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A Literature Review of the Effects of Intensive Forestry on Forest Structure and Plant Community Composition at the Stand and Landscape Levels

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A Literature Review of the Effects of Intensive Forestry on Forest Structure and Plant Community Composition at the Stand and Landscape Levels

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ABSTRACT

The purpose of intensive forest practices is to improve the growth and future yield of young, primarily conifer stands in Maine (Maine Forest Service 2001a). Specific practices employed in Maine include plantation establishment, site preparation, vegetation control with herbicides, and precommercial thinning. Related to these practices is the use of clearcutting, a practice that went from 44% of the harvest in 1989 to 3.5% in 1999 (Maine Forest Service 2001a). The combined use of planting, precommercial thinning, and herbicide release of softwood regeneration from competition has occurred on about 4.7% (786,000 acres) of the timberlands through 1999 (Maine Forest Service 2001a).

The effects of intensive forest management on forest structure and plant community composition are not well documented, particularly with respect to the forests in the Northeast. Relevant studies from other regions do not indicate that clearcut harvests and other intensive forestry practices currently implemented in Maine have caused the complete loss of any plant species or communities from the forests in the region. Plantation forestry alters plant communities significantly, sometimes requiring several decades for understory species to recover. However, the impact of such changes at the landscape scale in Maine and the Northeast may not be important because plantations are not common in the region. Changes do, though, occur in forest vegetation communities in response to other intensive forestry practices used in Maine, and the increased fragmentation of habitat at the landscape scale by forestry practices has impacted certain plant species in other regions. Increases in species diversity and shifts in the relative abundance and species composition of overstory tree, understory herb, and shrub communities are the most common effects of intensive forestry practices. Often these changes are short-term; that is, the plant communities shift back toward their pre-treatment character within 10 years. Sometimes the changes in the various components of forest plant communities are long-term. For example, a clearcut harvest in spruce-fir and mixedwood stands can result in either no softwood regeneration or regeneration suppressed by hardwood sprouts unless the clearcut is followed by herbicide application or pre-commercial thinning. Amounts of coarse woody debris and moribund trees are typically reduced by intensive forest practices. Changes in some non-vascular plant populations appear to correspond to similar changes in vascular plant components of the plant community, but some bryophyte and lichen species are dependent on the woody

debris and moribund trees associated with specific stages of forest development, and therefore, may be more sensitive to intensive forestry practices. These structural features can also require several decades to recover, unless the woody debris is intentionally left. The changes in plant communities created by intensive forestry practices have resulted in variable responses from tree pests. The greatest risk for increased pest problems is associated with planted species but not with the surrounding forest.

This review of the literature revealed the following list of gaps in the understanding of the effects of intensive forestry practices.

- The majority of the research on the effects of intensive forest management on plant communities, as well as on soils, water quality, and forest vertebrates and invertebrates, reports the results of short-term studies. Even in areas of North America where intensive forestry is widespread, sites that have undergone multiple rotations of management are rare. Therefore, the cumulative long-term impact of these practices on native plant communities and other components of forest ecosystems may only be speculated based on the currently limited information.
- More information is needed on the function of understory vascular and non-vascular plants in ecosystem processes and the impacts of intensive forestry on individual species and functional groups. However, studies about the effects of management practices on some uncommon or rare species may prove problematic. The abundance of many taxa is so low that measures of their response cannot be statistically analyzed, and few appropriate late-successional sites exist in Maine for comparison.
- With respect to coarse woody debris and moribund trees, it is unclear as to how much of each structural feature is necessary to maintain vulnerable species and important processes. It is also not known whether it is necessary to maintain these features in every stand or if representation at the landscape level is sufficient.
- There is little information to indicate the amount, the patch size, and the spatial pattern of mature forest that is required to maintain populations of plants at the landscape scale to span the range of forest succession types.

While intensive forestry practices have the potential to affect forest structure and plant community composition, many of the effects of the methods used in high-yield silviculture can be intentionally mitigated through additional forestry practices not addressed in this review.

INTRODUCTION

Maine's forests have been harvested for a variety of reasons since the time of European settlement (Smith 1972; Wood 1971; Coolidge 1963), and presumably to some extent before that by Native Americans (Bonnicksen 2000). The methods and scale of harvesting and the application of different management practices have varied considerably because of changes in technology, markets, and the forests themselves. Starting in the 1970s, for example, clearcutting became more widespread in the state (Seymour 1992) due to an extensive spruce budworm outbreak, increased sawmill capacity (Canada), new markets for small trees (e.g., biomass), and improvements in mechanized harvesting equipment. Although the rate of clearcutting declined from 44% in 1989 to 3.5% in 1999 of all lands harvested annually (Maine Forest Service 2001a), the public has become increasingly involved in debates over what constitutes desirable forestry practices.

Some of the key issues of these debates are questions concerning the rate at which Maine's forestland is being harvested relative to the overall growth rate of the timber supply and the environmental effects of different harvesting and management techniques. During the last decade, the area of forestland harvested annually has increased from 325,000 to 532,000 acres (Maine Forest Service 2001a). Under current management techniques, the rate of harvest could exceed that of growth during the next 50 years, as demonstrated by two separate analyses that project shortfalls in the spruce-fir wood supply for the early 21st century (Gadzik et al. 1998; Seymour 1985). Several recent reports suggest that increasing the area of Maine's forestland under intensive forest management could improve long-term forest sustainability and continue to meet timber demands (e.g., Maine Forest Service 2001a; Gadzik et al. 1998). Additionally, applying intensive forest practices to more acres in Maine could potentially increase the amount of land available for conservation efforts (Seymour and Hunter 1992).

In general, the purpose of intensive forest practices is to improve the growth and future yield of young, primarily conifer stands in Maine (Maine Forest Service 2001a). However, the environmental effects of intensive forest management are not well documented, particularly with respect to the Northeast. In the context of the following review, intensive forest management refers to those practices considered high-yield silviculture. Specific practices employed in Maine include plantation establishment, site preparation, vegetation control with herbicides, and precommercial thinning with the objective of increasing softwood fiber production

and value. Few in the preceding list of practices are currently applied to the management of hardwood forest types in Maine. Because clearcutting is the harvesting method commonly associated with use of high-yield practices, it is included. Lastly, the rate and pattern of land area harvested are addressed in this review, as the potential expansion in the use of intensive management techniques in Maine may also influence the landscape-scale characteristics of the environment.

Intensive forestry practices vary in the relative frequency of their use in the 17 million acres of Maine's commercial forest. Clearcutting as a harvesting method was a widespread practice during salvage operations associated with the spruce budworm outbreak of the 1970s and 1980s and peaked at 44% of the harvested land in 1989 (Maine Forest Service 2001a). By a decade later, clearcutting was significantly reduced to approximately 10% of the lands harvested annually (Maine Forest Service 2001a). Planting, precommercial thinning, and herbicide release of softwood regeneration from competition have only been applied in Maine since the late 1970s (Maine Forest Service 1999). These combined practices have been applied to about 4.7% (786,000 acres) of the state's timberlands through 1999 (Maine Forest Service 2001a).

Questions arise about how these practices affect the compositional, structural, and functional attributes of plant communities, soils, water quality, and native vertebrate and invertebrate species at both the stand and landscape scales. While the effects of intensive forestry practices are being investigated, the findings are not readily accessible to those discussing and making decisions about forest management policy. Moreover, information about these topics is incomplete with respect to Maine's forests. The geographical focus of this review is Maine and the Acadian forest region, a mixture of northern hardwoods, red spruce, and boreal forest conifers that extends across the Northeast into Atlantic Canada. However, research on the ecological implications of intensive forest management is more common from other areas of North America, Scandinavia, and northern Europe, where intensive forest management is generally applied to larger areas and has a longer history of use. Thus, this review is dominated by information from these sources.

Literature on the impacts of intensive forestry practices is more extensive for some aspects of the ecosystem than others, and literature reviews and comprehensive studies of a few of the topics already exist (Table 1) and are not all addressed in this paper. Our paper focuses on the effects of intensive forestry practices on the structure and composition

Table 1. Existing literature reviews, annotated bibliographies, and comprehensive studies that address the effects of forest management on various ecosystem components.

Topic	Reference
general biodiversity	Freedman et al. 1994 Bunnell and Huggard 1999
wildlife/vertebrates	Harlow et al. 1997 deMaynadier and Hunter 1995 Lautenschlager 1993 Sweeney et al. 1993
invertebrates and aquatic organisms	Freedman et al. 1994 Pierce et al. 1993 Adamus et al. 1986
water quality	Kahl 1996 Stafford et al. 1996 Binkley and Brown 1993 Hornbeck et al. 1993 Sidle and Hornbeck 1991 Martin et al. 1984
dead organic matter	Freedman et al. 1996
soils and nutrient dynamics	Briggs et al. 2000 Vejre 1999 Worell and Hampson 1995 Pierce et al. 1993 Hornbeck et al. 1990 Federer et al. 1989 Mann et al. 1988 Smith et al. 1986 Jurgensen et al. 1986

of vegetation, a broad topic area that has not been specifically reviewed for the forest types in the Northeast. In addition, a summary of the effects of forest management on dead organic matter from a review by Freedman et al. (1996) and other recent papers (e.g., Hagan and Grove 1999) is also included.

While not addressed in our review, forest management also needs to consider the temporal and spatial habitat requirements of other components important to ecosystem functioning, such as vertebrates, invertebrates, fungi, and bacteria, as well as soil nutrient dynamics. However, living plants in all structural layers are critical components of forest ecosystems due to their functions as primary producers and habitat for many organisms. Woody debris and other elements of dead organic matter are

also important as habitat and function in numerous ecosystem processes.

Therefore, we address the following questions relevant to increasing fiber production primarily of conifers:

- 1) How will intensive forest management likely affect native plant communities, their species composition, and function at the scale of the stand?
- 2) What changes can occur in the quality and quantity of the components of dead organic matter (snags, coarse woody debris, and the forest floor) within intensive forest management areas?
- 3) How could changes in structure and composition of forest vegetation caused by intensive management affect tree pests?
- 4) What are the likely impacts on plant composition and structural diversity at the landscape level, if the area under intensive forest management increases?

Much of the research relevant to the effects of intensive forestry has examined changes in overstory tree and understory plant communities (diversity indices, species composition, and richness) and in the horizontal and vertical structure of vegetation. The majority of the studies report on vegetation development at the stand level. Because intensive forest management has only become extensively used in the United States within the last 50 years, the temporal scale of these studies is short, commonly covering the first 10 to 30 years after treatment. Although the responses of vegetation to clearcutting and herbicide applications dominate the literature, there are also reports on changes due to mechanical site preparation, planting, and thinning.

This review presents a six-part synthesis of the literature. The first section considers the effects of intensive forestry practices within the context of naturally regenerated stands. The second section reviews the changes associated with the planting of conifers in softwood sites, as well as those previously occupied by hardwood and mixed-wood stands. The third examines the impacts of intensive management specifically on bryophytes and lichens. The fourth section discusses changes in dead organic matter components of the stand and the fifth with the impact on tree pests. The final section views the effects of intensive forestry from the landscape-scale perspective and is followed by summary and conclusions. While this paper provides a summary of scientific information, it does not recommend policy or propose how the forest should be managed.

METHODS

Peer-reviewed journals (i.e., scientific journals in which two to three specialists in the topic area anonymously review each of the articles and recommend whether they merit publication) were the main sources of the literature cited in the text. Information from Forest Service reports, symposia proceedings, and chapters from edited volumes were also incorporated. Literature relevant to the chosen topics was primarily sought by means of the AGRICOLA database. We also used the FORESTRY ABSTRACTS database to a limited extent. The articles listed in the output of “subject” searches were initially scanned for content in the library. Those papers that we thought to be relevant were photocopied. Each of the articles, research reports, and reviews was read by one of the authors. Reference sections were then examined for additional sources. As a result of this, we read some, but not all, of the studies cited in the review papers.

The information presented in this literature review is based on the results of the research reported in the papers. Where trends in the literature are reported for a specific topic, these represent the results of two or more works. Sometimes the reported trends are based, in part, on information documented in cited reviews, and, therefore, the conclusions presented are not drawn entirely from empirical data. Conflicting results among studies are presented if they occur. While this review of the literature is fairly comprehensive, it is not exhaustive, particularly for the coarse woody debris, bryophyte and lichen, and landscape sections. The review does provide, at least, an introduction to the issues and concerns relevant in each topical section. Literature published after 2001 is not included.

NATURAL REGENERATION FOLLOWING CLEARCUT HARVESTING

Response of Tree Species

In the following studies, the stands were clearcut and allowed to regenerate naturally. No additional treatments were applied between the harvest and the vegetation surveys. Few studies of this nature have been conducted in the Acadian forest region, and they are not common for any one area. Therefore, results are reported from several different locations and forest ecosystem types. The studies are quite variable with respect to the method of clearcut harvest (conventional or whole-tree, silvicultural or “commercial”), the season of harvest, and the

vegetation characteristics recorded. The basis for determining vegetation changes also differed. Some studies compared the vegetation characteristics of the harvested stands to the pre-harvest vegetation (untreated), while others examined vegetation differences between harvested areas and mature, second growth stands or old-growth stands in the same forest ecosystem types. Most of the research reports the effects of harvesting on the woody species. The harvest may remove the entire canopy or only the merchantable stems. The latter treatment is termed a “commercial” clearcut where overstory trees and sub-canopy, small diameter trees of poor form and for which there are no markets remain to become part of the regenerating stand. Table 2 summarizes the studies of tree species responses to clearcuts and some of their results.

In general, established tree species and shrubs create a canopy of lower stature a few years after a clearcut. For five to 20 years, the canopy of the developing stand remains fairly uniform until specific differences in height growth rates begin to be expressed (Wang and Nyland 1996; Radosevich and Osteryoung 1987). In the Northeast, raspberries and the sprouts of hardwood species, such as pin cherry, red maple, beech, and aspen can dominate sites from 10 to 25 years following the removal of the overstory in softwood and hardwood stands (Pierce et al. 1993; Newton et al. 1987). The density of tree and woody shrub species is much greater than that of a mature stand during this period, and basal area is distributed among the numerous stems of smaller diameter (e.g., Norland and Hix 1996; Gilliam et al. 1995; Leopold et al. 1985). The composition of the stand may be altered as more light-tolerant species colonize and/or increase in their abundance through vegetative reproduction. The effects of clearcutting on plant diversity were measured for trees, as well as woody shrubs, in all of the reviewed studies and reported in terms of species composition, species richness, and sometimes with diversity indices. In most, changes in vegetation were recorded for less than 30 years of post-harvest development. In most of the studies for which diversity measures were presented, tree and woody shrub diversity increased during the earliest stages of stand development after clearcutting (Elliott et al. 1997; Norland and Hix 1996; Elliott and Swank 1994; McMinn and Nutter 1988; Hix and Barnes 1984). Tree species losses were rarely reported. Like many types of forest disturbances, clearcutting often altered the relative abundance (measured as percent cover or importance values) of species in all vegetation layers (see Tables 2 and 3).

Table 2. Summary of the impact of clearcutting on tree species comparing the overstory species to regenerating species in naturally regenerated forest types. Note that species composition and species relative abundance are represented by different columns. (a) Pre-canopy closure, that is, less than approximately 20 years after harvest. (b) Post-canopy closure, that is, more than 20 years after harvest.

Location	Reference	Forest Cover Type	Years Post-Harvest	Species Richness ^a	Diversity Changes ^b	Change?		Relat. Abund. Change?	Control Stand Age
						Over-story	Shrub/Regen.		
(a)									
New Brunswick	Roberts et al. 1988	northern hardwoods	1 and 2	>	ooo	ooo	(+)	y	pc
Quebec	Archambault et al. 1998	balsam fir and yellow birch	5, 10 and 20	nc	ooo	(-)	(+)	y	m
Quebec	Harvey and Bergeron 1989	balsam fir-white birch-spruce	7	>	ooo	nc	nc	y	m
New York	Walters and Nyland 1989	northern hardwoods	13	nc	ooo	nc	ooo	y	pc
Upper Michigan	Albert and Barnes 1987	sugar maple	6	>	ooo	(+)	ooo	y	ud
Ohio	Norland and Hix 1996	mixed hardwoods	8	ooo	ooo	(+)	(+)	y	m
Ontario	Brumelis and Carleton 1988	black spruce	1 to 20	>	ooo	(+)	ooo	y	ud/m
Montana	Muir 1993	lodgepole pine	10 to 20	nc	nc	nc	ooo	y	m
West Virginia	Gilliam et al. 1995	mixed hardwoods	20	>	nc(s-w)	nc	(+)	y	m
North Carolina	Elliot and Swank 1994 (ws)	cove hardwoods with pine-oak	8 and 13 (1st cut)	nc	> (s-w)	nc	ooo	y	pc
North Carolina	Elliot and Swank 1994 (ws)	cove hardwoods with pine-oak	7 (2nd cut)	nc	> (s-w)	nc	nc	y	pc
North Carolina	Elliot and Swank 1994 (ws)	cove hardwoods with pine-oak	14 (2nd cut)	<	nc	nc	(-)	y	pc
North Carolina	Elliot et al. 1997 (ws)	cove hardwoods	3,5,10,19	<	<	nc	(+)	y	pc
		mixed oak	3,5,10,19	<	<	nc	(+)	y	pc
		oak-pine	3,5,10,19	<	<	nc	(+)	y	pc
Georgia	McMinn 1992; McMinn and Nutter 1988	Oak-pine	10	>	ooo	(+)	(+)	y	***
(b)									
Upper Michigan	Albert and Barnes 1987	sugar maple	50	>	ncns	nc	(-)	y	ud
Upper Michigan	Hix and Barnes 1984	hemlock	36-59	>	>	(+)/(+)	(+)	y	ud
Ohio	Norland and Hix 1996	mixed hardwoods	26	ooo	ooo	(+)/(+)	ooo	y	m
Ontario	Brumelis and Carleton 1988	black spruce	>40	nc	ooo	nc	ooo	y	ud/m
Ontario	Groot and Horton 1994	black spruce	50 to 70	nc	ooo	nc	ooo	y	ud
Ontario	Carleton and MacLellan 1994	black spruce	<55	nc	ooo	nc	ooo	y	m
Montana	Lesica et al. 1991	grand fir-pine	70	>	ooo	(+)	ooo	y	ud
North Carolina	Elliot and Swank 1994 (ws)	cove hardwoods with pine-oak	29	nc	< (s-w)	nc	nc	y	pc
North Carolina	Leopold et al. 1985 (ws)	cove hardwoods with pine-oak	23 (1st cut)	nc	>	nc	ooo	y	pc
		cove hardwoods with pine-oak	21 (2nd cut)	ooo	ooo	(-)	(+)	y	pc

^aincludes species of all vegetation layers recorded

^bS-W and S indicate Shannon-Weiner and Simpson's diversity indices

Key: (+) = added species

(-) = loss of species

nc = no change

pc = pre-treatment condition

ws = data collected in entire watershed

>/< = either species added/lost or increase/decrease in diversity indices

ooo = not reported

bold number was age used for changes recorded in table

m = mature second growth stands ud = undisturbed/old growth stands

Table 3. Summary of the impact of clearcutting on the understory vegetation of naturally regenerated stands. (a) Precanopy closure, that is, less than approximately 20 years after harvest. (b) Post-canopy closure, that is, more than 20 years after harvest.

Location	Reference	Forest Cover Type	Years Post-Harvest	Species Richness ^a	Diversity Changes ^b	Change? Species Composition			Change? Relat. Abund.	Control Stand Age
						Shrub	Herb	Bryophytes/Lichens		
(a)										
Nova Scotia	Crowell and Freedman 1994	mixed hardwoods	1,2, 6	>	> (s-w)	(+)	(+)	(-)	y	m
Quebec	Archambault et al. 1998	balsam fir and yellow birch	5,10, 20	nc	ooo	(+)	(+)	ooo	y	m
Quebec	Harvey and Bergeron 1989	balsam fir- white birch-spruce	7	nc	ooo	nc	ooo	ooo	y	pc
Ontario	Brumelis and Carleton 1989	black spruce (nutrient poor)	<20	>	ooo	(+)	(+)	(+)	y	ud/m
		black spruce (nutrient rich)	<20	>	ooo	(+)	(+)	(+)	y	ud/m
Upper Michigan	Albert and Barnes 1987	maple	6	>	ooo	ooo	(+)	ooo	y	ud
Michigan	Roberts and Gilliam 1995a	big tooth aspen (dry)	<15	nc	nc (s-w)	nc	nc	ooo	y	m
		big tooth aspen (mesic)	<15	>	> (s-w)	(+)	(+)	ooo	y	m
West Virginia	Gilliam et al. 1995	mixed hardwoods	20	>	nc (s-w)	(+)	ncns	ooo	y	m
North Carolina	Elliot et al. 1997 (ws)	cove hardwoods	3,5,10, 19	<	< (s-w)	(+)	(-)	ooo	y	pc
		mixed oak oak-pine	3,5,10, 19	<	< (s-w)	(+)	(-)	ooo	y	pc
Sweden	Hannerz and Hanell 1997	Norway spruce	8	<	< (s)	ooo	(-)	(-)	y	pc
Estonia	Zobel 1993	Scots pine (dry acidic)	5	ncns	ncns (H')	ooo	ooo	ooo	y	pc
		Scots pine (paludifying acidic)	5	ncns	ncns (H')	ooo	ooo	ooo	y	pc
		Scots pine (moist acidic)	5	>	> (H')	ooo	ooo	ooo	y	pc
		Scots pine (dry neutral)	2	ncns	ncns (H')	ooo	ooo	ooo	y	pc
		Scots pine (dry calcareous)	2	ncns	ncns (H')	ooo	ooo	ooo	y	pc
(b)										
Upper Michigan	Albert and Barnes 1987	maple	50	ncns	ooo	nc	nc	nc	y	ud
Upper Michigan	Hix and Barnes 1984	hemlock	36-59	>	>	(+)	(+)	ooo	y	ud
Oregon (ws)	Halpern and Spies 1995	Douglas fir-hemlock	40	nc	ooo	(-)	(-)	ooo	y	ud/pc
Montana	Lesica et al. 1991	grand fir-pine	70	>	> (s-w)	(+)	(+)	(+)/(-)	y	ud

^aincludes species of all vegetation layers recorded

^bS-W, S, and H' indicate Shannon-Weiner, Simpson's, and Shannon's diversity indices

Key: (+) = added species

m = mature second growth stands

pc = pre-treatment condition

ws = data collected in entire watershed

ooo = not reported

(-) = loss of species

nc = no change (nsdifferences not statistically significant)

ud = undisturbed/old growth stands

>/< = either species added/lost or increase/decrease in diversity index

bold number was age used for changes recorded in table

The early shifts in the relative abundance of tree species following a clearcut were not always a temporary stage in stand development. We noted that conifer forests and certain types of site conditions appeared to be more susceptible to long-term changes in species composition than other types. In some cases, changes persisted into older post-cut stands (i.e., stages after canopy closure/30 to 60 years after cutting) when compared to mature and uncut stands of the same forest type (Carleton and MacLellan 1994; Newton et al. 1987; Albert and Barnes 1987; Hix and Barnes 1984). Fifty years after commercial clearcuts in two forest types in Upper Michigan, the tree-species composition in hemlock-dominated stands differed from that in stands in adjacent, uncut forests of the same type, while species composition in the maple-dominated stand remained unchanged (Albert and Barnes 1987; Hix and Barnes 1984). Clearcutting the stand originally dominated by hemlock resulted in the virtual elimination of hemlock from the overstory and understory (Hix and Barnes 1984). In boreal forests, mesic and nutrient-rich sites appear to be more susceptible than poor quality sites to shifts from predominantly softwood in mature stands to post-harvest stands of mixed-wood composition (Groot and Horton 1994; Brumelis and Carleton 1988; Newton et al. 1987).

One cause of long-term changes in tree species composition is the effect on regeneration of forest floor disturbance resulting from harvesting activities. Regeneration mechanisms and competitive ability of different species respond differently to varying types of disturbance (Carleton and MacLellan 1994; McMinn 1992; White 1991; Brumelis and Carleton 1988; Roberts et al. 1998; McCormack 1984; Frisque et al. 1978). There are several tree species in the Northeast that reoccupy harvested sites primarily through advance regeneration (e.g., large seedlings and saplings of shade-tolerant spruce, fir, and sugar maple established prior to a cut). It has long been acknowledged that preserving advance regeneration is important in maintaining spruce and fir in post-harvest forests of this type and others in northern New England (e.g., Seymour 1985; Hix and Barnes 1984; McCormack 1984; Westveld 1953). If advance regeneration is lacking or destroyed during harvesting, then hardwoods generally have the advantage over conifers in openings created by clearcutting. Hardwood species tend to produce abundant seed at more frequent intervals, exhibit rapid juvenile growth as seedlings or sprouts, and germinate readily in hardwood or softwood litter and the mineral soil exposed by harvesting operations (Newton et al. 1987). The season during which harvesting occurs and the type of harvesting equipment used strongly

influence the degree of soil disturbance. Frozen ground mitigates forest floor disturbance, regardless of the harvest system, and snow cover protects advance regeneration from damage (Brumelis and Carleton 1988; McCormack 1984; Frisque et al. 1978). In Maine, spruce, fir, and sugar maple rely primarily on advance regeneration (and probably most woody and herbaceous species in the forest floor stratum, see Ruben et al. [1999]). These species benefit from winter harvesting operations and relatively low-impact harvesting systems (for some system comparisons see Seymour [1985]).

There are several examples in which clearcutting shifted softwood stands to mixed wood or hardwood-dominated stands as a result of severe disturbance to the forest floor (e.g., Archambault et al. 1998; Gadzik et al. 1998; Hughes and Bechtel 1997; McMinn 1992; Harvey and Bergeron 1989; Newton et al. 1987; Hix and Barnes 1984). The long-term shifts in species composition at all of the sites were attributed to one or more of the following causes: destruction of the existing advance regeneration, harvesting prior to the establishment of advance regeneration of the overstory species, and aggressive competition from hardwood species. In many situations, clearcutting can alter the competitive balance between conifer species and shift the composition of the forest to deciduous hardwoods and shrubs. Although shifts in species composition are associated with most ecological disturbances, some changes are more permanent than others are. Based on surveys conducted prior to and seven years after clearcutting in northwestern Quebec, Harvey and Bergeron (1989) concluded that the balsam fir dominating the post-harvest stand had permanently replaced much of the black and white spruce, major components of the forest prior to the cut. Changes like this alter the canopy architecture/structure, influence susceptibility to certain forest pests, and can affect the next generation of understory vegetation through differences in light transmittance (Freedman et al. 1994; discussed in future sections).

Reports of the effects of successive clearcuts on the same site do not exist for the conifer and mixed wood forests of Maine and the surrounding region. In one of the few reported studies in an experimental watershed in North Carolina, vegetation inventories were conducted prior to the first harvest in 1939. Inventories were continued during the 22 years before the second cut in 1962 and during the 29 years after that harvest (Elliott and Swank 1994; Leopold et al. 1985). Composition and relative importance (abundance) of tree species underwent major changes from 1939 to 1991. With the exception of chestnut lost to the blight, species composition of the forest

following the first cut was comparable to that of the early inventory (Leopold et al. 1985). However, the 23 years between harvests were not enough time for red and white oak to establish advance regeneration. These two oak species and pitch pine, present in the original stand, declined significantly after 1962. Structural differences between the stands established after the successive clear-cuts also occurred. There were more stems in the larger diameter classes 21 years after the 1962 cut than 23 years after the 1939 cut. Leopold et al. (1985) attributed this to the greater sprouting ability and growth rate of the young hardwood stumps remnant of the second harvest. Similarly, Albert and Barnes (1987) noted that, although maple still dominated the overstory 50 years after harvest in Michigan, a successive clearcut would create a stand of different composition. The authors suggested that the dense overstory of maple that had developed since the harvest was inhibiting the establishment of sufficient amounts of maple advance regeneration in this site.

In summary, the responses to clearcut harvest described above are relevant to the mixed conifer and mature hardwood stands in Maine. If the composition of subsequent stands is dependent on natural regeneration alone, the following scenarios are possible in some forest types in Maine. Hardwoods only temporally dominate spruce-fir and other mixed conifer types if advance regeneration of these conifer species is preserved in an overstory removal type of clearcut. Conifer sites are subject to long-term shifts to hardwoods if there is no advance regeneration present and softwood species do not become established following the harvest or if advance regeneration does not persist under the hardwoods (McCormack 1985). In similar situations hardwood stands dominated by shade-tolerant species like sugar maple may become composed of hardwood species that are established by sprouting and less shade-tolerant species if no advance regeneration is present.

Response of Herbaceous and Shrub Species

The removal of the canopy in clearcut harvesting causes significant changes to the understory plant community primarily due to greatly increased light levels and reduced competition for other resources. Forest floor disturbance from harvesting equipment exposes mineral soil habitats for the establishment of ruderal herbaceous and shrub species. Residual shrubs also increase in abundance or dominance. Initially, this causes a shift in the distribution of biomass to the lower strata. The density of vegetation increases substantially from the predominantly woody species in the canopy to an understory mixture of herbaceous and woody taxa (e.g., Elliott et al.

1997; Crowell and Freedman 1994). The increased density of the understory is a significant, but usually temporary, alteration to stand structure.

Most of the research addressing the effects of forestry practices on understory vegetation has been conducted outside the Northeast (Elliott et al. 1997; Hannerz and Hanell 1997; Gilliam et al. 1995; Roberts and Gilliam 1995a; Duffy and Meier 1992; Brumelis and Carelton 1989; Albert and Barnes 1987; Hix and Barnes 1984). In many of the studies, the species richness of stands within 10 years of harvest was usually equal to or greater than the species richness of unharvested sites (see Table 3). Freedman et al. (1994) noted that the species richness of the vascular-plant communities in Maritime Canada was generally greater for approximately one to six years after the harvesting of predominantly softwood stands when compared with the richness of mature/older stands of similar forest types. Ferns, monocots such as sedges and grasses, dicotyledonous herbs (particularly species of the Asteraceae family), raspberries, blackberries, birch, red maple, and pin cherry commonly dominated the early successional communities of these stands in Canada. Most herbaceous species that had constituted the plant communities prior to harvest recovered their pre-cut abundances a few years after the harvest (Freedman et al. 1994). In other areas, species composition was the characteristic more likely to change. For example, several of the less common species recorded in a 1952 inventory of a hardwood-dominated watershed in North Carolina were not found 17 years after a clearcut. Moreover, other more common but late-successional plants had not recolonized the inventoried sites in the three forest types studied (Elliott et al. 1997). The composition of many of the stands >30 years old at the time of the vegetation survey differed from that of the mature secondary or old-growth stands used for comparison. In contrast with this result, a study conducted in Northeast hardwoods found that most herbaceous species had recovered in old clearcut forests. Ruben et al. (1999) compared the composition and density of understory species in 25- and 60-year-old clearcuts in northern hardwood stands to those of adjacent stands of secondary forest. Using indices based on densities of the herbaceous plants across the boundaries of the stands of different age, the responses of the species to clearcutting were classified as "sensitive," "insensitive," "enhanced," or "edge-enhanced." Short-term reductions in density identified species as sensitive to the harvesting practice. Six of the 23 most common understory species in the 25-year-old stands were classified as sensitive, and only one of these six (*Medeola virginiana* or Indian cucumber

root) remained significantly less dense 60 years after the cut. However, the authors could not determine whether this result was due to differences in logging methods dating to the two periods or recovery time since the harvest. We found that the most consistent impact on understory vegetation in the studies reviewed for both softwood and hardwood forest types was change in the relative abundance of species (see Table 3).

Many of the herbaceous species in Maine are fairly common, with extensive geographic ranges throughout the state. Sixty-three percent of the state's vascular-plant species are considered widespread or ubiquitous (Gawler et al. 1996). However, many other vascular plants in Maine's forests are considered rare, threatened, or endangered at the state or regional level. Many of these species are those that are growing at the northern or southern limit of their range in Maine's transition between the boreal and northern hardwood forests. While forest-dwelling species make up the largest proportion of the rare, threatened, or endangered plants, the sporadic inventories conducted to date indicate that most of Maine's forests do not contain rare flora (Gawler et al. 1996). There is much uncertainty about the effects of intensive forestry practices on many of the less common species; however, it is difficult to experimentally determine the effects on such species because they are not common. A report on the biological diversity in Maine states that some herbaceous species in the state's forests appear to be sensitive to harvesting (i.e., local populations do not survive or readily reestablish following heavy overstory removals; Gawler et al. [1996]). Giant rattlesnake plantain, wild leek, blunt-lobed woodsia, and American ginseng are some examples of such species. In general, the habitat requirements and response to harvesting of most herbaceous species are yet unknown.

It is difficult to generalize about the effects of clearcutting on the understory vegetation. The results of three studies conducted in forests outside of the Northeast demonstrate that the response of understory species can vary according to differences in overstory cover type and site type. Changes in the understory species richness and composition of two forest types in Upper Michigan were assessed by comparing stands clearcut 50 years earlier with those in undisturbed areas (Albert and Barnes 1987; Hix and Barnes 1984). The species composition in harvested hemlock stands differed from that in the undisturbed forests. Three species recorded in the uncut stands were absent from the harvested sites, and 18 new species became established in the cut

areas and persisted throughout the 50 years since harvest. In contrast, clearcutting the maple stands did not significantly affect the understory vegetation. The same herbaceous species groups were represented in cut and uncut maple forests (Albert and Barnes 1987). Roberts and Gilliam (1995a) compared the effects of clearcutting on stands having the same overstory cover type but growing in mesic and dry-mesic site conditions. While understory diversity and species richness differed between mature and cut stands in mesic sites, clearcutting caused little change in the understory of stands in the dry-mesic sites. Similarly, a study conducted in Estonia examined the response of the vegetation communities of Scotch pine stands growing along soil moisture and pH gradients (Zobel 1993). Changes in the early-successional communities recorded two to five years after clearcutting were site dependent. In some site types (e.g., moist acidic sites) the difference between the communities in mature and cut sites was significant, while in others little change was noted (e.g., dry calcareous sites).

Response of Vegetation to Herbicide Release

Herbicide application and thinning are two management treatments that are commonly associated with clearcut harvesting. Although these two treatments are applied during different stages of stand development and target different components of the plant community, both practices reduce the amount of vegetation competing with the crop species for resources. This reduction accelerates growth rates and provides merchantable-sized trees within a shorter period of time. These treatments alter vegetation structure, but are not intended and generally do not eliminate plant taxa (Freedman et al. 1994). There are a few studies addressing the effects of these stand treatments on the non-crop vegetation in naturally regenerated stands. Their results are summarized in Table 4.

Early in post-harvest stand development, aggressive deciduous trees and shrubs suppress the growth of conifer crop species, particularly in highly disturbed and better-quality sites in the Acadian forest region (Seymour 1992; Newton et al. 1987; McCormack 1984). Herbicides applied from the air and ground are currently used in Maine to release conifers from this source of competition in both naturally regenerated and planted sites (Gadzick et al. 1998; Newton et al. 1992). Currently, though, the area of forest treated with herbicides in Maine, New Brunswick, and Ontario has been declining following a peak in 1989 (McCormack 1994). Applied within two to 10 years (typically two to three years)

of harvest, the primary effect of herbicide release in the Northeast is a change in the relative abundance of hardwoods and softwoods (Freedman et al. 1993; Newton et al. 1992, 1989; Schaertl 1991).

Hardwood species show differential susceptibilities to the various herbicides and varying rates of recovery. Because many of the commonly applied herbicides (e.g., glyphosate) are not completely effective on all non-coniferous plants, and the tree-shrub layer often physically shields ground layer vegetation (e.g., bunchberry, twinflower, Canada mayflower, violet species, and forbs of the Composite family), mixed communities of plants often develop after silvicultural herbicide treatments (Freedman et al. 1994). The soil seed bank, seed rain from off-site sources (depending on the size of the treated area), and the sprouting abilities of different species all contribute to shorten the duration of the changes caused by herbicide application (Freedman et al. 1994). Two and nine years after application to spruce-fir forests in Maine, species of deciduous trees and shrubs present before treatment continued to be represented in the stands but with reduced abundance (Newton et al. 1992). At the time of the vegetation survey, vertical heterogeneity was greater in the treated stands than in the untreated stand. The herbaceous cover was greatest in the treated stands and scattered canopy hardwoods and shrub patches survived amidst the dominant softwoods, whereas the untreated stands were in the stem exclusion stage with little cover in the herbaceous layer.

Thinning

Thinning also manipulates plant community structure in treated stands. Thinning is conducted after canopy closure and is sometimes used to alter tree species composition (e.g., pre-commercial thinning in which spruce is favored over fir or unwanted hardwood species). Results from a study conducted in spruce-fir stands showed that the response of fir to pre-commercial thinning was greater than that of red spruce (Frank 1985 in Seymour 1992). Due to its vigorous growth rate, the conditions created by thinning may favor balsam fir and allow it to dominate the overstory of stands harvested on rotations of a length that does not allow red spruce to mature (Seymour 1994). There are some examples of populations of herbaceous species that grow beneath forest canopies in Maine but expand in thinned stands in response to increased light levels in the understory (Gawler et al. 1996). Commercial thinning in regions outside of the Northeast has been shown to hasten the development of multi-storied stands from a single-storied state, as well as increase the mean diameter of individuals in the residual overstory (Bailey and Tappeiner 1998; Yanai et al. 1998; Alaback and Herman 1988; Table 4). Species composition of the understory changes as shrubs and tree seedlings become established. Initial increases in the richness and composition of ground vegetation can result. In some northern forest types high thinning levels allow for the dominance of the understory by a few favored species (Sean et al. 1999). However, 15 to 20

Table 4. Summary of the response of non-crop vegetation to competition control treatments in naturally regenerated stands.

Location	Reference	Forest Cover Type	Stand Age	Treatment	Yrs. Since Treatment	Change? Species Composition			Species Richness ^a	Control Stand Age	Change? Rel. Abund.
						Overstory	Shrub/Seedling	Herb.aceous+			
Oregon	Alaback and Herman 1988	spruce	33	thinning	17	ooo	c	nc	>	m/pc	y
Oregon	Halpern and Spies 1995	hemlock	33	thinning	17	ooo	c	c	nc	m/pc	y
Oregon	Bailey and Tappeiner 1998	Doug. fir-hemlock	40	thinning	5,10,20, 40	nc	c	c	nc	ud/pc	y
Oregon	Bailey and Tappeiner 1998	Douglas fir	40–100	thinning	10–25	ooo	c	nc	ooo	ud	y
Pennsylvania	Yanai et al. 1998	central hardwoods	50–55	thinning	15	ooo	c	ooo	>	m/pc	y
Maine	Newton et al. 1992	spruce-fir	16	herbicide release	9	ooo	nc	c	>(herb)	pc	y

^aincludes species of all vegetation layers unless noted

Key: c = change in species composition

m = mature second growth stands

pc = pre-treatment condition

y = shift in relative abundance (% cover) of one or more species

bold number was age used for changes recorded in table

herbaceous+ = includes ferns

nc = no change (ns not statistically significant)

ud = undistributed/old growth stands

ooo = not reported

years after treatment, these changes may no longer be apparent due to the development of a dense shrub cover or canopy closure. Although thinning enhances the vertical heterogeneity of the stand, the spatial distribution of stems in treated multi-story stands is more uniform than that observed in multi-story old-growth forests (Bailey and Tappeiner 1998).

PLANTATIONS

Site Conversion

Conversion of a site from naturally regenerated forest to a plantation of tree species not native to the site is the management practice with the greatest potential to alter the forest. Due to the success of natural regeneration in the Northeast, plantations are not as common in this region as they are in the northern boreal forest of Canada and Scandinavia and forests in southeastern and western regions of the United States. Currently plantations are established on a small fraction of the industrial forest in Maine each year (Seymour 1992). Planted species include local and genetically improved seedlings of native conifer species, often black and white spruce. The total number of acres planted in Maine over the last 25 years represents about 1.2% of the forestland (Maine Forest Service 2001a). However, the use of planting may expand in the future (Gadzick et al. 1998). The impact of plantation establishment on the vegetation at a site varies with the age and composition of the replaced stand (Freedman et al. 1994), in addition to other factors related to site conditions, whether tree species native to the region or exotics (not common in Maine) are planted, and the silvicultural practices employed. Changes to the plant community can be significant when a hardwood or mixed-wood stand in the later stages of succession is converted to a conifer plantation. Although the changes were not apparent during the early stages of stand development, the understory plant community of a mature plantation forest in New Brunswick, Canada, differed significantly from that of the natural forest (Freedman et al. 1994). Freedman et al. (1994) attributed the differences to changes caused by the physical structure of conifer canopy and chemical influences of its litter. In several sites in southern England, differences in the mix of planted species, soil types, and subsequent tending practices all played roles in the effects of plantation establishment on the understory vegetation (Kirby 1988). The understory flora in stands planted in mixtures and pure stands of beech, pine, spruce, and oak was compared with that of secondary, mixed hardwood forests of approximately the same ages. Kirby (1988) noted that the ground flora in dense stands of planted conifers

and stands of planted beech were composed of many fewer species when compared with that of the natural mixed-oak woodlands. Understory species were more likely to survive through the dense stem-exclusion stage in mixed plantations of oak and spruce than in sites where pure stands of pine or spruce were planted. Thinning in the planted sites during this stage of development improved light conditions in the understory, which allowed also for the persistence of some species associated with the original stands and the recolonization of others. Changing the overstory tree species in base-rich soil types appeared to alter the composition of the understory flora more than planting on sites with predominantly acid soils (Kirby 1988). In Maine, stands with productive soils and occupied by low-quality hardwoods with a history of high-grading have usually been selected as sites for softwood plantations (Seymour 1992), but no research into the effects on ground flora has been conducted.

Site Preparation

Although it is also used with natural regeneration processes, site preparation is commonly associated with plantation establishment. Machinery (mechanical), herbicide applications, and prescribed burning are all used to manage residual vegetation and harvesting debris to prepare the site for planting. No published research on the effects of these practices in Maine was found, probably largely due to the fact that site preparation is not often practiced in Maine. Table 5 summarizes the results of studies from the southeastern and northwestern states and areas in western Canada covering all three kinds of site preparation techniques. Because sites are prepared early in succession, the setback in stand development is not great. The impact appears to depend on the technique and the intensity of its application. However, intense site preparation also impacts residual plant species by delaying their recovery in the stand (Schoonmaker and McKee 1988). The greatest impact of site preparation may be on the dead organic matter component (Freedman et al. 1996, 1994); this will be addressed in a later section.

In all cases, site preparation initially increased herbaceous species cover at the expense of the recovering shrub layer (Harper et al. 1997; Locasio et al. 1991; Swindel et al. 1989; Schoonmaker and McKee 1988; Stransky et al. 1986). The use of multiple methods of site preparation or those types that cause the severe soil disturbance promoted the early dominance of a few invading herbaceous species, particularly grasses and sedges (Schoonmaker and McKee 1988; Stransky et al. 1986; Abrams and Dickmann 1982). For example, Scherer et al. (2000)

Table 5. Summary of the response of vegetation to site preparation in planted stands.

Location	Reference	Forest Cover Type	Treatment	Years Since Treatment	Change? Species Composition	Species Richness ^a	Diversity ^b	Change? Relative Abund.	Age of Control Stand
British Columbia	Harper et al. 1997	spruce	herbicide glyphosate	12	c	<(herb)	< (S)	y	pc
			herbicide hexazinone	12	c	nc	nc (S)	y	pc
Oregon	Schoonmaker and McKee 1988	Douglas fir-hemlock	burning	5,10,20, and 40	c	<	< (S-W)	y	ud
Georgia	Locasio et al. 1991	loblolly pine	mechanical	6	c	nc	> (SH)	y	m
Texas	Stransky et al. 1986	loblolly pine	mechanical and burning	1, 8, and 10	nc	nc	***	y	pc/m
Texas	Swindel et al. 1989	loblolly-slash pine	mechanical and chemical	5		<(severe)	<(SW and S)	y	pc

^aincludes species of shrub and herb vegetation layers

^bS-W, SH, and S indicate Shannon-Weiner, Shannon, and Simpson's diversity indices

Key: c = change in species composition

nc = no change (ns not statistically significant)

ud = undisturbed/old growth stands

ooo = not reported

m = mature second growth stands

pc = pre-treatment condition

y = shift in relative abundance (% cover) of one or more species

bold number was age used for changes recorded in table

compared the response of understory vegetation among several different residue treatments, noting little difference between most treatments and the controls. The dominance of one or two species in the understory only occurred in sites where the broadcast burning and chopping treatments were applied. Research conducted by Harper et al. (1997) showed that chemical applications primarily reduced the tall shrub layer, while mechanical methods and burning altered all layers indiscriminately. Regardless of site preparation method, differences in plant community characteristics between treated and control plots had generally diminished within 10 years. Forty years after forests in Oregon were broadcast burned and planted with Douglas fir, plant inventories were conducted in the treated sites and natural forests of the same ecosystem type. All but two species (mycotrophs) found in natural stands were present in the managed stands (Schoonmaker and McKee 1988).

Herbicide Release

Herbicide treatments in Maine and other regions are typically applied to softwood plantations within five years of the previous harvest. The release of the planted conifers from the hardwood competition that naturally regenerates on the site reduces the biomass of competing deciduous trees and shrubs. True to the objective of herbicide application, the relative abundance of conifers increased in all of

the studies that we reviewed (Miller et al. 1999; Lautenschlager et al. 1998; Sullivan et al. 1996; Boyd et al. 1995; Freedman et al. 1993; May et al. 1982; Table 6). The studies documented changes in the vegetation over the 8 years or less following the herbicide applications. The results generally showed that the species present in the plant communities of the untreated controls were little different from those in the treated stands (Lautenschlager et al. 1998; Sullivan et al. 1996; Boyd et al. 1995; Freedman et al. 1994; May et al. 1982). While conifers dominated the upper layers of the canopy, the relative abundance of the herbaceous species and deciduous tree and shrub taxa in treated stands remained below untreated levels.

In one operational-scale study conducted in northwestern Ontario, the effects on the vegetation by four methods of competition control were compared in northern mixed-wood forest that had been clearcut and planted with spruce four to seven years prior to study (Lautenschlager et al. 1998; see also Bell et al. 1997). Vegetation response to two mechanical methods (brushsaws and Silvana Selective cutting head) and two commonly used herbicides (glyphosate and triclopyr) was compared with untreated blocks and plots in the adjacent, unharvested forest. Reported comparisons were made through measures of relative percent cover in eight vegetation groups three years after the treatments. While plant diversity indices indicated little difference among the release

Table 6. Summary of the response of vegetation (all but deciduous trees and shrubs) to herbicide release treatments in planted sites.

Location	Reference	Forest Cover Type	Treatment	Years Since Treatment	Change? Species Composition	Species Richness ^a	Species Diversity	Change? Relative Abund.	Age of Control Stand
British Columbia	Sullivan et al. 1996	sub-boreal spruce	herbicide	5	ooo	nc herb/<shrub	nc	y	pc
Nova Scotia	Freedman et al. 1993	mixed-wood	herbicide	1,2,4 and 6	nc	nc	nc	y	pc
Ontario	Lautenschlager et al. 1998	mixed-wood to spruce	herbicide glyphosate	3	ooo	ncns	ooo	y (>grasses)	pc
		mixed-wood to spruce	herbicide triclopyr	3	ooo	ncns	ooo	y (<ferns)	pc
		mixed-wood to spruce	brushsaw	3	ooo	ncns	ooo	y	pc
		mixed-wood to spruce	Silvana	3	ooo	ncns	ooo	y	pc
Georgia	Miller et al. 1999	mixed pine-hardwood	herbicide	11	nc	ncns	ncns	y	pc
Georgia	Boyd et al. 1995	loblolly pine	herbicide	7	nc	nc	ncns	y	pc
Texas	Swindel et al. 1989	loblolly-slash pine	herbicide	5	c	c	<	y	pc

^aincludes species of shrub and herb vegetation layers

Key: c = change in species composition

nc = no change (ns not statistically significant)

ud = undisturbed/old growth stands

ooo = not reported

m = mature second growth stands

pc = pre-treatment condition

y = shift in relative abundance (% cover) of one or more species

bold number was age used for changes recorded in table

alternatives, the herbicide blocks had the highest species richness of the treated blocks and the greatest reduction in the shrub and fern vegetation groups. The same vegetation groups were represented in unharvested forest and planted areas; however, the plantation generally had less moss cover and more herb, grass, and sedge species than the unharvested forest. Only the cover of the deciduous tree group in the herbicide-treated blocks was statistically lower than its cover in the untreated blocks.

BRYOPHYTES AND LICHENS

Both as ground cover and epiphytic inhabitants of the trunks of trees, bryophytes and lichens are ubiquitous structural components of forests of many types and ages. Bryophytes, particularly those growing on rotting logs, create moist microclimates that support the establishment of the seedlings of trees and herbs (Gawler et al. 1996), but little else is currently known about the importance these organisms to ecosystem function. Because we encountered few studies that addressed the effects of intensive forest management on bryophytes and lichens, responses to all treatments are discussed in this section and

summarized in Table 7. The responses of bryophyte and lichen communities to disturbance by management practices were quite variable and forest-type dependent. These organisms typically declined in response to management activities, and common species, at least, appeared to increase to pre-treatment levels as the forest recovered (Newmaster et al. 1999; Hannerz and Hanell 1997; Freedman et al. 1994). Clearcutting generally altered the abundance of bryophytes and lichens more than vascular plants (Hannerz and Hanell 1997; Niippola 1992; Lesica et al. 1991; Brumelis and Carleton 1989). However, one study comparing conventional clearcutting to whole-tree with slash removal documented no change and concluded that bryophytes were indifferent to logging residue treatments (Olsson and Staaf 1995). Changes in species composition appeared to relate to the effect of the disturbance on specific microenvironment conditions or habitat structure. In northwestern Ontario, herbicide treatment reduced the abundance and species richness of bryophytes and lichens for at least two years following the application. Only the group of species considered "common" in the study appeared to recover toward pretreatment levels (Newmaster et al. 1999). Two papers reported the

Table 7. Summary of the effects of forest management on the bryophyte and lichen communities.

Location	Reference	Forest Cover Type	Mean Stand Age	Treatment	Years Since Treatment	Change? Understory		Change? Bryophyte/Lichen		Age of Control Stand
						Composition	Relative Abund.	Composition	Relative Abund.	
Ontario	Brumelis and Carleton 1989	black spruce	5 through 30	clear-cut	5 through 30	c	y	c	y	ud/m
Montana	Lesica et al. 1991	fir-pine	ooo	clear-cut	70	c	y	c	y	ud
Oregon	Alaback and Herman 1988	spruce-hemlock	variable	thinning	17	nc	nc	c	y	pc
Finland	Nieppola 1992	scotch pine	15 149	clear-cut thinned	<20 <30	c nc	y y	c nc	y y	pc pc
Sweden	Hannerz and Hannell 1997	Norway spruce	8	clear-cut	8	c	y	c	y	pc
Sweden	Olsson and Staff 1995	spruce-pine	ooo	cut and slash removal	8 and 16	c	y	nc	nc	pc
Ontario	Newmaster et al. 1999	aspen-spruce	4	herbicide	1 and 2	ooo	ooo	ooo	y	pc
Sweden	Soderstrom 1988	spruce-pine	ooo	clearcut and thinning	50	ooo	ooo	c	y	ud

Key: c = change in species composition
nc = no change
ud = undisturbed/old growth stands
ooo = not reported

m = mature second growth stands
pc = pre-treatment condition
y = shift in relative abundance (% cover) of one or more species
bold number was age used for changes recorded in table

effects of the thinning of mature stands. A thinning study conducted in Finland observed no change in the bryophyte and lichen communities (Nieppola 1992). Seventeen years after treatment in Oregon, groundcover mosses had increased in abundance in the plots thinned in a spruce-hemlock forest (Alaback and Hermon 1988). The increase was attributed to the shady conditions created by a corresponding increase in hemlock seedling establishment.

A moderate amount of information is available about the mosses and lichens of Maine (Gawler et al. 1996). No studies have directly examined the impact of forest practices on these species in the Northeast. However, there are several species of lichen that appear to be largely restricted to old-growth forests in Maine (Selva 1994). Additionally, three species of moss considered "of special interest" grow at the northern edge of their distributions in Maine (Allen 1996). These species all require tree trunks and rock in woodlands as habitat and are included in a list of species that are declining in Maine as a result of habitat destruction, the causes of which were not specified (Allen 1996).

Some mosses and lichens in other regions are also associated with specific stages of forest development as a result of their habitat requirements. Research

conducted in Montana, Ontario, the Pacific Northwest, and Sweden demonstrated such associations (Halpern and Spies 1995; Lesica et al. 1991; Brumelis and Carleton 1988; Soderstrom 1988). Several moss and lichen species are epiphytic (growing on tree trunks and/or branches) or epixylics (inhabiting substrates other than the ground surface or living trees, commonly woody litter). A few of these species rely on the presence and distribution of particular structural features, like coarse woody debris and moribund trees that develop as the stand matures. The results of three studies reported moss and lichen species restricted to undisturbed stands (old-growth) in which the woody litter and trees of advanced age were abundant and well distributed throughout the stand (Halpern and Spies 1995; Lesica et al. 1991; Soderstrom 1988). In these same studies, there were also species found in second-growth stands that were not present in the old-growth sites.

The reviewed studies suggest that mosses and lichens are potentially more sensitive to the effects of intensive forest practices than vascular plants. While many species are able to recover to pre-treatment levels, several bryophyte and lichen species possess habitat requirements that are dependent on structural elements and micro-site conditions

associated with specific stages of forest development. Maintaining the moribund trees and woody debris and other structural elements would likely offset the reduction of sensitive species.

(Note: Eve Schuller recently studied the effects of intensive forestry practices on bryophytes in Maine. Publication forthcoming.)

DEAD ORGANIC MATTER

Another consideration at the stand-scale is the loss of structural heterogeneity resulting from the reduction of dead organic matter associated with intensive forestry practices. Freedman et al. (1996) reviewed this topic thoroughly with respect to its implications for ecosystem-wide biodiversity. Because of the influence of dead organic matter on stand structure and function, we will summarize the findings of this report, reiterate some important points, and further support them with the results of recent research.

Dead organic matter is comprised of cavity trees, snags, coarse woody debris, and the organic horizon of the forest floor. The aboveground structural elements of dead organic matter provide habitat for vertebrate and invertebrate species, as well as for vascular plants, bryophytes, lichens, and fungi. Studies have demonstrated the importance of the spatial distribution and decay stage of dead organic matter as preferred habitat for bryophyte, lichen, and saprophytic and mycorrhizal fungal species that have roles in nutrient cycling and plant nutrition (Hagan and Grove 1999; Freedman et al. 1996; Berg et al. 1994; Lesica et al. 1991; Soderstrom 1988). Coarse woody debris can also be an important substrate for seedling establishment and, thereby, influence the tree species composition of stands (McGee and Birmingham 1997; Szewczyk and Szwagrzk 1996). In addition, "dead shade" created by slash left on clearcut spruce-fir sites protects the smaller advance regeneration from the extensive mortality that often results from exposure (Seymour 1986). The organic horizon of the forest floor functions to influence site quality by storing quantities of organically bound nutrients; playing an important role in anion and cation exchange capacity, water-holding capacity, and carbon storage; and by affecting soil properties like acidity (Freedman et al. 1996; Jurgensen et al. 1986). The decline in the quality, quantity, and spatial distribution of the different components of dead organic matter, as well as the loss of species associated with these habitats, can alter stand function and various ecosystem processes (Freedman et al. 1996).

The short-term effects of intensive forestry practices on the components of dead organic matter depend on the nature of the preharvest stand, the method used to harvest the stand, the management techniques applied during post-harvest stand development, and the length of the rotation. The temporal pattern of the changes in dead organic matter quantity and quality following clearcutting without additional treatments has been reported for both northern hardwood and spruce-fir stands in the Northeast (Sturtevant et al. 1997; McCarthy and Bailey 1994; Gore and Patterson 1986). While the temporal dynamics differ slightly, the general pattern of change in the abundance of dead organic matter in both forest types follows a bimodal distribution. Amounts of woody debris are greatest during the early and late stages of stand development, as long as small diameter slash and residual trees are left on site after a cut. The quantity of dead organic matter in the young stand reaches its lowest level after 30 to 50 years when harvest slash and other debris have decomposed and entered soil pools. Approximately 50 to 80 years after the harvest, the mature canopy begins to break up, contributing woody debris and enhancing the structural heterogeneity of the stand. Although the time sequence differs from that documented for the Northeast, a similar pattern of development also occurs in the Pacific Northwest where the abundance of coarse woody debris peaks immediately after a harvest and again in the mature/old-growth stages (Spies et al. 1988).

Numerous studies have indicated that mature, managed stands of both hardwoods and softwoods do not have snags, cavity trees, and coarse woody debris in the overall volumes that are found in old-growth stands. Moreover, the proportion of these structural components in large-diameter classes or in later stages of decay is also less than that documented in old-growth forests (Duvall and Grigal 1999; Linder and Ostland 1998; Goodburn and Lorimer 1998; Shifley et al. 1997; Sturtevant et al. 1997; Freedman et al. 1996; Tyrell and Crow 1994; Lesica et al. 1991; Soderstrom 1988). Intensive forest management practices appear to exacerbate the differences between managed and unmanaged stands with respect to volume and quality of coarse woody debris. Usually few snags or residual trees remain when site preparation follows conventional clearcutting or whole-tree harvesting. Mechanical site preparations (e.g., crushing) and burning rapidly reduce the size and, thus, the volume of coarse woody debris derived from the harvesting residues (slash). The coarse component of dead organic matter is immediately added to the soil pool, removing habitat and hastening the rate of decomposition and

nutrient release (Freedman et al. 1996). The open conditions after clearcutting and characteristic of young plantations further enhance decomposition rates of the woody debris and further diminish the coarser components of dead organic matter. Also, during these early stages of succession, inputs from plant litter are low. The effects of whole-tree harvesting are greater because this practice removes the treetops and limbs that create slash (woody debris) from the site. In a review of soil organic matter losses for eastern forests, Jurgensen et al. (1986) found that logging slash is a major contributor to soil organic matter. While woody residues and soil organic matter have been shown to be an important factor in soil water and nutrient availability in forests in North America and Europe, the long-term impacts of residue removal on nutrient availability and site productivity are uncertain (Hagan and Grove 1999; Vejre 1999; Fay and Leak 1997; Worrell and Hamson 1995; Jurgensen et al. 1986).

High-yield plantations tend to be spatially uniform and fast growing. Because such plantations are often managed to maximize timber production on shortened rotations, few moribund trees develop and little woody debris accumulates during the intervals between harvests (Freedman et al. 1996; Hansen et al. 1991; Gore and Patterson 1986). Thinning, maintaining reserve trees, and leaving some coarse woody debris in plantations are three practices applied under this system that can potentially offset the trend toward reduced volume of woody debris, snags, and cavity trees (Duvall and Grigal 1999; Hagan and Grove 1999; Berg et al. 1994). While thinning creates some small-diameter coarse woody debris, McCarthy and Bailey (1994) point out that it could also limit contributions of large-diameter debris during later stages of stand development.

All components of dead organic matter are important contributors to the structure and function of forest ecosystems as habitats and as elements of nutrient cycling and plant nutrition. Unless residual coarse woody material and moribund trees are left after a harvest, the studies indicate that intensive silviculture reduces large diameter classes of dead organic matter and late stages of wood decay. Exposure of the ground surface following heavy overstory removals can also increase the decomposition rate of the debris left on site, which may, in turn, affect the nutrient dynamics of the soil and possibly understory and overstory species composition of the regenerating stand. The effects of intensive forestry practices on coarse woody debris appear to be consistent across the studies reviewed from various regions, with no apparent difference between hardwood and conifer stand types. Therefore, the implications of the results

of the reviewed studies should be considered in the management of Maine's forestlands.

IMPACT OF INTENSIVE FORESTRY ON TREE PESTS

Changes in structure and composition of forest vegetation will affect the dynamics of tree pests. This review is limited to pest complexes that are commonly associated with the intensive forestry in Maine including spruce budworm, beech bark disease, pests of spruce plantations, and decay associated with thinning spruce/fir stands.

Spruce Budworm

As mentioned earlier, much of the clearcutting in Maine was a response in large part to the spruce budworm (*Choristoneura fumiferana*) outbreaks causing defoliation and mortality on more than 7 million acres in the 1970s and 1980s (Livingston 1998; Witter et al. 1984). As the following discussion indicates, future outbreaks will be affected by how the newly developing forests are managed.

Larvae of the spruce budworm moth can defoliate conifers over a period of years causing especially high mortality in balsam fir (Kucera and Orr 1981). Outbreaks occurred in Maine from 1972 to 1986, 1913 to 1919, and possible in the early 1800s (Seymour 1992). Another outbreak from 1949 to 1959 caused defoliation of trees but low mortality (Irland et al. 1988).

The natural composition of Maine's spruce-fir forest was influenced by spruce budworm defoliation even before the 20th century, and this disturbance regime favored mixed, multiaged forests consisting predominately of young fir and older spruce (Seymour 1992). This was the case in Maine after the last spruce budworm outbreak on uncut sites (Livingston 1998). However, heavy cutting in response to widespread fir mortality during the last outbreak removed the spruce overstory on those sites (Livingston 1998). The species composition of the sites subjected to overstory removal shifted to dominance by hardwood sprouts and fir regeneration. The advanced conifer regeneration will presumably replace the hardwood sprouts, and Gadzik et al. (1998) project that the spruce-fir forest will increase in merchantable growth. These forests are likely to be dominated by balsam fir because most of the mature spruce has been removed from these stands while the seedlings and saplings are dominated by balsam fir (Livingston 1998).

Stand susceptibility to mortality due to spruce budworm defoliation in Maine will increase with the increased proportion of balsam fir in the stand (MacLean 1980; Diamond et al. 1984; Witter et al.

1984). Based on inventory data (Livingston 1998), average balsam fir mortality (>8 in dbh) between 1982 and 1995 inventory periods went from 39% to 49% as percent basal area in balsam fir increased from 1% to 15% to 45% to 100%. Presumably, this mortality is mostly the result of the 1972-1986 outbreak. The inventory data also indicated high mortality in young balsam fir (5–8 in dbh) with mortality averages of 23% to 32% as the proportion of balsam fir increased. MacLean (1996) and Su et al (1996) found that defoliation of balsam fir in New Brunswick increased from 30% or less to more than 60% if hardwoods were less than 40% of the stand's basal area. Needham et al. (1999) analyzed stand data from the last spruce budworm outbreak and found a similar result in that balsam fir mortality increased if the hardwood proportion in a stand was less than 50%.

The trends in Maine are similar to those reported in New Brunswick in that stands with a lower percentage of spruce-fir had less mortality and presumably less defoliation during the outbreak. In addition, the Maine data confirm the expectation of red spruce being less susceptible to damage by spruce budworm (Diamond et al. 1984; Witter et al. 1984). Red spruce mortality averaged 10%–18% for large and small trees during the last outbreak (Livingston 1998). Therefore, an increasing proportion of balsam fir in Maine's forest will result in an increase in future vulnerability to widespread mortality during spruce budworm outbreaks.

Due to the high density of balsam fir regeneration on clearcut sites, pre-commercial thinning of these stands is viewed as key to improving their productivity (Gadzick et al. 1998). Thinning to increase the spacing between trees also affects balsam fir susceptibility to defoliation and mortality caused by spruce budworm. Bauce (1996) suggested that thinning conducted two years prior to budworm outbreak could reduce susceptibility because of increased foliage production. However, thinning during an outbreak could increase vulnerability because the chemical changes in needles after thinning favor larval feeding. Pothier (1998) reported no survival of balsam fir in stands that had up to 30% of the basal area removed 10 years prior to the outbreak in Quebec. Dobesberger (1998) used a simulation model to predict that thinned, open grown balsam fir could have compensatory growth after defoliation. However, MacLean and Piene (1995) suggest another scenario after examining data from Nova Scotia stands that were thinned at ca. 15 years old in 1971. After the last outbreak, mortality reached 94%–100% in the severely defoliated thinned stands. In contrast, unthinned stands had pockets of fir that survived.

The authors strongly recommend that crop trees of balsam fir on thinned sites, even young trees, will need protection during future outbreaks of severe defoliation by the spruce budworm.

Intensive forestry practices can increase the future vulnerability of Maine's spruce-fir forest to spruce budworm defoliation. Clearcutting has removed the more resistant red spruce from the overstory and reduced its presence in the forest. Herbicide treatments decrease hardwood composition and increase the proportion of susceptible balsam fir. Precommercial thinning can increase balsam fir susceptibility to defoliation. Another possible adverse consequence of the increasing proportion of balsam fir in Maine forests is an increase in frequency and severity of spruce budworm epidemics (Blais 1985).

Blum and MacLean (1984) describe ways in which intensive forestry also has the potential to reduce risk to future budworm outbreaks if it can reduce the balsam fir component, increase red spruce and non-host species in the spruce-fir stands, and maintain host vigor. At a regional scale, between-stand diversity in species composition and age structure is an additional key goal. The authors indicate clearcutting can increase stand diversity, but the practice can create problems as outlined earlier. Stand conversion to black spruce plantations is another recommendation because of this species' high resistance to budworm defoliation. Shelterwood systems combined with thinning are additional recommendations that have proven effective in reducing the amount of balsam fir in a stand. Two- and three-stage shelterwood treatments combined with thinning-out the fir has increased red spruce growing stock from 11%–25% to 41%–55% in 17 years (Frank 1985). Red spruce regeneration also increased from 2%–7% to 40%–75% of the stems in 16 to 29 years.

In conclusion, the future application of intensive forestry practices will have a major influence on the vulnerability of Maine's spruce fir forests to mortality resulting from spruce budworm outbreaks.

Beech Bark Disease

Beech bark disease (Houston 1994; Houston and O'Brien 1983) is caused by a disease complex. A scale insect (*Cryptococcus fagisuga*) feeds on the bark of living beech and weakens the phloem cells in the area of the feeding. Once weakened, a pathogenic fungus (*Nectria coccinea* var. *faginata*) can enter the tissue and kill patches of bark. The disease complex was introduced into Nova Scotia from Europe around 1890, and American beech has little resistance to this combination of pests. Stands of large beech were killed by the complex in Maine during the 1930s and

40s. However, the roots were not killed, and dense stands of beech sprouts have replaced the original overstory. The disease complex does not kill the smaller trees, but does cause extensive cankers on the stem surface resulting in disfiguration, reduced growth, and reduced mast production. Only a few trees per acre show an ability to completely resist the scale insect.

Presumably due to heavy harvesting in response to the spruce budworm outbreak, the number of beech stems in Maine forests increased from 88.6 million in the 1982 inventory (Powell and Dickson 1984) to 169 million in 1995 (Griffith and Alerich 1996). Therefore, the amount of beech bark disease in the state is increasing substantially because the sprouts will retain the parent tree's susceptibility to the disease. As with the vulnerability of spruce-fir forests to spruce budworm defoliation, intensive forestry offers increased risks and opportunities in dealing with beech bark disease. While clearcutting favors regeneration of beech sprouts, herbicide spraying is a practical way to remove the susceptible beech component from the existing forest (Burns and Houston 1987; Kelty and Nyland 1986; Ostrofsky and McCormack 1986). Understory herbicide applications can target the diseased beech stems but leave resistant beech and other species to grow on the site. If there is no intervention, eastern hemlock can slowly replace beech in the overstory in some stands over time (Runkle 1990; Twery and Patterson 1984).

In conclusion, beech bark disease will have an increasingly adverse impact on Maine's managed forests unless actions are taken to reduce the number of beech sprouts.

Plantation Pests

Monocultures of trees are more susceptible to pest outbreaks (Cowling 1978). Little acreage is planted in Maine, just over 10,000 acres per year (Maine Forest Service 2001b) yielding a total acreage of ca. 200,000 acres in the state (Maine Forest Service 2001a). The predominant species being planted is spruce, mostly black spruce and some white spruce. In Maine, the primary pests identified in spruce plantations are *Armillaria* root disease (Livingston 1990) and the yellow-headed spruce sawfly (*Pikonema alaskensis*) (Maine Forest Service 1998).

Armillaria root disease is a common problem in forest plantations because the ubiquitous fungus can survive in cut stumps from which it can infect planted seedlings (Hood et al. 1991). On eastern conifers, the primary species killing planted seedlings is *Armillaria ostoyae* (Gerlach et al. 1997; Wiensczyk et al. 1997; Livingston 1990). Infection level in spruce plantations are 1%–32% in Ontario (Wiensczyk

1996) and accumulated mortality could exceed 10% (Whitney 1988). In Maine, *Armillaria* root disease is found in most spruce plantations, but less than 1% of the trees (<11 years old) in the stands were recently killed (Livingston 1990). The low mortality levels indicate that *Armillaria* infection is not a problem for Maine's spruce plantations.

An estimated 3,500 acres of black spruce plantations have suffered from defoliating outbreaks of the yellow-headed spruce sawfly (*Pikonema alaskensis*) (Maine Forest Service 1998). To combat the outbreaks, carbaryl (Sevintm XLR Plus) was applied to 1,098 acres in 1997. Carbaryl has a very low toxicity to mammals and other vertebrates (Kuhr and Dorough 1976). However, it is highly toxic to several insect groups, the best-known being honeybees (Kuhr and Dorough 1976). Some aquatic invertebrates are also sensitive to carbaryl toxicity (Courtemaunch and Gibbs 1980; Gibbs et al. 1984). Carbaryl breaks down rapidly in plants and soil and will typically completely degrade within a couple of months (Kuhr and Dorough 1976). However, carbaryl residues can be detected in contaminated ponds over a year beyond the treatment year (Gibbs et al. 1984).

Pest problems in spruce plantations have affected very few trees in Maine, and there is no indication that they will cause major problems in the future.

Decay and Precommercial Thinning

Pre-commercial thinning of dense, regenerating spruce-fir stands is viewed as key to improving their productivity (Gadzick et al. 1998). A risk associated with thinning is increased incidence of wood decay. Cruickshank et al. (1997) found *Armillaria ostoyae* capable of colonizing 12% to 52% of residual stumps after precommercial thinning of Douglas-fir plantations resulting in an increased threat of infection for crop trees. However, Entry et al. (1991) did not find increases in *Armillaria* infections of Douglas-fir after thinning, but *Armillaria* infections did increase if thinned sites were fertilized. Fertilization decreased defensive compounds in the tree bark and increased the food in bark tissue that the fungus needs during infection (Entry et al. 1991). Whitney (1993) found a decrease in incidence of *Tomentosus* root rot (*Inonotus tomentosus*) in thinned white spruce plantations. On balsam fir in Maine, incidence of decay at stump height tended to be lower for pre-commercially thinned stands (36%) than unthinned stands (55%) 10 to 24 years after treatment (Tian 2002). Red spruce decay incidence was much lower (5%–7%) and was unaffected by treatments. Based on existing reports, thinning of spruce-fir stands is not expected to adversely impact incidence of decay in Maine.

MANAGEMENT IMPACTS FROM THE LANDSCAPE-SCALE PERSPECTIVE

Overview

Forest-management activities influence the characteristics of forest stands with respect to changes in plants and woody debris. The stand-scale impact of intensive forestry practices can appear significant, particularly its effects on dead organic matter and overall structural complexity of stands in the absence of the mitigating practices. However, it is important to assess the impact of forest practices from the landscape perspective, that is, the regional pattern of forest patches. Each managed stand and residual forest represent a patch in the landscape mosaic. Therefore, the basis for the evaluation of impacts at this spatial scale is the distribution and proportion of area under different combinations of forest management practices (Hepinstall et al. 1999; Freedman et al. 1996; McComb et al. 1993; Hansen et al. 1991). This perspective is relevant for understanding the interaction between and influence of areas subject to intensive management practices with the species inhabiting the adjacent forest patches. Several authors suggest that landscape-scale patterns should be the basis for the forest management designs in the future (e.g., Crow and Gustafson 1997; Diaz and Bell 1997; Hunter 1990). This section examines some of the changes in the forested landscape resulting from management activities and the potential effects of the landscape changes on plant communities.

Landscape-scale patterns are dependent on natural and man-made disturbances. Forestry, agriculture, and other land management and development activities impose an anthropogenic patch dynamic on the landscape. This landscape pattern differs in many ways from the mosaic created by natural disturbances. Studies of the spatial patterns in the forested landscapes of Michigan and the Pacific Northwest characterized some of these differences (Spies et al. 1994; Mladenoff et al. 1993; Ripple et al. 1991). In these regions, managed landscapes generally differed from natural landscapes (i.e., those subject to natural disturbance agents only) in the predominance of small forest patches in second growth, the presence of fewer patches of unmanaged forest, simpler patch shapes (e.g., straight edges), and low continuity between forest patches (high-contrast edges). Increase in abundance of edge environment, decrease in the availability of interior habitat, and isolation of remnant patches in a matrix of managed forest have caused habitat fragmentation for a variety of organisms in areas outside the Northeast (Jules 1998; Spies et al. 1994; Mladenoff et al. 1993; Ripple et al. 1991). The differences between managed and

natural landscapes have additional consequences for biological diversity due to changes in attributes such as structural complexity of vegetation and species composition within and between stands. Several authors believe that these changes might, in turn, have implications for ecosystem function (Crow and Gustafson 1997; Halpern and Spies 1995; Freedman et al. 1994; Matlack 1994; Mladenoff et al. 1993; McComb et al. 1993; Hansen et al. 1991).

Three primary concerns arise from an examination of the potential effects of changes in the pattern of the forested landscapes on plant communities. These three concerns include (i) increases in the proportion of early successional species, (ii) the implications of habitat fragmentation and associated changes in forest edge characteristics on the resistance and recovery of non-tree plant species to disturbances caused by forest management activities, and (iii) the large-scale reduction in the structural complexity of forest stands, on which other forest organism and ecological processes may be dependent.

All of these issues, changes in forest cover types, habitat fragmentation, and related issues are relevant to the forests of Maine. Based on 1993 satellite images, an estimated 11% of the state's land area was in clearcut, early regeneration, or late regeneration (Hepinstall et al. 1999). Based on state records, the Maine Forest Service (2001a) estimates that in 1999 the cumulative use of plantations, pre-commercial thinning, and herbicide application occurred on approximately 4.7% of the state's timberlands. Clearcutting has been reduced from 44% of the harvest in 1989 to 3.5% in 1999 (Maine Forest Service 2001a). Although the rate at which sites are repeatedly subject to clearcut harvesting (rotation length) varies greatly, Seymour and Hunter (1992) point out that extensive clearcutting and the associated road systems have created a fragmented landscape in some regions of Maine. The effects of this type of fragmentation, that is, the break up of continuous tracts of forest, on understory plant species have not been studied in Maine and are just beginning to be documented in other areas (e.g., Jules 1998).

If intensive forest management practices are applied extensively and harvest rotations are shortened relative to the rotation of natural disturbances associated with the forest type, the cumulative effects of the harvesting rates can cause a significant proportion of the landscape to be dominated by early successional forest. The expansion of early successional forest types increases the density of the seed rain from the associated species and augments their establishment in patches produced by anthropogenic and natural disturbances (Spies et al. 1994). As a result, early successional species become increas-

ingly common in the landscape. Concomitantly, the return intervals introduced by harvest rotations in some areas limit the development of late-successional forests, which also affects the species and ecological processes dependent on them. Landscape-level changes in species proportions have been observed in Ontario (Carelton and MacLellan 1994). A similar situation also developed in parts of the boreal forest in central Sweden from the 1920s to 1950s as a result of the introduction of clearcutting on a large scale (Linder and Ostland 1998). During the 1960s and 1970s efforts were directed toward diminishing the high proportion of early successional deciduous trees that had become established in favor of the conifers that had previously dominated the region. One result of this management action was a drastic reduction in numbers of older deciduous trees, an important habitat for some species whose populations had expanded following the extensive clearcutting. The landowners in this region of Sweden continue their attempts to identify and re-establish the "natural" balance between coniferous and deciduous species in these forests.

Although not extensively documented for vascular and non-vascular plants, landscape-scale fragmentation caused by forest practices is potentially problematic for species that are habitat-specialists or edge sensitive, are represented at low population densities, or possess poor colonizing abilities (Brunet and Von Oheimb 1998; Matlack 1994; Probst and Crow 1991). The results of demographic plant research conducted in a watershed in Oregon illustrate possible effects of habitat alteration and fragmentation caused by forest management activities. Jules (1998) examined the demography of a common understory herb of western forests, *Trillium ovatum*, with respect to spatial and temporal patterns of forestry-related disturbance. The mortality of trillium was almost complete in parts of the watershed that had been clearcut and planted with conifers. New individuals had not been recruited into stands that were cut as many as 30 years before the survey. Additionally, forest edge populations of *Trillium*, those growing within 65 m of a clearcut edge, had nearly no recruitment during the 30 years since adjacent sites were harvested. In contrast, populations in forest interiors showed continuous levels of *Trillium* recruitment. The change in the *Trillium* population was attributed to three possible, harvest-related causes: the limitations imposed by ant-mediated seed dispersal, changes in microclimate at clear-cut edges relative to the interior forest, and/or increased seed predation at clear-cut edges resulting from changes in the small mammal populations associated with harvesting. This research indicates that some

species do require certain types of habitat and that the fragmentation of habitat can significantly affect common plant species, not just rare ones.

The colonization rates of woodland plant species were studied in Sweden in 30- to 75-year-old deciduous tree plantations that had been established on abandoned agricultural fields (Brunet and Von Oheimb 1998). All of the plantations were adjacent to undisturbed deciduous woodlands. The authors' objective was to determine the time required for species that had become locally extirpated through clearcut harvests and planting to recover to former population levels. After 70 years, the richness of woodland species in the plantation was the same as that in the undisturbed forest only within 30 to 35 m of undisturbed forest edge. Moreover, some of the forest species not adapted to long-distance dispersal had not become established in all of the sampled transects.

Conclusions about the importance of landscape level patterns and the need for additional research have been made for the state by the Maine Biodiversity Project (Gawler et al., 1996). As noted in an earlier section, there are few species in Maine about which habitat requirements and response to harvesting are well known. To date, relevant studies from areas outside of Maine and works examined by the Maine Biodiversity Project (Gawler et al. 1996) indicate an increase in species richness and no loss of common plants in response to intensive silvicultural practices. Gawler et al. (1996) noted that these few studies compared plant species composition and structure in forests managed intensively or at short rotations to that in forests in late successional stages of development. In most cases, the characteristics of the pre-harvest forest were used to detect responses in vegetation. This type of study design is necessary because much of the forestland in Maine has already been altered by management practices. While this leaves few natural forest sites (defined as maintaining the integrity and continuity of natural processes) for controls, there are some forested stands that have been less impacted by management than others. The availability for future studies of late successional stages in Maine's forests is becoming limited because of a large increase in the acreage of seedling/sapling stands and early successional forest types in Maine (Gadzick et al. 1998). In addition, the quality and quantity of natural forests are not representative of all the recognized forest types in Maine (Gawler et al. 1996). The results of the Maine Biodiversity Project demonstrate the importance of determining the effects of forest management practices on native plants at the stand and landscape scales in Maine, but careful design will be needed to ensure proper

comparisons are made between the range of possible forest types in the region.

Management at the Landscape Scale: Examples

While some investigators have compared and documented differences in the characteristics of managed and natural forestlands at the landscape scale and examined their effects on individual species, other managers and scientists have attempted to design management plans for forested landscapes using the results and recommendations of such studies. The work of Hann et al. (1998) indicates that large landscape may offer a buffering capacity to broad-scale trends in changes in characteristics like vegetation composition and structure, demonstrating the importance of landscape-scale considerations in management. The following section summarizes the key recommendations and points to a few examples where the concepts and ideas have been implemented.

Several authors suggested that management designs for forests at the landscape scale incorporate considerations of stand size, connectedness, and age-structure through time as well as in space (Fries et al. 1998; Halpern and Spies 1995; Roberts and Gilliam 1995b; Freedman et al. 1994; McComb et al. 1993; Hansen et al. 1991; Probst and Crow 1991). Many further noted that knowledge of how plant populations respond to the temporal scale, as well as spatial patterning of forest management activities is needed to create management designs that maintain a range of habitat and species integrity supporting biodiversity in forested regions (Jules 1998; Diaz and Bell 1997; Halpern and Spies 1995; Roberts and Gilliam 1995b; Matlack 1994; McComb et al. 1993).

As one step in the process of designing and refining landscape-scale management plans, Roberts and Gilliam (1995b), Niemela (1999), and others proposed that the entire sequence of succession following natural disturbances be used as the standard for comparing the effects of management activities on plant and other community characteristics. An example of this approach occurred in part of the Willamette National Forest in Oregon where forest management activities were based on natural disturbance regimes reconstructed from various lines of evidence for the range of past ecosystem conditions (Swanson et al. 1997). This information was used to implement flexible management practices that allowed for variable rotation lengths, varying levels of tree removal at each cutting, and cutting units of sizes and spatial patterns as defined by natural patterns. Diaz and Bell (1997) and Hann et al. (1998) likewise recognized that baseline information about

ecosystem processes was needed to create management strategies that will ultimately maintain sustainable conditions at the landscape scale in British Columbia. Similar approaches to forest management have been undertaken in Sweden where timber production and maintaining biodiversity are goals of equal importance for the landscape-scale design (Fries et al. 1998).

Understanding the complex interactions of landscape-scale patterns and processes and implementing them into management designs for large forested areas are challenges. While this section offers only a brief introduction to the topic, the information provided points out the importance of considering the forested context of the stands to which high-yield silvicultural practices (as well as other management activities) are applied. Landscape-scale management designs have the potential to modify the impact of intensive practices through the thoughtful incorporation of the management of the surrounding forest. Many aspects of forest ecosystems in Maine and other regions require additional research to better understand the interaction of structure and function at the scale of landscapes. Rather than wait for the results of such research, management designs should use the information currently available but remain dynamic so that new information can be readily incorporated (Niemela 1999).

CONCLUSIONS

Intensive forestry practices are silvicultural methods that are applied to forest stands with a variety of objectives. The effects of the methods on forest vegetation depend on the management objectives. In Maine these methods are typically used to manage extensive areas of spruce-fir stands and limited areas of softwood plantations established on sites with productive soils but previously occupied by low-quality hardwoods. Although management goals in Maine's forests continue to undergo changes as the timber land base is increasingly separated from paper mills and as technology utilizing hardwood pulp is incorporated by industry, a major management objective for part of Maine's forests is still to increase softwood fiber production by minimizing competition from non-crop vegetation through the planting of softwoods, herbicide applications, and precommercial thinning.

Although it may have an "intensive" impact, a clearcut harvest is not truly intensive forestry if it is not associated with one or more of the other practices mentioned above. Clearcutting of spruce-fir and mixedwood stands without intensive forestry practices often results in either no softwood regen-

eration or regeneration suppressed by hardwood sprouts which reduce fiber production.

With these distinctions in mind, studies to date do not indicate that clearcut harvests and the intensive forestry practices currently implemented in Maine have caused the loss of any plant species or communities from the forests in the region. However, changes do occur in forest communities in response to these practices. This review of data from the Northeast and other regions indicate some general trends as well as knowledge gaps of how intensive forest management potentially affects plant communities and coarse woody debris in Maine and the Acadian forests. While the following list summarizes the responses of forest vegetation to the previously defined set of intensive forestry practices, many of the effects of high-yield silviculture can be intentionally mitigated through additional forestry practices not addressed in this review.

1. The response of tree species to intensive forest practices is relatively well understood at the stand scale. Clearcut harvests, planting, herbicide applications and thinning often increase species diversity. Species composition and relative abundance of the overstory tree species are also usually altered, as these are the intended objectives of most of these management practices.
2. In contrast, the effects of harvesting and intensive practices on most understory vascular and non-vascular plants were not considered until very recently. As with overstory species, studies indicate that the use of intensive forestry practices typically increases the species diversity of understory herbs and shrubs. Shifts in species composition and relative abundance in understory plant communities are usually temporary. Occasionally these changes appear to be long-term.
3. The response of non-vascular plant species to intensive forestry practices is similar to that of other understory plants. However, some species of bryophytes and lichens may be more strongly dependent on structural features (e.g., moribund trees and woody debris) associated with specific stages of forest development and, therefore, may be more sensitive than vascular plants to intensive forestry practices that remove such substrate materials.
4. Plantation forestry significantly alters plant communities. Research in Scandinavia has shown that it may take a century or more for locally extirpated woodland species to recover in intensively managed sites even if there is an adjacent source of propagules. However, relevant studies

in Maine and the Northeast are few, and the impact of these changes at the landscape level may not be important because of the infrequent use of plantation forestry in the state.

5. Amounts of coarse woody debris and moribund trees are typically reduced by intensive forest practices, unless such structural features are intentionally left. The reduction of debris and removal of snags and large diameter trees affects the natural structural complexity of stands, which in turn, alters the availability of habitat and nutrients in the stand.
6. Responses of tree pests to intensive forestry are variable. Risk to spruce budworm could be reduced or increased depending on whether forest practices reduce or increase the amount of balsam fir in a stand. Reducing the beech component of a stand could reduce beech bark disease. Plantation forestry will likely increase pest problems for the planted species but not for the surrounding forest.
7. Increases in the fragmentation of mature, second growth and unmanaged forest patches have occurred. There is also evidence from some regions that the fragmentation of habitat by forestry practices has impacted certain plant species.

Knowledge gaps:

1. The majority of the research on the effects of intensive forest management on plant communities, as well as on soils, water quality, and forest vertebrates and invertebrates, reports the results of short-term studies. Even in areas of North America where intensive forestry is widespread, sites that have undergone multiple rotations of management are rare. Therefore, the cumulative long-term impact of these practices on native plant communities and other components of forest ecosystems may only be speculated based on the currently limited information.
2. More information is needed on the function of understory vascular and non-vascular plants in ecosystem processes and the impacts of intensive forestry on individual species and functional groups. However, studies about the effects of management practices on some uncommon or rare species may prove problematic. The abundance of many taxa is so low that measures of their response cannot be statistically analyzed, and few appropriate late-successional sites exist in Maine for comparison.
3. With respect to coarse woody debris and moribund trees, it is unclear how much of each of

the structural features is necessary to maintain vulnerable species and important processes. It is also not known whether it is necessary to maintain these features in every stand or if representation at the landscape level is sufficient.

4. There is little information to indicate the amount, the patch size, and the spatial pattern of mature forest that is required to maintain populations of plants at the landscape scale to span the range of forest succession types.

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