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Rationale and methods for conserving biodiversity in plantation forests

Mitschka J. Hartley*

Department of Wildlife Ecology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA

Abstract

Industrial forest managers and conservation biologists agree on at least two things: (1) plantation forests can play a role in conserving biodiversity, and (2) plantations will occupy an increasing proportion of future landscapes. I review literature from around the world on the relationship between biodiversity and plantation management, structure, and yield. The dynamics of plantation ecology and management necessarily differ by landscape, geographic area, ecosystem type, etc. This review provides a broad array of management recommendations, most of which apply to most regions, and many patterns are evident. I suggest a new plantation forest paradigm based on the hypothesis that minor improvements in design and management can better conserve biodiversity, often with little or no reduction in fiber production. There is ample evidence that these methods do benefit biodiversity, and can also entail various economic benefits. Adherence to these recommendations should vary by plantation type, and depending on the proportion of the surrounding landscape or region that is or will be planted. Stand-level variables to consider include socio-economic factors, native community type and structure, crop species composition, and pest dynamics. During establishment, managers should consider innovations in snag and reserve tree management (e.g. leave strips), where mature native trees and/or understory vegetation are left unharvested or allowed to regenerate. Polycultures should be favored over monocultures by planting multiple crop species and/or leaving some native trees unharvested. Native species should generally be favored over exotics. Site-preparation should favor methods that reflect natural disturbances and conserve coarse woody debris. Plantations that have already been established by traditional design can also conserve biodiversity via small modifications to operations. Earlier thinning schedules or longer rotations can strongly affect biodiversity, as can reserve trees left after plantation harvest to remain through a second rotation.

Keywords: Biodiversity; Conservation; Intensive silviculture; Plantation

1. Introduction

Currently 3% of the world's forests are plantations, comprised of 60 million hectare in developed nations and 55 million hectare in developing nations (WRI, 1998; FAO, 1999). In some regions, plantations comprise a major proportion of forest area, including 44% in Japan, 20% in New Zealand, and over 90% in Britain (Donald et al., 1997; FAO, 1999). Though tropical forest cover is declining throughout the world, tropical plantation area has increased dramatically, "from about 10 million hectare in 1980 to about 44 million hectare in 1990" (Lugo, 1997). Demand for wood products has increased for decades, and will continue to increase into the 21st century (Nambiar, 1984; FAO, 1999). Unless members of the public reduce their use of wood products and/or increase recycling efforts, their increased demands must largely be met by growing more fiber on plantations. Plantations already produce more of the world's

* Present address: Audubon New York, 200 Trillium Lane, Albany, NY 12203. Tel.: +1-207-581-2939; fax: +1-207-581-2858. *E-mail address*: hartley@umenfa.maine.edu (M.J. Hartley).

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commercial timber (34%) than do old-growth forests (30%), managed second-growth forests (22%), or minimally-managed second-growth forests (14%) (Sedjo and Botkin, 1997).

There is a common belief that forest management negatively influences biodiversity (Wagner et al., 1998), in that increasing fiber yield decreases biodiversity. However, for most forest-types, we have a limited understanding of the functional relationship between biodiversity and fiber production (Barbour et al., 1997). Compared to naturally regenerated forests, plantations are often viewed unfavorably both by the public and conservation biologists (Perley, 1994; Potton, 1994), largely because they lack biodiversity relative to natural forests (Friend, 1982; Freedman et al., 1996). Most, but not all comparisons of unmanaged forests to plantations have found an impoverished flora or fauna in the latter (reviewed in both Moore and Allen, 1999; Palik and Engstrom, 1999). For example, Carlson (1986) found that densities of forest-interior birds were two to three orders of magnitude greater in tropical forests than in replacement plantations. On the other hand, in terms of a functioning natural community, plantations compare favorably to many other intensive industrial land uses such as annual crop agriculture or human developments (Moore and Allen, 1999).

Depending on the type of plantation and the natural structure of surrounding native forests, planted stands usually cannot be thought of as similar to, or a substitute for natural forests. Plantations usually include exotic species, non-local native species, or native species not typically forming extensive, pure stands. However, as different or biologically impoverished as they are, plantations still contribute to biodiversity conservation through various means. Most directly, plantations can contain substantial components of biotic diversity across many taxa (Ferns et al., 1992; Allen et al., 1995; Michelsen et al., 1996; Chey et al., 1997; Estades and Temple, 1999), including rare species in some cases (Norton, 1998; Tucker et al., 1998; Wilson and Watts, 1999). Even exotic plantations can help restore native biota to degraded sites (Lugo, 1997), by stabilizing soil and creating site conditions favorable for native animals and plants to recolonize. Plantations are most likely to contribute positively to biodiversity conservation when used to reforest degraded or deforested areas (Moss et al., 1979; Evans, 1982; Moore and Allen, 1999). In addition, plantations can benefit landscape composition (Estades and Temple, 1999). Some ecological processes, e.g. avian nest predation rates, are related to large-scale factors such as the proportion of a landscape that is forested (Robinson et al., 1995; Hartley and Hunter, 1998). Plantations can buffer edges between natural forests and non-forest lands, and improve connectivity among forest patches, which might be important for some metapopulations (Norton, 1998). Finally, forests of any type play a role in reducing global warming by acting as carbon sinks (Trexler, 1995).

Many conservationists have accepted the role that plantations can play in relieving timber demands from natural, native forests (Seymour and Hunter, 1994; Hunter and Calhoun, 1995), because plantations produce much more fiber on a much smaller land base (Greenwood et al., 1988). In theory, this can allow for natural forests to be managed less intensively or set aside as ecological reserves. Indeed, some calculations indicate that plantations could meet most industrial fiber demands on <10% of the world's forest land area (Sedjo and Botkin, 1997). Also, increasing fiber production in temperate areas lessens pressures to meet global wood demands by harvesting tropical forests, which are of the utmost value for global biodiversity (Lambeth and McCullough, 1997). It may seem that the best use of all plantations would be to maximize fiber production while minimizing costs (Moore and Allen, 1999), but this assumes that plantations will increase the amount of natural forests that are taken out of production or harvested minimally (Hunter and Calhoun, 1995). However, there are several reasons and conditions whereby biodiversity should be given greater consideration in plantation design and management: (1) plantation establishment may not result in natural forests being taken out of production or managed less intensively, (2) some regions have already become so dominated by plantations that native forest-types have largely been replaced (Tucker et al., 1998), (3) even in areas where plantations make up a relatively small proportion of forest area, this proportion is likely to increase steadily in coming decades, and (4) most plantations can be managed such that biodiversity is given greater consideration, yet with little loss of fiber production (Norton, 1998). Especially where this is true, managers should obviously modify their management if doing so yields ecological and social benefits without incurring economic costs.

I review literature from around the world that examines the major aspects of plantation design, structure, and management, and relates biodiversity to fiber production. The term ''plantation'' is broad and without universal definition. Depending on the user and context, this word refers to a wide range of stand types from regularly spaced exotic monocultures to stands comprised of a patchy mosaic of planted native species and competing vegetation with much horizontal and vertical structure. Thus, what some define as a plantation others do not, and recommendations that are relevant to one type of plantation will not be important for another type. Also, given the complexity of this subject it should not be surprising that research on plantations and biodiversity sometimes results in contradictory conclusions. Variables that can differ among studies include: climate, site conditions, management methods, response variables (e.g. plants, insects, birds, mammals, etc.), scale, stand age, stand structure, and species composition. I offer a set of general management recommendations, many of which can be applied to a range of stand types from tropical to boreal. However, an approach that is effective in one region might not work in a distant forest of a different type. Some of the methods I propose have not been scientifically evaluated across a wide range of ecosystems or crop species, and thus, represent hypotheses to be tested experimentally.

2. Landscape context

Arguably, the single most important consideration in managing any individual stand for biodiversity is its larger spatial context (Wigley and Roberts, 1997; Díaz et al., 1998). Managers should vary in their response to the recommendations of this paper depending on the regional and landscape context within which their stands are located. The most important factors to consider are plantation size, location (Díaz et al., 1998), extent to which a landscape or region has been and will be harvested and planted, degree to which the landscape is natural (Hunter, 1996a) versus degraded, the similarity of plantation structure to natural vegetation (Gjerde and Saetersdal, 1997), and what habitats are being converted into plantation. Obviously, managers of plantations that are small, comprised of native species, and in a largely natural landscape are least in need of basing their management on the recommendations of this paper. This paper is aimed at managers for which one or more of the following is true: their plantations are large, a native forest-type is being converted, exotic species are used, and/or the surrounding landscape is already heavily planted or degraded. If landscapes are carefully planned and managed, optimal juxtaposition of different stand ages, sizes, and types (including plantations) can ameliorate many of the negative effects associated with plantations, and even increase regional biodiversity (Gjerde and Saetersdal, 1997). Because landscape considerations and recommendations have been treated extensively elsewhere (Harris, 1984; Hunter, 1990; Norton, 1998), this paper focuses on stand-level characteristics and strategies for conserving biodiversity within individual plantations.

3. Harvest considerations

The single best correlate between animal species diversity and plantation structure is the amount of native vegetation found within a plantation (Staines, 1983; Parker et al., 1994). In converting natural stands to plantations, especially to exotic species, biodiversity is strongly affected if some native vegetation is left after harvest or allowed to regenerate during site-preparation or tending (Zanuncio et al., 1998). Harvests can be designed to allow some large-diameter, mature trees to be left as scattered individuals (dispersed retention), in clumps (aggregated retention), or in linear strips (Franklin et al., 1997). Deep-rooted, windfirm individuals are the best candidates to use if trees are retained for the purpose of shade, vertical structure, or to be harvested later. However, if retention trees are written off for the ecological balance sheet and selected primarily for biodiversity, then many species are acceptable. One of the most important roles of retention trees is that they can provide future inputs of coarse woody debris (Freedman et al., 1996). Thus, whether alive or dead—standing or fallen—retention trees maintain high ecological value even when damaged or killed during or after site-preparation, whether from herbicides, wind, or fire. The lack of standing snags and fallen logs is typically the most conspicuous difference between planted and natural forests (Hunter, 1990; Freedman et al., 1996; Stokland, 1998).

Retaining live native vegetation allows for a higher species diversity throughout the rotation of the planted stand and provides a source for seeds, spores, or individuals to reinhabit the growing plantation (Woodley and Forbes, 1997). Native vegetation can also be retained in patches, sometimes referred to as microreserves or lifeboats (Franklin et al., 1997). Lifeboats are especially useful for sensitive species that would be adversely affected by the climatic and environmental conditions associated with early successional stands, and species with limited dispersal capabilities or slow colonization rates, e.g. lichens (Franklin, 1992). Remnant patches provide critical habitat for those native species that persist within them, even when these species are not found within the planted stands (Friend, 1982; Lindenmayer et al., 1998). Patch size is an important consideration, as larger patches ameliorate many of the physical factors (e.g. excessive light or desiccation) that might render individual retention trees unsuitable for sensitive species such as mosses or shade-loving herbaceous plants (Franklin et al., 1997). The total basal area of native vegetation to be left within a stand should be a function of the surrounding landscape and regional context. As the proportion of a landscape or region that is converted to exotic species increases so should lifeboat sizes within each plantation, and the obligation or frequency of leaving native vegetation patches within plantations. Woodley and Forbes (1997) advise that native species comprise at least 5% of planted stands, but in heavily planted landscapes and large, exotic plantations retention goals of 10% of stand area might be more appropriate.

On some sites it might be operationally desirable to leave unharvested vegetation in linear ''leave strips''. These can be marked before harvest, or incorporated later by incomplete herbicide applications. Leave strips can be arranged in parallel rows to facilitate herbicide applications and minimize shading of crop trees. For example, leave strip spacing could approximate the width of a helicopter spray boom, if this is how herbicides are typically applied. If rows are widely separated and narrow (e.g. only as wide as a single tree), crop trees can be planted at a normal spacing, just as if the strips were absent. Leave strips can look like hedgerows if every stem in the strip is retained. Another option is an ''orchard row'', where individual retention trees are chosen and marked along a transect, using a pre-arranged spacing (e.g. every 15 m), and/or choosing trees with specific ecological (e.g. cavities) or economic (e.g. high-value as veneer) reasons to be left through the next rotation. Leave strips can also be used to buffer natural features in the plantation, such as the edge or perimeter of existing aquatic habitats (e.g. streams, rivers, wetlands, or lakes). Aquatic buffer strips contain important elements of biodiversity (Carey and Johnson, 1995), and often serve to connect other habitats within a landscape (Estades and Temple, 1999). These ecotypes are among the most desirable areas to leave unharvested in terms of biodiversity (Freedman et al., 1996), and also because operating in or around them can be logistically difficult, uneconomical (Morrison and Meslow, 1984), or prohibited by regulations (Norton, 1998). deMaynadier and Hunter (1995) proposed two-tiered buffers strips with a 10–25 m no cutting zone on each side of streams surrounded by a wider zone where partial harvesting can take place. In a highly planted landscape, different plantations can be separated and dissected by networks of native vegetation, optimally in broad, interconnected corridors.

In cases, where patches or strips of residual vegetation cannot be retained in new plantations, a small number (e.g. 15% of stems) of dispersed native trees can play a disproportionately important role in retaining biodiversity after harvest (Bibby et al., 1989; Fuller, 1995). In the Pacific northwest, Hansen et al. (1995) examined avian abundance along a continuum of 0–150 retention trees per hectare in Douglas-fir (*Psuedotsuga menzeseii*) plantations, and found that bird densities increased little beyond 5 trees/ha. These trees can provide major benefits to managers by serving as shield or nurse trees to prevent frost or drought-related regeneration failures (Nilsson, 1990; Groot and Carlson, 1996), and inhibiting insect pest outbreaks (Stiell and Berry, 1985). Given a fixed basal area of non-crop trees to be left, Bibby et al. (1989) argue that widely scattered trees are more beneficial to birds than are clumps of trees. However, Schieck et al. (2000) found that boreal bird communities in harvested areas were more similar to those in old-growth forest when >80% of the large residual trees were retained in clumps. Aggregated retention was also recommended for conserving forest amphibians (deMaynadier and Hunter, 1995). Currently, we lack scientific evidence on the relative benefits of dispersed versus aggregated retention for most species and biomes (Franklin et al., 1997). Given the many taxa that rely on native vegetation within plantations, both aggregated and dispersed residual vegetation are important to consider in landscapes dominated by large plantations (Franklin et al., 1997; Estades and Temple, 1999).

In many regions, older plantations more closely resemble native forest communities than do younger plantations (Friend, 1982; Clout, 1984; Peterken et al., 1992; Parker et al., 1994; Allen et al., 1995; Gill and Williams, 1996; Norton, 1998), and animal and plant diversity and abundance often increase with plantation age (Donald et al., 1998). The economically-optimum rotation age is usually much younger than the ecological optimum for a stand (Ferns et al., 1992; Fuller, 1995). Lengthening rotations of managed stands will often have dramatic benefits for biodiversity (Currie and Bamford, 1982; Peterken et al., 1992; Allen et al., 1995), but can entail major economic compromise. One option for large landowners to consider is harvesting most plantations at their economical rotation age, but leaving some stands—or large parts of harvested stands—to continue to age (Currie and Bamford, 1982; Peterken et al., 1992; Woodley and Forbes, 1997). Varying rotation periods, from 50 to 200 years at higher latitudes (Fries et al., 1997), represents a compromise between economic and ecological considerations. By not trying to recoup initial investments as quickly as possible managers can gain access to different product markets (e.g. larger diameter lumber) and increase values on a per-tree and unit area basis without the additional investments of regenerating a new stand.

Mature plantations are almost always harvested by clear-cutting, but this does not mean other options are economically or operationally infeasible (Norton, 1998). Plantations can be harvested by a variety of silvicultural options, though few have been attempted and compared. Unless innovative, unconventional methods are used and evaluated, it will remain unclear as to whether or not they can result in economic gains or losses, and how they relate to biodiversity. Theoretically, plantations can be harvested by even or uneven-aged systems such as shelterwood or patch cuts. Methods that differ from clear-cutting can have major ramifications for conserving biodiversity (Peterken et al., 1992). Relative to short-rotation clear-cuts, long rotations with multiple entries provide quicker and more frequent returns on investments, produce high-value timber, and spread out risks related to poor market conditions and possible stand damage or disturbance (Seymour and Hunter, 1994; Carey and Johnson, 1995). In addition to these financial benefits, selection systems maintain greater structural diversity—and, thus, biodiversity—over time (Hunter, 1990). Irregular shelterwoods and seed–tree cuts can be a cost-effective way to regenerate some plantations. Especially in large plantations of shade-tolerant species, a series of smaller harvest gaps or strips might be effectively regenerated by seeds from the canopy, possibly eliminating planting or herbicide costs. The ability to control stocking and use genetically-improved seedlings are important advantages of planted versus natural stands, so ''natural'' regeneration methods might be undesirable in situations where these factors are seen as crucial.

In areas where nutrients are limited, how trees are harvested and delimbed also has important implications for long-term productivity. A high priority should be placed on delimbing trees as near as possible to where they were cut, and leaving tops on site. Foliage and branches contain such disproportionately high nutrient levels that if they are left on site after logs are removed, most of the total nutrients on that site will be conserved (Stanley and Montagnini, 1999). However, logging residues (i.e. slash) can make a site difficult to plant if not chopped, crushed, or burnt (Smith, 1986), which generally reduces its value for biodiversity (see Sections 6 and 8.3).

4. Native versus exotic species

From a biodiversity perspective, the most contentious aspects of plantation forestry are the widespread use of exotic species, and the fact that large areas have been converted into unnatural forest-types (Keenan et al., 1995; Tucker et al., 1998). For the purposes of this section, I lump together exotic plantations and those where crop species are native to the region, but were previously uncommon, found on different ecotypes, or rarely formed pure stands. Critics of plantations argue that exotic stands are ''biological deserts'' (Allen et al., 1995), and that exotic species often 'escape' from plantations, encroaching upon and degrading adjacent native forests (Potton, 1994; Gill and Williams, 1996; Estades and Temple, 1999). Defenders of plantations assert that even exotic plantations usually contain more biodiversity than other intensive, human-influenced habitats such as cropland, and residential or commercial developments (O'Loughlin, 1995). Both points are valid, and ought to be taken into account by both sides. In recognition of these arguments, some countries (e.g. New Zealand) now prohibit the conversion of native forests to plantations and mandate that plantations replace formerly farmed land (Norton, 1998). If this policy was implemented in most regions, especially those already heavily planted, it would reduce concerns related to two controversial aspects of plantations: (1) that they contribute to loss of natural forests, and (2) they typically occupy sites with superior soils and drainage relative to surrounding areas, and thus, eliminate habitat for organisms restricted to these site conditions.

From a biodiversity perspective, native tree species should be favored over exotics, in part because there are a multitude of species (especially invertebrates and microorganisms) that are virtually unstudied, but might be adapted only to native trees. In many areas, there are native tree species with many of the same desirable characteristics as exotic trees and these should be used whenever differences are marginal or even moderate (Sedjo and Botkin, 1997). Some native tree species are disproportionately valuable for biodiversity because they provide resources such as mast, fruit, nectar, or cavities (e.g. *Populus* in temperate conifer plantations). Individuals and/or clumps of these species that are interplanted within exotic plantations or left during tending can have important ramifications for conservation (Norton, 1998). Interplantings can be done on areas that were disturbed during harvesting (e.g. skid trails), or used to buffer sensitive areas such as wetlands or watercourses.

Plantation genetics are also important to consider from a conservation perspective (Lambeth and McCullough, 1997), as genetic diversity is the fundamental unit of biodiversity (Hunter, 1996b). Individuals native to a given area can be uniquely adapted to local conditions. Conserving global and regional genetic diversity can prove to be economically invaluable, if a new pest or disease outbreak arises and only a few individuals are found to be resistant (Hunter, 1996b). If managers maintain genetic diversity among their planting stock they have more opportunity for long-term economic viability in the case of global climate change, pest outbreak, or other problems, because some individuals will respond better than others to changing conditions (Lambeth and McCullough, 1997).

5. Mixed-species versus monoculture

There is a long standing debate over whether to use mono- or polycultures when establishing plantations (Ball et al., 1995; Stanley and Montagnini, 1999). There are many benefits attributed to planting a mix of species, including: (1) more efficient nutrient use, thus, trees grow bigger, faster, (2) site quality and yields are conserved over time, (3) reduced risk of catastrophic damage from storms, insects, or disease outbreaks, (4) some 'nurse' species provide structure beneficial to primary crop species, e.g. training, shade, or protection from frost, (5) reduced economic risk by hedging bets against future markets, and (6) public opinion favors mixes over monocultures because they are thought to have higher ecological integrity due to higher species diversity. I review evidence for each of these assertions below. Note that mixed-species stands can be achieved by planting multiple species and by retaining native trees during pre-establishment harvest or thinning.

Mixed-species can use nutrients more efficiently than do pure stands because of differences among species in rooting patterns, mycorrhizal associations (Perry et al., 1992), shade-tolerance (Assmann, 1970), growth rate (Smith, 1986), form (Menalled et al., 1998), phenology (Keenan et al., 1995), nutrient demands (Kelty, 1992), soil mineralization rates (Matthews, 1989), litterfall, and abilities to fix nitrogen (Morgan et al., 1992). Many studies have found that species mixtures produced higher yields than do monocultures of individual species (Cannell et al., 1992; Kerr et al., 1992; Morgan et al., 1992; FAO, 1992; Khanna, 1997; Menalled et al., 1998), though some did not (Smith and Long, 1992). This so-called "mixture effect" is largely a function of a site's limiting factor(s), whether light, moisture, nutrients, etc. (Kelty, 1992). Mixes of species that differ in height (rather than diameter) growth, form, shade-tolerance, and phenology are most likely to increase site productivity (Kelty, 1992). Fiber yields are most likely to be higher if stratified stands are formed by intolerant species growing above shade-tolerant ones (Smith, 1986). Yields are also likely to increase when nitrogen-fixing species are planted on nutrient-poor sites. Cases such as these involve species with good ecological combining ability, meaning that they perform better in mixture than either does in monoculture (Menalled et al., 1998).

In an extensive review of studies from temperate and boreal regions, Burkhart and Tham (1992) showed that species mixes usually had equal or higher yields than did pure stands. Mixtures tend to outperform monocultures on poor sites (Binkley, 1992; Montagnini et al., 1995), whereas pure stands of a highly productive species can have higher merchantable yields on high quality sites (Burkhart and Tham, 1992; Kelty, 1992). The mixture of hardwoods in conifer stands is especially likely to be useful in temperate or boreal regions where nutrients are often limited by decomposition rates (Bowen and Nambiar, 1984). Species mixtures often have increased decomposition rates, in part because the carbon:nitrogen ratio of litter is improved and acidity is reduced. These changes stimulate microbial activity that increases nitrification and overall nutrient availability on sites (Matthews, 1989; Kelty, 1992). In spruce (*Picea*) stands in Sweden, benefits persisted even after hardwoods had disappeared from the stand (Bowen and Nambiar, 1984).

Monocultures are widely believed to be more vulnerable and susceptible to pest outbreaks (Lugo, 1997). Contradictions do exist, and overall experimental evidence is scant (Watt, 1992; Keenan et al., 1995). In the tropics, non-crop nurse trees have long protected species of the Meliaceae against attack by *Hypsipyla* insects (Ball et al., 1995). Risch (1981) shows how polycultures in general support lower densities of insect pests than do monocultures. Montagnini et al. (1995) found that some tropical plantations with mixed-species suffered less insect damage than did pure stands. Relative to heterogeneous stands, monocultures are (1) more vulnerable to pest outbreaks, and (2) suffer more damage during outbreak (Bragança et al., 1998). There is abundant evidence that spruce budworm (*Choristoneura fumiferana* (Clemens)) damage to fir (*Abies*) is less frequent and severe in mixed stands, with resistance and resiliency related to the proportion of hardwoods in the stand (Needham et al., 1999). In New Brunswick, a hardwood mix increased fir yields when defoliation was relatively high (>45%), but at low defoliation levels hardwoods reduced net fir yields by costing more in growing space than they "earned" in pest resistance (Needham et al., 1999). Here, a mixed-species strategy requires a greater land base for a given softwood volume, but also includes economic benefits from hardwood harvest. In addition, insect protection measures are necessary to avoid total losses during outbreaks in pure fir stands, but these costs are unnecessary in mixed-species stands.

Species mixtures often include retention of mature overstory nurse trees, chosen for its beneficial effects on the main crop species. In addition to nutrient synergisms (Kelty, 1992) and pest resistance (Stiell and Berry, 1985), these trees are used to protect crop species from frost (Nilsson, 1990; Groot and Carlson, 1996) and drought (Nilsson, 1990; Marsden et al., 1996); provide side shelter for training tree form (Smith, 1986); and increase wind stability (Kerr et al., 1992; Lugo, 1997). The retention of overstory trees in a young plantation can obviously have many benefits, but the costs are less clearly understood. Crop yields can be increased or decreased, depending on the species, site, canopy stocking, etc. Plantations of shade-tolerant species are the best candidates for canopy-retention above seedlings. Growth rates of spruce and fir in Maine were highest under 65% gap fraction, compared to open grown seedlings (McConville, 1998). In a review of temperate studies on spruce, fir, and cedar (*Thuja*), McConville (1998) found that four of nine studies showed maximum growth rates under some degree of canopy versus none, though this result did not extend to high quality sites in that study. If retention trees are used in plantations of shade-intolerant species (e.g. pine), yields are likely to decline. However, the loss of fiber can be small enough to be acceptable, if it is seen as a worthwhile tradeoff for the ecological and socio-economic benefits gained from having multi-structured stands. A model in Sweden indicated that leaving 10 mature pines per hectare will reduce pine yields by 5–10% over the rotation (B. Elfving, personal communication).

Polycultures reduce risks associated with the uncertainty of future economic markets (Kerr et al., 1992), and sometimes provide higher returns than do pure stands (Ball et al., 1995). In developing countries, mixed-species plantations might follow an agroforestry model, which allows for a wider range of products (e.g. coffee or cacao) for consumption or sale. Compared to timber, these commodities usually are available earlier and over a longer time frame (Keenan et al., 1995). Planting polycultures also avoids risks associated with lack of site suitability, establishment failures, and nutrient depletion (Evans, 1982; Kerr et al., 1992). Although, some experimentation will be necessary to optimize the species mix and ratio, plantation mixtures show much promise and should be seriously considered by managers (Stanley and Montagnini, 1999). Most studies support the public view that polycultures have more abundant and diverse flora and fauna than do monocultures (Bibby et al., 1989; Butterfield and Malvido, 1992; Donald et al., 1997). Especially where native species are planted, polycultures generally host many more animal species than monocultures because of the strong relationship between native plant diversity and animal diversity within a stand (Bibby et al., 1989; Bragança et al., 1998; Donald et al., 1998).

6. Site-preparation

Decisions related to preparation of a site for planting and initial control of competing vegetation have important implications for biodiversity. As discussed above, residual native vegetation within planted stands is most important to biodiversity. Many plant and animal species recorded within plantations are associated with "skips", where herbicide applications missed native vegetation (Morrison and Meslow, 1984; Santillo et al., 1989a). Whether by accident or design, the less perfectly that competing vegetation is eliminated from the stand the better, for most species. Because of unsuccessful attempts at elimination, some plantations contain a high proportion of the native woody plant species found on unplanted stands (T. Needham, personal communication), though this is likely less true for herbaceous plants.

On some sites scarification, plowing, crushing, or other intensive methods can promote rapid leaching of nutrients which can decrease long-term site productivity. Intensive site-preparation also has acutely negative impacts on biodiversity, because many species such as salamanders and invertebrates are associated with or entirely restricted to the forest floor (deMaynadier and Hunter, 1995). Most forest floor fauna have not been studied in terms of how they are affected by forest management (Freedman et al., 1996). In general, minimizing intensive site-preparation best conserves coarse woody debris and thus biodiversity (Carey and Johnson, 1995). In temperate or boreal regions the forest floor plays a critical role as a source of nutrient reserves, as it can contain more nutrients than the combined above-ground biomass or the mineral soil (McColl and Powers, 1984). Depending on how it is managed, the forest floor can either inhibit or enhance regeneration of crop trees.

In ecosystems adapted to fires, crop trees will respond positively when fire is used for site-preparation, and burned sites often will have more native plant and animal species (McColl and Powers, 1984; Fries et al., 1997). In the southeastern United States, burning maintains a diverse groundcover characteristic of longleaf pine (*Pinus palustris*) forests, even on planted sites that have been converted to other *Pinus* species (Tucker et al., 1998). This is important because the historic range of longleaf pine forests has been reduced by 97% (Frost, 1993), and many of the native species associated with this ecosystem decline within 3–5 years after burning (Tucker et al., 1998). Fortunately, burning is compatible with commercial forest management because it is an economical and effective way to reduce competing shrubs and increase growth and yield of crop species (Bower and Ferguson, 1968). Some species that benefit from burning also respond positively to thinning operations (Wilson and Watts, 1999). Not all taxa respond well to burns (e.g. amphibians, deMaynadier and Hunter, 1995), thus their conservation depends upon using a variety of management systems across the landscape mosaic. Also, in regions where fire is uncommon, burning can inhibit crop tree growth and reduce coarse woody debris and the biodiversity associated with it (Freedman et al., 1996).

7. Tending

How a site is managed in the first half of its rotation is of the utmost importance to both fiber production and biodiversity (McColl and Powers, 1984; Bailey and Tappeiner, 1998). Understory vegetation comprises one of the most important elements of biodiversity within plantations, and often is the single best predictor of animal diversity (López and Moro, 1997; Humphrey et al., 1999). Thinning young stands stimulates the regeneration and development of shrub and other understory layers, increases the survival and growth of intermediate and suppressed trees, and leads to structural attributes that more closely resemble old-growth forests (Carey and Johnson, 1995; Barbour et al., 1997; Bailey and Tappeiner, 1998). Earlier and heavier thinnings than normal will usually result in more plant and animal diversity (Peterken et al., 1992), and can still be economically viable (Barbour et al., 1997). Wider spacing can have positive economic implications because it increases diameter growth of individual crop trees, even if it does not maximize stand volume. Some animals prefer dense, unthinned thickets; so some plantations on the landscape or selected portions of many plantations should be left unthinned. Conversely, thinnings can incorporate variable spacing (e.g. 40–80 m wide strips) to provide spatial heterogeneity within the stand (Carey and Johnson, 1995). In some plantations this practice will benefit managers, because the cost of thinning is saved, and dense stands can produce high wood volumes (Barbour et al., 1997) and valuable knot-free timber (Fries et al., 1997).

As biodiversity often is influenced strongly and positively by the extent of native, non-crop vegetation associated with a plantation (Staines, 1983; Gill and Williams, 1996; Díaz et al., 1998), conserving biodiversity seems inherently at odds with pre-commercial tending that maximizes fiber production by minimizing competing vegetation. However, understories that contain much biodiversity are not necessarily bad for managers. Some models show that high structural diversity can be achieved by thinning regimes that produce reasonably similar volumes and qualities of timber (Barbour et al., 1997). Locasio et al. (1990) found that among five types of site-preparation, those that produced the best understory vegetation for forage biomass also exhibited average or above-average timber growth. In Spanish pine plantations, crop tree density had little effect on bird communities as long as some understory vegetation was conserved (López and Moro, 1997).

Much of the public controversy over plantation management relates to the use of chemical pesticides and fertilizers (Wagner, 1993; Wagner et al., 1998). In terms of biodiversity, herbicide applications generally reduce plant species and structural diversity of young stands, and thus can result in somewhat impoverished communities of birds (Morrison and Meslow, 1984; Santillo et al., 1989a; Parker et al., 1994), herpetofauna (Moore and Allen, 1999), and mammals (Santillo et al., 1989b; Lautenschlager, 1993). Though more research is needed, most studies to date have shown relatively minor differences between herbicide-treated and untreated areas. Where differences exist, they tend to be species–specific, related to seral associations, and generally do not persist for many years (Lautenschlager, 1993). The same can probably be said for fertilizers, which are used often in plantations (Moore and Allen, 1999), but have received little study in terms of how they affect biodiversity. In one study on industrial sludge as a fertilizer, effects on biodiversity were minor and due to changes in habitat structure (Vera and Servello, 1994). In a manner opposite to herbicides, fertilizers can increase vegetative structure, especially in the understory. Thus, both chemicals predictably affect some species positively and others negatively. Plant species richness can be maintained even on sites with repeated herbicide applications, especially when chemicals are applied in narrow strips directly along rows of seedlings (Moore and Allen, 1999).

The public perception that most pesticides and fertilizers harm wildlife directly is not generally shared by the scientific community (Lautenschlager, 1993; Wagner, 1993; Wagner et al., 1998), though there are important issues related to how chemicals affect biodiversity. Of greatest concern is that pesticides are often toxic to non-target species as well as those they are intended to kill. Where they occur, rare plants or insects that are not detrimental to plantations—and may even be beneficial—are often unintentionally killed by managers in addition to pest species. Similarly, chemicals end up in non-target areas such as aquatic ecosystems, where they can be more harmful to biodiversity—and to a broader range of taxa—than in terrestrial ecosystems. Also, pesticide compounds persist in some animal populations for decades after use (Perkins et al., 1998). Although these are important issues, economics dictate that pesticide use will usually be a necessary part of plantation forest management. Though pesticide use in plantations will likely remain controversial with the public (Wagner et al., 1998), regulations often are or can be put in place to ensure careful applications of pesticides. Also, the public can appreciate the fact that pesticides are used much less frequently in forestry than in annual agricultural systems, and will be applied only as frequently as economically necessary.

8. Summary of management recommendations

8.1. Harvest considerations

When converting natural stands to plantations or harvesting mature plantations, leave as many snags and cavity trees as possible. Plan to leave native vegetation as biological legacies throughout the second rotation, through one or more of the following: (1) dispersed individual retention trees, (2) aggregated clumps (i.e. microreserves or lifeboats), (3) linear strips (hedgerows or orchard rows), or (4) buffer strips along aquatic habitats. Delimb trees near the stump, and leave tops on site. Manage some plantations on longer rotations. Instead of clear-cutting all mature plantations, manage some via irregular shelterwood, seed–tree cuts, or selection silviculture.

8.2. Species composition

When possible favor native species over exotics. Where exotics are used widely, begin or increase planting of native species, increase emphasis on retaining areas of native vegetation, and spatially and temporally juxtapose exotic and native stands within a landscape. Retain or underplant especially important plant species that provide mast, fruit, nectar, or cavity resources. Maintain genetic diversity in all landscapes by using a variety of planting stock, and by retaining some local gene stock. Avoid widespread use of seed from a limited number of individuals, or clones. Instead of monocultures as the rule, they should be the exception in plantations. There are many ecological, operational, and economic benefits to having multiple crop or non-crop species within plantations, even if one species comprises 90% of a site. Mixed-species stands can be managed by planting multiple crop species, retaining desirable native species during harvest or tending, thinning (but not cleaning) competitor species to a desirable level, and augmenting monocultures either by underplanting established stands, or stocking a mix of species into natural or harvested gaps.

8.3. Site-preparation

Avoid intensive site-preparation that disturbs soil nutrients, promotes leaching and soil erosion, and destroys or reduces coarse woody debris. Leave some snags and downed coarse woody debris after site-preparation to maintain the many species associated with these structural elements. Where fires are naturally frequent, controlled burning is desirable over at least part of the landscape to promote native understory plants. Controlled burn frequency should approximate natural disturbance rates, which also reduces risk of fire damage to crops and controls competing shrubs.

8.4. Tending

Thin some plantations earlier and heavier than normal, to stimulate or maintain a diverse understory plant community. Leave other plantations (or sections thereof) unthinned to create a mosaic of relatively open areas and dense thickets. Allow incomplete herbicide applications that skip some areas, or thin competing vegetation to acceptable levels instead of trying to clean stands completely. This maintains a mixture of plant species that will better conserve biodiversity by providing habitat and forage for a wide array of native animals.

9. Discussion

Plantations have long been viewed strictly as tree farms, but I argue for a new perception that they have potential to conserve biodiversity while efficiently producing fiber. Managers with multiple plantations can view these stands as part of a replicated experiment that can be manipulated and examined across space and time to determine how fiber production and biodiversity are related in that system. With innovations in management and research on yield response and biodiversity, optimal designs can be chosen for each landowner or manager, in any context. I have presented many cases above where improvements in plantation management resulted in better conserving biodiversity without reducing fiber production, or with only moderate declines. However, this will not always be the case. Methods that are effective in one region might not work in another region, especially if applied to different crop species. Shade-intolerant systems are especially challenging in terms of finding "win–win" strategies for biodiversity and fiber production. In the Pacific northwest, Hansen et al. (1995) found that leaving only a few trees per hectare substantially increased abundance of birds, but caused declines in yield. In the same region, Birch and Johnson (1992) showed that leaving only 5 trees/ha over a 60-year rotation resulted in a volume only 70% that of stands that had been completely clear-cut.

In plantations, economic considerations are generally given more weight than in other industrial forest practices due to higher establishment and tending costs. This translates to a narrow focus on fiber production, but a neglect of biodiversity and other multiple-use considerations (Spellerberg and Sawyer, 1995). It can be difficult to compare the economic tradeoffs associated with practices that conserve biodiversity, but reduce fiber production (Richardson, 1994), and some speculation is involved. The best economic models and forecasts might not predict that a polyculture plantation will be much more valuable than a monoculture if the primary market for a given forest product closes or changes during the decades that the stand develops.

There are many relatively recent developments in society that shape how the public views forest management, for example: environmental movements and organizations, global-access to information via the internet, media coverage of the Rio Summit, biodiversity treaties, etc. (Hughes, 1994). Public opinion does and arguably should influence how forests are managed in some situations, e.g. timber concessions on public lands, increased forest legislation in many states and nations, green-certification, and consumer preferences. Public opinion heavily favors more natural forest management over artificial or intensive methods (Wagner et al., 1998). Thus, the public does not look favorably on traditional plantations even though this position is inconsistent with the fact that their personal efforts to conserve resources through recycling and reduced consumption lag. Foresters are often considered to have an ethical obligation to ensure that forest ecosystem processes are conserved or enhanced (Kenk, 1992). Failure to consider public opinion can be costly for foresters (Perley, 1994; Spellerberg and Sawyer, 1995), though it is difficult to estimate these costs and weigh them against silvicultural alternatives that can lower yields somewhat. With this in mind, it seems likely that proactive managers will be rewarded over time for including biodiversity considerations in plantation management practices, and for risking possible fiber reductions in order to experiment and evaluate potentially beneficial innovations in plantation management.

10. Conclusions

As human populations grow there will be continued growth in global demand for wood products (Moore and Allen, 1999), and much of this fiber likely will be grown on plantations. Plantation flora and fauna are typically impoverished compared to natural forests, so it is often assumed that they have little value for conserving biodiversity. However, plantations occur along a continuum from exotic monocultures with a very simple structure to heterogeneous stands of native species. There is abundant evidence that management of planted stands at any point along this continuum can be improved, so that they better conserve biodiversity while maintaining similar levels of fiber production and profitability. However, there is much work yet to be done in most areas to understand how various management methods affect fiber production (Burkhart and Tham, 1992), not to mention biodiversity (Keenan et al., 1995). Many of my recommendations can be viewed as hypotheses yet-to-be-tested in a given region or plantation type. Because of the complexity (Freedman et al., 1996) and long-term nature of these ecosystems and the research upon them (Wagner, 1993), critical comparisons and evaluations between traditional management methods and those recommendations suggested in this and other papers (Keenan et al., 1995) should be undertaken as soon as possible.

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References

Allen, R., Platt, K., Wiser, S., 1995. Biodiversity in New Zealand plantations. New Zealand For. 39 (4), 26–29.

Assmann, E., 1970. The Principles of Forest Yield Study. Pergamon Press, Oxford, 506 pp.

Bailey, J.D., Tappeiner, J.C., 1998. Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. For. Ecol. Manage. 108, 99–113.

Ball, J.B., Wormald, T.J., Russo, L., 1995. Experience with mixed and single species plantations. Common For. Rev. 74, 301–305.

Barbour, R.J., Johnston, S., Hayes, J.P., Tucker, G.F., 1997. Simulated stand characteristics and wood product yields from Douglas-fir plantations managed for ecosystem objectives. For. Ecol. Manage. 91, 205–219.

Bibby, C.J., Aston, N., Bellamy, P.E., 1989. Effects of broad-leaved trees on birds of upland conifer plantations in north Wales. Biol. Conserv. 49, 17–29.

Binkley, D., 1992. Mixtures of nitrogen-fixing and non-nitrogen-fixing tree species. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 99–123.

Birch, K., Johnson, K.N., 1992. Stand-level wood-production costs of leaving live, mature trees at regeneration harvest in coastal Douglas-fir stands. West. J. Appl. For. 3, 65–68.

Bowen, G.D., Nambiar, E.K.S., 1984. Nutrition of Plantation Forests. Academic Press, New York, 516 pp.

Bower, D.R., Ferguson, E.R., 1968. Understory removal improves short-leaf pine growth. J. For. 66, 421–422.

Bragança, M., De Souza, O., Zanuncio, J.C., 1998. Environmental heterogeneity as a strategy for pest management in Eucalyptus plantations. For. Ecol. Manage. 102, 9–12.

Burkhart, H.E., Tham, Å., 1992. Predictions from growth and yield models of the performance of mixed-species stands. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 21–34.

Butterfield, J., Malvido, J.B., 1992. Effect of mixed-species tree planting on the distribution of soil invertebrates. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 255–265.

Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young- and old-growth forests. Ecol. Appl. 5, 336–352.

Cannell, M.G.R., Malcolm, D.C., Robertson, P.A., 1992. The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, 312 pp.

Carlson, A., 1986. A comparison of birds inhabiting pine plantation and indigenous forest patches in a tropical mountain area. Biol. Conserv. 35, 195–204.

Chey, V.K., Holloway, J.D., Speight, M.R., 1997. Diversity of moths in forest plantations and natural forests in Sabah. Bull. Ent. Res. 87, 371–385.

Clout, M.N., 1984. Improving exotic forests for native birds. New Zealand J. For. 29, 193–200.

Currie, F.A., Bamford, R., 1982. The value to bird-life of retaining small conifer stands beyond normal felling age within forests. Q. J. For. 76, 153–160.

deMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the north American literature. Environ. Rev. 3, 230–261.

Díaz, M., Carbonell, R., Santos, T., Tellería, J.L., 1998. Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. J. Appl. Ecol. 35, 562–574.

Donald, P.F., Haycock, D., Fuller, R.J., 1997. Winter bird communities in forest plantations in western England and their response to vegetation, growth stage and grazing. Bird Study 44, 206–219.

Donald, P.F., Haycock, D., Fuller, R.J., Evans, A.D., Gough, S.J., 1998. Effects of forest management and grazing on breeding bird communities in plantations with broad-leaved and coniferous trees in western England. Biol. Conserv. 85, 183–197.

Estades, C.F., Temple, S.A., 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. Ecol. Appl. 9, 573–585.

Evans, J., 1982. Plantation forestry in the tropics. Oxford University Press, New York, 472 pp.

FAO, 1992. Mixed and pure forest plantations in the tropics and subtropics. United Nations Food and Agriculture Organization, Forestry Paper no. 103, Rome.

FAO, 1999. State of the world's forests 1999. United Nations Food and Agriculture Organization, Rome, 154 pp.

Ferns, P.N., Cowie, R.J., Weir, A.G., 1992. Managing conifer plantations for the benefit of granivorous birds and mammals. Aspects Appl. Biol. 29, 83–88.

Franklin, J.F., 1992. Scientific basis for new perspectives in forests and streams. In: Naiman, R. (Ed.), Watershed Management:

Balancing Sustainability and Environmental Change. Springer, New York, pp. 5–72.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century. Island Press, Washington, DC, pp. 111–139.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., Woodley, S., 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4, 238–265.

Friend, G.R., 1982. Bird populations in exotic pine plantations and indigenous eucalypt forests in Gippsland, Victoria. Emu 82, 80–91.

Fries, C., Johansson, O., Pettersson, B., Simonsson, P., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. For. Ecol. Manage. 94, 89–103.

Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Hermann, S.M. (Ed.), The Longleaf Pine Ecosystem: Ecology, Restoration, and Management. Proceedings of the Tall Timbers Fire Ecology Conference, Vol. 18, pp. 17–43.

Fuller, R.J., 1995. Bird-life of Woodland and Forest. Cambridge University Press, New York, 244 pp.

Gill, A.M., Williams, J.E., 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. For. Ecol. Manage. 85, 261–278.

Gjerde, I., Saetersdal, M., 1997. Effects on avian diversity of introducing spruce (*Picea* sp.) plantations in the native pine (*Pinus sylvestris*) forests of western Norway. Biol. Conserv. 79, 241–250.

Greenwood, M.S., Seymour, R.S., Blumenstock, M.W., 1988. Productivity of Maine's forests underestimated—more intensive approaches are needed. Coop. For. Res. Unit Info. Rep., Vol. 19, 6 pp.

Groot, A., Carlson, D.W., 1996. Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. Can. J. For. Res. 26, 1531–1538.

Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., Raphael, M.G., 1995. Alternative silvicultural regimes in the Pacific northwest: simulations of ecological and economic effects. Ecol. Appl. 5, 535–554.

Harris, L.D., 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago, 211 pp.

Hartley, M.J., Hunter Jr., M.L., 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conserv. Biol. 12, 465–469.

Hughes, H.R., 1994. Towards sustainable plantation forestry. New Zealand For. 39 (2), 16–18.

Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Koan, R., Jukes, M.R., 1999. Relationships between insect diversity and habitat characteristics in plantation forests. For. Ecol. Manage. 113, 11–21.

Hunter, M.L. Jr., 1990. Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity. Prentice-Hall, Englewood Cliffs, NJ, 370 pp.

Hunter, M.L., 1996a. Benchmarks for managing ecosystems: are human activities natural? Conserv. Biol. 10, 695–697.

Hunter, M.L., 1996b. Fundamentals of Conservation Biology. Blackwell Scientific Publications, Cambridge, MA, 482 pp.

Hunter, M.L., Calhoun, A., 1995. A triad approach to land use allocation. In: Szaro, R., Johnston, D. (Eds.), Biodiversity in Managed Landscapes. Oxford University Press, New York, pp. 447–491.

Keenan, R., Lamb, D., Sexton, G., 1995. Experience with mixed-species rainforest plantations in north Queensland. Common For. Rev. 74, 315–321.

Kelty, M.J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M.J. (Ed.), The Ecology and Silviculture of Mixed-species Forests. Kluwer Academic Publishers, The Netherlands, pp. 125–141.

Kenk, G.K., 1992. Silviculture of mixed-species stands in Germany. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 53–63.

Kerr, G., Nixon, C.J., Matthews, R.W., 1992. Silviculture and yield of mixed-species stands: the UK experience. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of trees. Blackwell Scientific Publications, Oxford, pp. 35–52.

Khanna, P.K., 1997. Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. For. Ecol. Manage. 94, 105–113.

Lambeth, C.C., McCullough, R.B., 1997. Genetic diversity in managed loblolly pine forests in the southeastern United States: perspective of the private industrial forest land owner. Can. J. For. Res. 27, 409–414.

Lautenschlager, R.A., 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. Can. J. For. Res. 23, 2286–2299.

Lindenmayer, D.B., Pope, M.L., Cunningham, R.B., Donnelly, C.F., Nix, H.A., 1998. Conserving biodiversity in intensively-managed exotic softwood plantations in Australia: preliminary results from a landscape-scale fragmentation experiment, Abstract. In: Gustafsson, L., Weslien, J.O., Palmer, C.H., Sennerby-Forsse, L. (Eds.), Biodiversity in Managed Forests—Concepts and Solutions, Sweden 1997. Report 1/98. The Forestry Research Institute of Sweden, Uppsala.

Locasio, C.G., Lockaby, B.G., Caulfield, J.P., Edwards, M.B., Causey, M.K., 1990. Influence of mechanical site-preparation on deer forage in the Georgia Piedmont. South. J. Appl. For. 14 (2), 77–80.

López, G., Moro, M.J., 1997. Birds of Aleppo pine plantations in southeast Spain in relation to vegetation composition and structure. J. Appl. Ecol. 34, 1257–1272.

Lugo, A.E., 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. For. Ecol. Manage. 99, 9–19.

Marsden, B.J., Lieffers, V.J., Zwiazek, J.J., 1996. The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. Can. J. For. Res. 26, 1015–1021.

Matthews, J.D., 1989. Silvicultural Systems. Clarendon Press, Oxford, 284 pp.

McColl, J.G., Powers, R.F., 1984. Consequences of forest management on soil–tree relationships. In: Bowen, G.D., Nambiar, E.K.S. (Eds.), Nutrition of Plantation Forests. Academic Press, New York, pp. 379–412.

McConville, D.J., 1998. Overstory canopy influences on height development of red spruce and balsam-fir saplings. Unpublished M.S. Thesis. University of Maine, Orono, ME, 59 pp.

Menalled, F.D., Kelty, M.J., Ewel, J.J., 1998. Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures. For. Ecol. Manage. 104, 249–263.

Michelsen, A., Lisanework, N., Friis, I., Holst, N., 1996. Comparisons of understorey vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. J. Appl. Ecol. 33, 627–642.

Montagnini, F., González, E., Porras, C., Rheingans, R., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Common For. Rev. 74, 306–314.

Moore, S.E., H.L. Allen, 1999. Plantation forestry. In: Hunter, M.L. Jr. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York, pp. 400–433.

Morgan, J.L., Campbell, J.M., Malcolm, D.C., 1992. Nitrogen relations of mixed-species stands on oligotrophic soils. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 65–85.

Morrison, M.L., Meslow, E.C., 1984. Response of avian communities to herbicide-induced vegetation changes. J. Wildlife Manage. 48, 14–22.

Moss, D., Taylor, P.N., Easterbee, N., 1979. The effects on songbird populations of upland afforestation with spruce. Forestry 52, 129–150.

Nambiar, E.K.S., 1984. Plantation forests: their scope and a perspective on plantation nutrition. In: Bowen, G.D., Nambiar, E.K.S. (Eds.), Nutrition of Plantation Forests. Academic Press, New York, pp. 1–15.

Needham, T., Kershaw Jr., J.A., MacLean, D.A., Su, Q., 1999. Effects of mixed stand management to reduce impacts of spruce budworm defoliation on balsam-fir stand-level growth and yield. North. J. Appl. For. 16 (1), 19–24.

Nilsson, N.-E., 1990. The forests. National Atlas of Sweden, 144 pp.

Norton, D.A., 1998. Indigenous biodiversity conservation and plantation forestry: options for the future. New Zealand For. 43 (2), 34–39.

O'Loughlin, C., 1995. The sustainability paradox—an examination of the plantation effect—a review of the environmental effects of plantation forestry in New Zealand. New Zealand For. 39 (4), 3–12.

Palik, B., Engstrom, R.T., 1999. Species composition. In: Hunter, M.L. Jr. (Ed.), Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, New York, pp. 65–94.

Parker, G.R., Kimball, D.G., Dalzell, B., 1994. Bird communities breeding in selected spruce and pine plantations in New Brunswick. Can. Field-Nat. 108, 1–9.

Perkins, D.W., Hodgman, T.P., Owen, R.B., Dimond, J.B., 1998. Long-term persistence of DDT in shrews, Soricidae, from Maine. Can. Field-Nat. 112, 393–399.

Perley, C., 1994. Biodiversity, sustainability and a land ethic. New Zealand For. 39 (1), 2–3.

Perry, D.A., Bell, T., Amaranthus, M.P., 1992. Mycorrhizal fungi in mixed-species forests and other tales of positive feedback, redundancy and stability. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 151–179.

Peterken, G.F., Ausherman, D., Buchenau, M., Forman, R.T.T., 1992. Old-growth conservation within British upland conifer plantations. Forestry 65, 127–144.

Potton, C., 1994. A public perception of plantation forestry. New Zealand For. 39 (2), 2–3.

Richardson, S.D., 1994. Economics and ethics: approaches to sustainable forest management. New Zealand For. 39 (1), 17–20.

Risch, S.J., 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 6, 85–98.

Robinson, S.K., Thompson III., F.R., Donovan, T.R., Whitehead, D.R., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987–1990.

Santillo, D.J., Brown, P.W., Leslie Jr., D.M., 1989a. Response of song-birds to glyphosate-induced habitat changes on clear-cuts. J. Wildlife Manage. 53, 64–71.

Santillo, D.J., Leslie Jr., D.M., Brown, P.W., 1989b. Response of small mammals and habitat to glyphosate application on clear-cuts. J. Wildlife Manage. 53, 164–172.

Schieck, J., Stuart-Smith, K., Norton, M., 2000. Bird communities are affected by amount and dispersion of vegetation retained in mixedwood boreal forest harvest areas. For. Ecol. Manage. 126, 239–254.

Sedjo, R.A., Botkin, D., 1997. Using forest plantations to spare natural forests. Environment 39 (10), 14–20, 30.

Seymour, R.S., Hunter, M.L. Jr., 1994. New forestry in eastern spruce-fir forests: principles and applications to Maine. Maine Agricultural and Forest Experiment Station, Misc. Publication, 716 pp.

Smith, D.M., 1986. The Practice of Silviculture. Wiley, New York, 527 pp.

Smith, F.W., Long, J.N., 1992. A comparison of stemwood production in monocultures and mixtures of *Pinus contorta* var. *latifolia* and *Abies lasiocarpa*. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 87–98.

Spellerberg, I.F., Sawyer, J.W.D., 1995. Multiple-use, biological diversity and standards. New Zealand For. 39 (4), 21–25.

Staines, B.W., 1983. The conservation and management of mammals in commercial plantations with special reference to the uplands. In: Harris, E.H.M. (Ed.), Forestry and Conservation. Royal Forestry Society, pp. 38–51.

Stanley, W.G., Montagnini, F., 1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. For. Ecol. Manage. 113, 91–103.

Stiell, W.M., Berry, A.B., 1985. Limiting white pine weevil attacks by side shade. For. Chron. 61, 5–9.

Stokland, J., 1998. Managed and unmanaged coniferous forests: differences in coarse woody debris and the diversity of wood-inhabiting fungi, Abstract. In: Gustafsson, L., Weslien, J.O., Palmer, C.H., Sennerby-Forsse, L (Eds.), Biodiversity in Managed Forests—Concepts and Solutions, Sweden 1997. Report 1/98. The Forestry Research Institute of Sweden, Uppsala.

Trexler, M.C., 1995. Keeping it green: tropical forestry opportunities for mitigating climate change. World Resources Institute, 60 pp.

Tucker Jr., J.W., Hill, G.E., Holler, N.R., 1998. Managing mid-rotation pine plantations to enhance Bachman's sparrow habitat. Wildlife Soc., Bull. 26, 342–348.

Vera, C.J., Servello, F.A., 1994. Effects of paper mill sludge in spruce-fir forests on wildlife in Maine. J. Wildlife Manage. 58, 719–727.

Wagner, R.G., 1993. Research directions to advance forest vegetation management in north America. Can. J. For. Res. 23, 2317–2327.

Wagner, R.G., Flynn, J., Gregory, R., Mertz, C.K., Slovic, P., 1998. Acceptable practices in Ontario's forests: differences between the public and forestry professionals. New For. 16, 139–154.

Watt, A.D., 1992. Insect pest population dynamics: effects of tree species diversity. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees. Blackwell Scientific Publications, Oxford, pp. 267–275.

Wigley, T.B., Roberts, T.H., 1997. Landscape-level effects of forest management on faunal diversity in bottomland hardwoods. For. Ecol. Manage. 90, 141–154.

Wilson, M.D., Watts, B.D., 1999. Response of brown-headed nuthatches to thinning of pine plantations. Wilson Bull. 111, 56–60.

Woodley, S., Forbes, G., 1997. Forest management guidelines to protect native biodiversity in the Fundy Model Forest. Unpublished report by New Brunswick Coop. Fish and Wildlife Research Unit. University of New Brunswick, New Brunswick, 35 pp.

World Resources Institute, 1998. World Resources 1998–1999. Oxford University Press, Oxford, 369 pp.

Zanuncio, J.C., Mezzomo, J.A., Guedes, R.N.C., Oliveira, A.C., 1998. Influence of strips of vegetation on Lepidoptera associated with *Eucalyptus cloeziana* in Brazil. For. Ecol. Manage. 108, 85–90.