curtis, and D. S. DeBell. 1997. Silvicultural systems and regeneration methods: current practices and new alternatives. Pages 151–164 *in* K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, D.C., USA.

Teclaw, R. M., and J. G. Isebrands. 1993. An artificial regeneration system for establishing northern red oak on dry-mesic sites in the Lake States, USA. Annals of Forest Science **50**:543–552.

ter Braak, C. J. F., and C. W. N. Looman. 1987. Regression. Pages 29–77 *in* R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, editors. Data analysis in community and landscape ecology. Pudoc, Wageningen, The Netherlands.

Truax, B., F. Lambert, and D. Gagnon. 2000. Herbicide-free plantations of oaks and ashes along a gradient of open to forested mesic environments. Forest Ecology and Management **137**:155–169.

Tuomela, K., J. Kuusipalo, L. Vesa, K. Nuryanto, A. P. S. Sagala, and G. Ådjers. 1996. Growth of dipterocarp seedlings in artificial gaps: an experiment in a logged-over rainforest in South Kalimantan, Indonesia. Forest Ecology and Management **81**:95–100.

Tworkoski, T. J., D. W. Smith, and D. J. Parrish. 1986. Regeneration of red oak, white oak, and white pine by underplanting prior to canopy removal in the Virginia Piedmond. Southern Journal of Applied Forestry **10**:206–210.

Weaver, P. L. 1987. Enrichment plantings in tropical America. Pages 259–277 *in* Management of the forests of tropical America: Prospects and technologies. Proceedings of a conference held in San Juan, Puerto Rico, 22–27 September 1986. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry, Rio Piedras, Puerto Rico, USA.

Wurtz, T. L., and J. C. Zasada. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Canadian Journal of Forest Research **31**:999–1011.

Youngblood, A. P., and J. C. Zasada. 1991. White spruce artificial regeneration options on river floodplains in interior Alaska. Canadian Journal of Forest Research **21**:423–433.

Zaczek, J. J. 2002. Composition, diversity, and height of tree regeneration, 3 years after soil scarification in a mixed-oak shelterwood. Forest Ecology and Management **163**:205–215.