Planted Forests and Biodiversity

Jean-Michel Carnus, John Parrotta, Eckehard Brockerhoff, Michel Arbez, Hervé Jactel, Antoine Kremer, David Lamb, Kevin O'Hara, and Bradley Walters

ABSTRACT

Expansion of planted forests and intensification of their management has raised concerns among forest managers and the public over the implications of these trends for sustainable production and conservation of forest biological diversity. We review the current state of knowledge on the impacts of plantation forestry on genetic and species diversity at different spatial scales and discuss the economic and ecological implications of biodiversity management within plantation stands and landscapes. Managing plantations to produce goods such as timber while also enhancing ecological services such as biodiversity involves tradeoffs, which can be made only with a clear understanding of the ecological context of plantations in the broader landscape and agreement among stakeholders on the desired balance of goods and ecological services from plantations.

Keywords: biological diversity, conservation biology, planted forests, stand management, landscape management

Plantation forests or planted forests are cultivated forest ecosystems established by planting or seeding or both in the process of afforestation and reforestation (Helms 1998), primarily for wood biomass production but also for soil and water conservation or wind protection. Although the total area of plantation forest (187 million ha) currently represents only 5% of the global forest cover (Food and Agriculture Organization [FAO] 2001), their importance is rapidly increasing as countries move to establish sustainable sources of wood fiber to meet the increasing demand for wood pulp and energy. This is particularly the case in Asia, where an estimated 62% of the global plantation forest estate is located. Industrial plantations (supplying industrial wood and fiber) account for 48% of the global plantation estate. These typically consist of intensively managed, even-aged, and regularly spaced stands of a single tree species (indigenous or exotic), often genetically improved, and are characterized by relatively short rotations when compared with naturally regenerated stands (i.e., "natural forests" in FAO terminology). Nonindustrial plantations, established for fuelwood, soil and water conservation (e.g., watershed rehabilitation), and wind protection, account for 26% of the world's plantation forests, and an additional 26% of plantation forests are established for other, unspecified, purposes (FAO 2001).

During the 1990s, while natural (i.e., naturally regenerated) forest and total forest areas continued to decline at the global level, forest plantation areas increased in both tropical (+20 million ha) and nontropical (+12 million ha) regions. In both tropical and nontropical regions, the conversion of natural forests and reforestation of nonforest areas have contributed in roughly similar proportions to these increases in forest plantation areas during this period (FAO 2001). It is worth noting that between 1990 and 2000, the rate of conversion of natural to plantation forests in tropical regions was about equal to the increase in natural forests, resulting from natural regeneration of nonforest areas, and only 7% of the area of natural forest converted to nonforestland uses. In nontropical areas the net increase in natural forest areas was more than three times the rate of conversion of natural to plantation forests.

About 60% of plantation forests are located in four countries (China, India, Russian Federation, and the United States). Species in the genera *Pinus* and *Eucalyptus* are the most commonly used in plantations (30%), although the overall diversity of planted tree species is increasing (FAO 2001). Table 1 provides a summary of plantation forest areas and their geographic distribution.

What Is Biodiversity?

Biological diversity is defined as "the variability among living organisms from all sources including . . . diversity within species, between species and of ecosystems" (*Convention on Biological Diversity*, United Nations 1992). Forest ecosystems shelter a major part of terrestrial biological diversity, including an estimated 80% of all terrestrial species; approximately 12% of the world's forests are presently in protected areas (FAO 2001). The importance of maintaining biodiversity in forest ecosystems has been emphasized in the past 10 years at political levels through many international conventions and agreements promoting sustainable forest management (SFM) including the Montreal and Pan-European Processes, and at commercial levels as part of forest certification schemes (e.g., Forest Stewardship Council and Programme for the Endorsement of Forest Certification). Thus, biodiversity is an issue of increasing relevance to plantation forests and their long-term sustainability; as a criterion for SFM, it is becoming clear that maintenance of biological diversity has direct implications for plantation forests and their management.

Biodiversity in a forest ecosystem is de-

Table 1. Plantation forests area by region, 2000.

Region	Total forest area (million ha)	Natural forest area (million ha)	Forest plantation area (million ha)	Total plantation area (%)
Africa	650	642	8	4
Asia	548	432	116	62
Europe	1039	1007	32	17
North and Central America	549	532	18	9
Oceania	198	194	3	2
South America	886	875	10	6
World total	3869	3682	187	100

Source: FAO 2001

termined and influenced by climatic and soil conditions, evolution, changes in species' geographical ranges, population and community processes, and natural or human-related disturbances. Ecological processes and biodiversity change over time as ecosystems recover from natural or human-induced disturbances. Disturbances can either increase or decrease biological diversity depending on the scales and measures of biodiversity being considered; for many measures, the highest levels of biodiversity are found in forests that have been subjected to intermediate frequencies, scales, and intensities of disturbance (Kimmins 2000).

Four components of biological diversity are of particular relevance to discussions on planted forests and their environmental impacts:

- Genetic diversity. The genetic variation within a population or a species.
- Species diversity. The frequency and diversity of different species in a particular area or community.
- Structural diversity. How forest plant communities are structured both horizontally and vertically, which changes continuously as stand development proceeds and is particularly significant in plantation forests. Structural diversity can be as important for animal species diversity as is the diversity of plant species in the forest plant communities.
- Functional diversity. Variation in functional characteristics of trees and other plant species, i.e., evergreen versus deciduous, shade tolerant versus light demanding, deep-rooted versus shallow-rooted, and others.

The aforementioned measures of biological diversity can be applied at various scales and are dynamic, changing over time. This change can be quite rapid, as a result of disturbance, or slow, as a result of climate change or species evolution. Much of the focus in discussions about biodiversity has been at the species and local ecosystem level; however, biodiversity measures at this level exhibit the greatest temporal variation.

In the following sections we will discuss and attempt to summarize the current state of scientific knowledge regarding the impacts of planted forests and their management on biodiversity. We will consider key issues related to intraspecific diversity, focusing on genetic diversity within tree plantations, as well as the influence of planted forests on interspecific diversity within planted forests and in surrounding landscapes. In addition, we will consider the role of biodiversity in planted forests and the strategies for managing planted forests to conserve and enhance biological diversity at various spatial scales from the forest stand to the landscape level.

Genetic Diversity

Characterization of Genetic Diversity in Tree Plantations. As a fundamental component of global biodiversity, genetic diversity includes the intraspecific variation between individual trees, e.g., genes, within populations and between populations (races, ecotypes, and provenances). This genetic diversity largely controls adaptability and resistance to abiotic and biotic disturbances.

In the past 10 years, the rapid development of tools (e.g., molecular markers) for analyzing the genetic variability of forest trees (Petit et al. 1997) has enabled scientists to better characterize and assess pollen fluxes between individuals and populations, spatial distributions of genetic diversity within stands, and to better understand the effects of silvicultural practices on the long-term evolution of genetic diversity of forest trees. Also, the molecular characterization of the plantation tree populations and improved varieties enable us to better manage and control the movements of forest reproductive materials (FRM; Ribeiro et al. [2002]).

Modification of Genetic Pools (New Species and Seed Transfer). Despite the growing body of scientific information available to assess the possible impacts of plantations on intraspecific genetic diversity of forest trees, broadly applicable generalizations remain elusive. This impact is influenced clearly by the type of FRM used in plantations, the quality of available and registered FRM genetic information, and the feasibility of controlling gene exchange in the field. In addition, the impact of plantations on genetic diversity depends on the level of genetic variability of the FRM itself, as well as on the possibility of gene exchanges between the planted FRM and surrounding forest tree gene pools. At the regional forest tree diversity level, the final impact of plantations established with a controlled FRM depends also on the total area afforested with this FRM and duration of its use. A key challenge for sustainable plantation forest management is to anticipate, evaluate, and manage risks posed by natural regeneration and spread of highly selected FRM outside of plantation areas, especially hybrid, clonal, or genetically modified (GM) varieties that are, initially, planned to be clearcut and replanted.

As has occurred earlier in agriculture, the introduction of genetically improved exotic species in forestry increases productivity and carbon-fixation efficiency. In some regions these introductions also have increased interspecific diversity at landscape and regional scales. In France, e.g., compared with 70 natural forest tree species, 30 introduced species are commonly used in plantation forestry, which often helps to increase the interspecific genetic diversity of forests at the local level (Le Tacon et al. 2000, 2001). More generally, in Europe, the forest flora was very diverse at the end of the tertiary period (approximately 1.6 million years ago), and numerous species disappeared during successive glacial periods. In Europe, at least, there is no doubt that the introduction of new species has partly restored this species richness.

Although popular in the past, introduction of exotic species lately has been limited in many countries because of greater concern about the risks associated with these introductions. Confirmation of long-term adaptation to environmental conditions (drought and frost resistance, tolerance to hydromorphic soil conditions, and so on)

and pest resistance is necessary for the use of exotic species in extensive plantation programs, to avoid severe damage. Also, exotic species can have negative impacts on native species and communities that need to be evaluated (Mack et al. 2000). For example, fast-growing species can replace native forest tree species because of their natural invasive potential, as has been observed, e.g., with eucalyptus in northwestern Spain and Portugal.

Impact of Using Genetically Improved FRM. FRM collected from registered seed stands results in plantation forests with a level of genetic diversity most often similar to the wild population from which it originates. The main genetic impacts depend on the level of adaptation of the introduced population to its new environment and the possible gene transfers from it to the surrounding native population. In this regard, the possible undesirable impacts of long-distance seed transfer require special consideration. With the development of selection programs for plantation tree species, the level of genetic diversity of the planted material has been progressively restricted, as with single or controlled mixtures of full-sib families, clonal varieties, or GM trees that may be used in the future. Consequently, such FRM could be expected to have a lower adaptability and pose increased ecological risks over the same rotation time (Gadgil and Bain 1999, Evans 1999, Wingfield 1999). However, those risks may be minimized by adapting management practices, including the quick turnover of short-rotation tree crops if the FRM is not adapted. Also, the genetic information that has been largely developed in recent years allows the forest owner to better balance the expected economic gains and the ecological risks, and there are relevant and well-known breeding strategies and gene conservation procedures that can facilitate maintenance of the genetic variability of the plantation species over several generations.

Clonal Varieties. A major concern arising from the use of clonal plantation forestry is the maintenance of stand adaptability, i.e., the ability to face an unexpected catastrophic perturbation due to biotic or abiotic causes. Does the increased use of clonal planting stock contribute to a decrease in stand viability? What is the optimal number of clones needed to minimize risks in clonal plantations? Although most regulations implicitly assume that planting more clones will minimize risks of plantation failure, theoretical investigations, based on simplified situations in which susceptibility to pest attack is controlled by one single diallelic locus (Bishir and Roberds 1999), have shown that there is no single answer to those questions and that risks can decrease, remain constant, or increase as the number of clones increases. To cover most situations, Bishir and Roberds (1999) recommend using clonal mixtures including 30–40 genotypes, beyond which the level of risks is unlikely to change significantly.

GM Trees in Commercial Varieties. Currently, gene transfer is being tested in most forest species undergoing intensive breeding activities (radiata pine, Scots pine, maritime pine, Sitka spruce, Norway spruce, eucalyptus, poplars, and others). In conjunction with other biotechniques such as somatic embryogenesis, rapid and important genetic gains can potentially be transferred to forestry. Transgenesis has been considered as an attractive tool for genetically improving trees for pest and insect resistance, wood properties, and lignin content (Jouanin 2000). Benefits expected from transgenesis are increased ecological sustainability and economic efficiency of wood production by improving and homogenizing target traits, increased adaptability and resistance to biotic and abiotic stresses, and reductions in the use of undesirable insecticides and other pesticides. For example, poplar, European larch, and white spruce have been engineered for a gene encoding an insecticide toxin from the soil bacterium *Bacillus thuringiensis* (Bt). To date, there are a total of 117 experimental plantations with GM trees belonging to 24 trees species around the world, but no commercial GM tree plantations have been reported. The main risks for biodiversity (Kremer 2002) are related to the dissemination of GM material that might result in introgression with related tree species (Matthews and Campbell 2000) and in the spread, through natural regeneration, of GM trees that are potentially better adapted to site conditions (Hayes 2001). As for annual crops, the potential use of transgenic trees in forestry has raised concerns in the public and among foresters and scientists and has motivated vandalism and other criminal acts. These unfortunate events illustrate the sharp controversy surrounding transgenic trees that exists not only between the public and the scientific community, but also within the scientific community. There is an urgent need for an in-depth debate on benefits and risks associated with transgenic technology in forestry, considering scientific, economic, social, and ethical aspects.

Interspecific Diversity

Species Diversity in Plantation Forests versus Naturally Regenerated Stands and Other Habitats. It is widely thought that plantation forests, typically, are less favorable as habitat than naturally regenerated stands for a wide range of taxa, particularly in the case of even-aged, single-species stands involving exotic species (Hunter 1990, Hartley 2002). In support of this notion, the bird fauna of single-species plantation forests has been reported to be less diverse than that of natural or seminatural forests (Helle and Mönkkönen 1990, Baguette et al. 1994, Gjerde and Sætersdal 1997, Fischer and Goldney 1998, Twedt et al. 1999). Carabid beetles were found to be more abundant and diverse in natural or seminatural forests than in spruce plantations in Ireland (Fahy and Gormally 1998) and Hungary (Magura et al. 2000). Similar results were obtained in studies of beetles in South Africa (Samways et al. 1996), dung beetles in Borneo (Davis et al. 2000), and arthropods in general in Brazil (Chey et al. 1997) and New Zealand. The vegetation in conifer plantations was found to be less diverse than that in seminatural woodlands in Ireland (Fahy and Gormally 1998) and in Great Britain (Humphrey et al. 2002).

However, we believe such findings should not be overgeneralized because in some cases the species diversity in plantation forests may be comparable with that in naturally regenerated stands. For example, species richness of indigenous birds in New Zealand was only slightly lower in pine plantation forests (Clout and Gaze 1984) and, in some cases, bird counts in these plantations exceed those of most naturally regenerated stands (Brockie 1992). Bird species richness in a *Lophostemon* plantation in Hong Kong was similar to that in secondary forests (Kwok and Corlett 2000). In Great Britain, the fungal and invertebrate communities in conifer plantations have been found to be similar to those in natural woodlands (Humphrey et al. 1999, 2000, 2002).

The differences in species composition and diversity between plantations and naturally regenerated stands can be attributed to a number of factors. The use of exotic tree species in plantations has implications for indigenous forest species (Kholi 1998), which may have certain requirements that are not met by the exotic tree species or the

Figure 1. Understory and plant species diversity in low-density, third-rotation *Pinus pinaster* plantations in the Landes region of Gascony in southwestern France. (Photo courtesy of the European Institute for Cultivated Forests/INRA, France.)

habitat they create. For example, exotic tree species in Britain are inhabited by far fewer herbivorous insects than are found in indigenous forests (Kennedy and Southwood 1984). By contrast, vascular plant species generally are not as discriminative and can colonize plantation forests regardless of the identity of the canopy species, provided the physical characteristics of the habitat are appropriate. Some plantations can have a highly diverse understory of indigenous species (Allen et al. 1995, Keenan et al. 1997, Oberhauser 1997, Viisteensaari et al. 2000, Yirdaw 2001, Brockerhoff et al. 2003). However, there is considerable variation in the richness and abundance of understory plants among planted forest stands. Some of this variation can be attributed to the amount of light available to understory plants (Cannell 1999, Brockerhoff et al. 2003), as illustrated in Figure 1. Particularly dense stands of spruce and Douglas fir can cast so much shade that they appear literally to shade out the understory vegetation (Humphrey et al. 2002). Likewise, single-species plantations of *Rhizophora* (Figure 2) may prevent site colonization of other, nonplanted mangrove species (Walters 2000, but see Bosire et al. 2003). In contrast, plantations with more open canopies have been found to have greater density, size, and richness of woody species colonizing the understory (Lemenih et al. 2004).

Generally, silvicultural and site management practices in planted forests have direct impacts on stand dynamics and structure and will greatly influence biodiversity. Intensity of site preparation, stand establishment, control of competing vegetation, precommercial or commercial thinning, pruning, methods, and timing of harvest largely

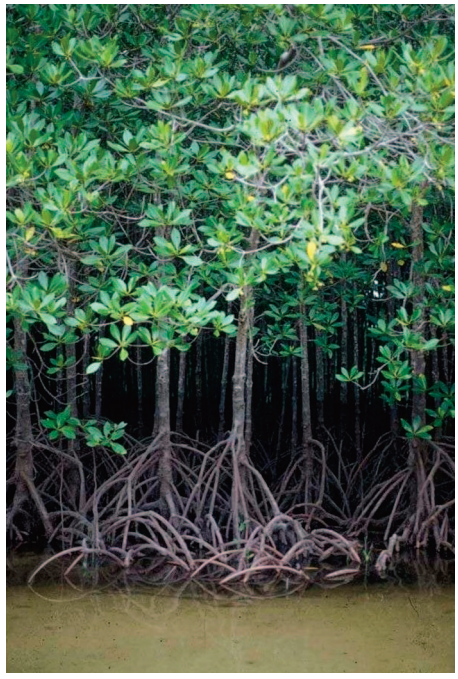

Figure 2. The use of dense spacing in tree plantings, such as these *Rhizophora stylosa* (mangroves) in the Philippines, reduces colonization of nonplanted tree species and hinders biodiversity recovery. (Photo courtesy of Bradley Walters.)

determine the rate of stand development, the initiation and duration of stem exclusion and other stages of stand development, and changes in tree architecture and stand structure. The harvesting method of clearcutting places a strong constraint on species inhabiting plantations and can dramatically change the species composition of understory plants (Allen et al. 1995), although the subsequent succession often restores the preclearcut understory vegetation (Brockerhoff et al. 2001). Fertilizer use can lead to reductions in the populations of some native plant species but increases in the populations of others, especially if the site was degraded before reforestation. Fertilization also may induce an increase in microbial diversity by accelerating turnover of organic matter (Nys 1999). There is limited knowledge of effects of planted forests on the diversity of soil biota compared with other land uses; it has been shown that longer rotations foster soil biodiversity for loblolly pine plantations in the southeastern United States (Johnston and Crossley 2002) and also that short-rotation plantations have positive effects on biological soil fertility in the Congolese savanna environment (Bernhard-Reversat 2001). Herbicide or insecticide application, which often is associated with intensive management of plantation forests, also can result in a temporary decrease in plant, fungi, and insect biodiversity (Dreyfus 1984). Short-rotation management also can reduce the quantity of dead wood that is beneficial to saproxylic insect species (Jukes et al. 2002) or bryophyte species (Ferris et al. 2000) and may decrease the opportunities for colonization by poorly dispersed, late-successional native plant species (Keenan et al. 1997). Short rotations also will limit the extent to which structurally complex understory development will occur, which can limit the suitability of plantation for some wildlife species.

But such comparisons are not necessarily the most appropriate ones to make. Although the conversion of old-growth forests, native grassland, or some other natural ecosystem to plantation forests rarely will be desirable from a biodiversity point of view, planted forests, in fact, often replace other land uses including degraded lands. Where they are established on abandoned pastures or degraded land, plantation forests usually are more beneficial to biodiversity than such modified agricultural areas. For example, in New Zealand pasture is known to be dominated by exotic species and to be a particularly poor habitat for indigenous species whereas the understory of pine plantations usually includes many indigenous plant species (Brockerhoff et al. 2001). In many circumstances plantations may be the only economic means by which to overcome large-scale degradation. In these circumstances the issue is not whether to establish plantations but, rather, what kind of plantation to establish.

Comparisons of plantations with other types of forests also are made more complex because the biodiversity in plantations depends very much on plantation age. Numerous studies performed during the past 15 years have indicated that planted forests, including plantation monocultures, can accelerate natural forest regeneration on degraded sites where persistent ecological barriers to succession would otherwise preclude recolonization by native forest species (cf. Parrotta and Turnbull [1997], Parrotta [2002]). This facilitative role of planted forests is due to their influence on understory microclimatic conditions, vegetation structural complexity, and development of litter and humus layers during the early years of plantation growth. This means biodiversity within plantations tends to increase over time. Documented examples of the "cata-

Figure 3. Plantation forests can have an understory of native plants, such as these tree ferns in a 27-year-old *Pinus radiata* stand in New Zealand. In such stands, the term "monoculture" only applies to the canopy species. (Photo courtesy of Eckehard Brockerhoff.)

Figure 4. A kiwi (*Apteryx mantelli*) in a pine plantation. These flightless birds are New Zealand's biodiversity icon, and large populations occur in several plantation forests that provide suitable habitat for this threatened species. (Photo courtesy of Rogan Colbourne.)

lytic effect" of forest plantings on degraded landscapes can be found in many tropical, subtropical, and temperate countries. In the Mediterranean region, e.g., artificial forests created at the end of the 19th century to rehabilitate overgrazed grasslands and for watershed protection, and, subsequently, thinned and harvested, have reverted naturally to mixed conifer-broadleaf forests similar in structure and species composition to those that existed before their degradation caused by overgrazing, overharvesting, and fire. These examples highlight the need for consideration of the land-use history when evaluating species richness in plantation forests.

Characteristics of Species That Can Benefit from Planted Forests. As a habitat for other species, plantation forests are characterized by some constraints resulting from their more- or less-intensive management (see above). Clearcutting and comparatively short rotations favor the occurrence of ruderal plant species whereas some long-lived climax species may not be present, and harvesting disturbance may enable invasive exotic plants to invade plantation forests (Allen et al. 1995). However, older stands can provide habitat for indigenous shade-tolerant species that are typical of the understories of naturally regenerated stands (cf. Allen et al. [1995], Brockerhoff et al. [2001]; Figure 3). Similar patterns have been observed for birds (Clout and Gaze 1984), typically for relatively common species. All such species benefit from the additional habitat provided by plantation forests if they have replaced less-suitable habitat. Plantation forests also can accommodate edge-specialist species (Davis et al. 2000) and generalist forest species that would benefit from any forest type (Christian et al. 1998, Ratsirarson et al. 2002).

Rare or threatened species often are not reported from plantation forests, but this is perhaps because of a lack of scientific study. Some notable cases of occurrence of such species exist, and these often are significant findings both as conservation issues and because they can have implications for the management of plantations. For example, large populations of threatened kiwi inhabit some pine plantations in New Zealand (Kleinpaste 1990). The occurrence of these flightless endemic birds and other threatened species challenges plantation forest managers (Brockerhoff et al. 2001; Figure 4). Another interesting case involves the critically endangered ground beetle, *Holcaspis brevicula*, a local endemic that has lost all of its natural habitat, primarily to agricultural land uses, and is today known to occur only in a plantation forest (Brockerhoff et al. 2005).

Spatial Considerations. The role of plantation forests in benefiting biodiversity at a regional level depends very much on the location of the plantation within the landscape. In some circumstances, plantation forests can potentially have negative effects on adjacent communities because of invasive natural regeneration of planted trees in adjacent habitats (Engelmark 2001) or alteration of hydrologic properties and aquatic life in connected watercourses through reductions in water yield as a consequence of afforestation or degradation of water quality by sediment movement generated from logging tracks, newly constructed roads, or poor management practices of riparian strips (Maclaren 1996). On the other hand, they also can make an important contribution to biodiversity conservation at the landscape level by adding structural complexity to otherwise simple grasslands or agricultural landscapes and fostering the dispersal of species across these areas (Hunter 1990, Parrotta et al. 1997, Norton 1998). Even plantation forests that are less diverse than naturally regenerated stands can increase bird diversity at landscape and regional scales, when they have habitat characteristics that are favored by some species and are located in appropriate places (Gjerde and Sætersdal 1997). In most tropical regions, wildlife species (especially bats and birds) are of fundamental importance as dispersers of seeds and soil microorganisms. Their effectiveness in facilitating plantation-catalyzed biodiversity development on deforested, degraded sites depends on the distances they must travel between seed sources (remnant forests) and plantations, the attractiveness of the plantations to wildlife (ability of plantations to provide habitat and food), and the condition of the forests from which they are transporting seeds (cf. Wunderle [1997]). Plantation forests adjacent to exposed remnants of indigenous forest therefore can be beneficial because they provide shelter, reduce edge effects, and enlarge the habitat for some species, and they also can serve to increase connectivity among forest fragments (Norton 1998). Such effects are most important in regions with sparse indigenous forest vegetation.

Of course not all plantations generate benefits such as these, and there still is much uncertainty about just how these outcomes might be achieved. Little is known, e.g., of just how much of a deforested landscape must be reforested to allow biodiversity and self-sustaining forest ecosystems to be reestablished. Likewise, little is known of where trees might be replanted in a fragmented landscape to achieve an optimal biodiversity outcome.

Plantations and Reduced Pressure on Natural Forests. It has been argued that plantations may protect natural biodiversity indirectly by enabling greater wood production from smaller, intensively managed areas, thus sparing remaining natural forests from harvesting pressure (cf. Sedjo and Botkin [1997], Rudel [1998]). Wood production from plantation forests is growing rapidly in many countries, yet there have been few attempts to assess whether such increased production actually has benefited natural forests and their biodiversity (Cossalter and Pye-Smith 2003). Mangrove

plantations in the Philippines have enabled some reduction in harvesting pressure from nearby natural stands (Walters 2004). In New Zealand, the importance of plantation forestry as a means of producing wood products has allowed the protection and conservation of indigenous natural forests; also, it is argued that through production and export of roundwood, which usually is obtained from old-growth forests, New Zealand plantation forests help to reduce exploitation pressure on old-growth forests in other countries (Maclaren 1996). However, a study of the Chilean forest industry found the contrary: harvesting pressure on natural forests actually increased as plantation production grew (Clapp 2001). In any case, understanding the relationship between plantations and natural forests is complicated by questions of timing and scale. There is a considerable time lag between when plantations are established and when they become producers of wood products that would otherwise be obtained from natural forests and the more regional and global markets for wood products there are, the more difficult it is to assess how changes in production from one forest impact production from others. These challenges notwithstanding, this is a topic that merits serious attention from forest researchers.

Figure 5. A 60-year-old mixed plantation of *Araucaria cunninghamii* and *Flindersia brayleyana* in southern Queensland, Australia. Both species have similar growth rates on this site although the *Araucaria* is more shade tolerant and has a deeper crown than the *Flindersia*. (Photo courtesy of David Lamb.)

Role of Biodiversity in Planted Forests

It is well known that living organisms, through their metabolism and growth, drive energy and matter flows that contribute to the structuring and functioning of ecosystems. It is more difficult to understand *how* the diversity of these organisms, i.e., species diversity, affects these ecosystem processes. This question is a key issue in modern ecology but also has practical implications for agriculture and forest management. It is indeed of great interest to understand how changes in biodiversity can affect forest ecosystem functions (e.g., primary productivity, nutrient element cycling, soil fertility, and trophic interactions) that in turn can affect crop yields.

Most of the experimental studies that show increasing biomass production with higher species diversity have involved grassland, wetland, or microbial species (Naeem et al. 1994, Yachi and Loreau 1999, Tilman et al. 2002, Loreau et al. 2002). Because of technical difficulties in manipulating and monitoring changes in biodiversity and ecosystem processes in systems dominated by long-lived species such as trees, relatively few controlled experiments have so far addressed this issue in forests. To date, the results of experiments comparing biomass production in single- and mixed-species plantations in boreal, temperate, and tropical regions have been inconsistent (cf. FAO [199], Petit and Montagnini [2004], Piotto et al. [2004], Pretzsch [2005], and Scherer-Lorenzen et al. [2005]), but the available data suggest that mixed-species plantations may be more productive than plantation monocultures *if* (a) the planted species are more or less equally well adapted to site conditions (so that one species does not dominate and ultimately suppress the other planted species), *and* (b) if the functional characteristics of the planted species are sufficiently different; in particular, if they exhibit significant temporal or spatial complementarity in their use of resources such as light, water, and soil nutrients (Figure 5). Where these conditions are met, as in some (though not all) studies involving two-species mixtures that included nitrogen-fixing trees on N-limited sites, increased biomass yields have been observed (Khanna 1997, Parrotta 1999, Binkley et al. 2003, Forrester et al. 2005).

Diverse forests can be more resistant to insect pests and diseases than single-species plantations, and thus the trophic dimension of the biodiversity-ecosystem functioning relationship needs to be considered. Several reviews indicate that forest monocultures in all climatic regions may experience insect outbreaks or pathogen epidemics that can cause considerable damage (Barthod 1994, Gibson and Jones 1977). Until recently, the evidence in support of the view that insect pest outbreaks occur more frequently in plantation forests as a result of their poor tree species richness was controversial (Gadgil and Bain 1999) because, in plantation forestry, confounding factors may occur such as even-age structure (Géri 1980, Schwerdtfeger 1981), use of exotic species (Watt and Leather 1988, Speight and Wainhouse 1989), and intensive silviculture (Ross and Berisford 1990, Jactel and Kleinhentz 1997). However, a recent review, based on a meta-analysis of more than 50 field experiments that compared pure stand versus mixed stand of the same tree species, showed a significant increase in insect pest damage in single-tree species forests (Jactel et al. 2005). Three main factors related to single-species forestry can predispose forest plantations to insect attack (Jactel et al. 2005). First, the lack of physical or chemical barriers provided by other associated plant species could reduce access of herbivores to the large concentration of food resources, i.e., the high density of host trees in the forest monoculture. Second, the low abundance or diversity of natural enemies often observed in forest plantations can result in limited biological control of pest insects. A third factor is the potential absence of a diversion process, i.e., the disruption effect on pest insects resulting from the presence in the same stand of another more palatable host tree species. A similar review indicates that tree species diversity also may make forests less susceptible to fungal pathogens (Pautasso et al. 2005). For instance, damage caused by *Melampsora* rust disease, *Heterobasidium annosum*, and *Armillaria* root rot diseases are significantly lower in mixed than in pure stands. Two mechanisms are proposed to account for this overall tree diversity–pathogen resistance relationship: (i) in mixed forests, even if a species is severely affected by disease, other less susceptible tree species may replace the severely affected species and perpetuate the forest ecosystem, i.e., the "insurance hy-

pothesis" (Loreau et al. 2002), and (ii) because most pathogens are passively dispersed, the mixture of tree species will slow the spread of disease (Pautasso et al. 2005). However, an important exception to the diversity-resistance paradigm is the case of polyphagous pest insects and generalist pathogens. Populations of such organisms can first build up on a preferred host tree species and then spill over onto associated less palatable tree species, leading to a contagion process (Jactel et al. 2005).

Because of technical and economic constraints, it is unlikely that plantation managers will convert single-species stands into mixed-species stands simply to reduce pest damage that is normally only of minor significance. On the other hand, they might do so if the commercially attractive tree species was especially valuable and the insect damage was significant. Keenan et al. (1995) described the advantages and required tradeoffs involved in using a temporary tree cover crop to minimize tip borer attack in redcedar (a member of the Meliaceae) in north Queensland. In this case insect damage on the target species was reduced in the multispecies plantation to an extent sufficient to make the plantation viable. On the other hand, the overstory canopy cover also reduced the growth rate of redcedar so that care had to be taken to balance survival against growth increment.

Alternative ways of achieving the functional benefits of diversity might be to increase plant diversity in the plantation understory, but proper field experiments are needed to test whether this would be effective. A second option might be to consider increasing tree diversity at the landscape level. Growing evidence suggests that enhancing habitat diversity in plantation forest landscapes may prevent the development of pest insect outbreaks. For example, a study on spruce budworm, *Choristoneura fumiferana*, reported lower balsam fir mortality in stands surrounded by nonhost deciduous forest than in stands within large conifer-dominated forest (Cappucino et al. 1998). Similarly, Jactel et al. (2002) showed that pure stands of maritime pine bordered by a mixed woodland of broad-leaved species suffered fewer attacks by the stem borer *Dioryctria sylvestrella* than pure stands situated within a monoculture of pine trees. These findings indicate that the preservation or restoration of mixed-species woodlands, e.g., in gaps where site conditions or stand accessibility make timber production less profitable, could provide the basis for a more sustainable management of plantation forests.

The role of biodiversity in modifying hydrologic processes in plantation forests is unclear. There appears to be little evidence that mixed-species plantations are any different than single-species plantations in terms of catchment water yields or water quality. The most that can be said is that fast-growing species tend to use more water than slow-growing species. On the other hand, there is clear evidence that structurally simple plantation monocultures without any significant understory or ground cover can foster significant erosion. Perhaps the most striking example is the heavy erosion that can occur under pure teak (*Tectona grandis*) plantations (Bruijnzeel et al. 2005). It also is possible that more diverse plantation systems might improve topsoil structural properties such as infiltration rates faster than monocultures on badly degraded sites. There still is no strong experimental evidence of this and any improvement is likely to take some time. Furthermore, any consequent decline in runoff and improvement in infiltration is likely to be masked by the increased rates of evapotranspiration caused by reforestation (Brujnzeel 2004).

Managing Planted Forests to Enhance Biodiversity: Suggestions for the Future

Genetic Resources. By combining scientific knowledge in forest and tree genetics with commonsense forest management, general suggestions for preserving and enhancing genetic diversity in plantation forestry can be elaborated (Arbez 2000):

• Monitoring and improving genetic diversity in breeding populations. The main concerns associated with the use of improved FRM are whether genetic gain and diversity can be simultaneously maintained at reasonable levels over successive generations during the whole selection program. As many operational tree breeding programs conducted on fast-growing species are entering their third or even more advanced generations, these questions have raised theoretical and experimental approaches that provide guidelines to geneticists for maintaining genetic diversity (Namkoong 1988, Eriksson et al. 1993, White et al. 1993). Furthermore, conservation strategies can enrich the genetic base at any moment and must be used as a necessary complement of the breeding process.

• Controlling quality of FRM. Quality of a given FRM is related directly to the quality of the genetic information available, allowing its final user to optimally balance expected gains and possible risks. It includes precise and reliable information on (i) geographic origin of the parent gene pool (natural population or selected genotypes); (ii) identities, number, genetic characteristics of the parents, and crossing scheme used to obtain the commercial variety; and (iii) selection procedures (description of the mono- or multisite experimental design, selected traits, and levels of genetic superiority assessed by comparison with well-known reproducible standards). This information can be used to control quality of FRM and to favor FRM resulting from a long-term breeding scheme combining recurrent selection and gene resource conservation.

• Diversifying genetic resources at stand or landscape levels through the parallel development of available genetically improved varieties and limited use of a given variety in space and time to prevent genetic uniformity. The risks associated with improved FRM and decreased genetic diversity can be minimized by (i) using multiclonal mosaic schemes, where genetic diversity within a stand at a given time is replaced by genetic diversity between stands at the landscape level; (ii) limiting the monoclonal plantation area at the regional scale as well as the time during which a given clonal variety is permitted to be used.

• Evaluating genetic risks, in particular, developing risk simulation methods and secured long-term trials to monitor impacts of introduction of GM trees in forest plantations before any commercial deployment and use (Kremer 2002). Economic and biological constraints limit the number of GM trees created and impose to deploy them through clonal varieties. The main recommendations for their use include (i) male sterility, preventing pollen contamination of the surrounding forest-related tree species; (ii) testing not only in classical clonal tests (comparing one clone with a limited number of standard other clones, in well-controlled conditions of experimental plantation) but also in long-term experimental field trials to evaluate environmental risks.

Stand Management. Enhancing biodiversity in plantations can generally be achieved by increasing variability when plantations are established or tended (Hartley 2002). The emphasis in the past has been on reducing variability to improve predic-

tive capabilities and efficiency of establishment, tending, and harvesting operations. As a result, there is little experience with enhancing variability in plantation management settings. It seems likely, however, that many future plantation owners, especially those operating on a small scale, will be seeking more than just timber production from their plantations and might be willing to trade efficiency and predictability for the sake of ecological services such as enhanced biodiversity.

This increased variability can be achieved in several ways. Perhaps the most obvious is to use multispecies plantations rather than monocultures. Random species assemblages are unlikely to be successful and care is needed to design mixtures that are stable as well as productive (FAO 1992, Montagnini et al. 1995, Lamb 1998). Various planting arrangements have been tested but alternate row plantings appear to be the most common. Plantations with more than one species planted in alternate rows may increase yields and facilitate removal of the slower-growing species in an intermediate thinning. These mixed-species plantation systems also may provide higher wood quality through mutual shading of lower limbs (Oliver and Larson 1996). The choice of species and the number to use in mixtures also will be affected by economic considerations. One of the potential advantages of diversity is that it provides insurance against future changes in market values but all potential species must have broadly similar values; if not, the opportunity cost of reducing the stocking of high-value species to use lower-value species may be too high.

Managers can modify the silviculture of plantations in other ways to enhance diversity. Small variations in the timing and type of site preparation can affect the development and composition of the understory. How and if competing vegetation is controlled or the timing of thinnings also will affect stand development (Figure 6). Because diversity is enhanced usually by lower density plantations, managers should try to avoid or minimize the process of stem exclusion where understory development is suppressed. Precommercial thinnings and commercial thinnings might occur earlier during rotations and be more severe to enhance understory development. Longer rotations also will favor the formation of a more diverse overstory and encourage the development of a more diverse understory. In coast Douglas-fir, rotations can be lengthened by thinning without an appreciable drop in mean annual increment (Curtis 1995). Another way of achieving enhanced variability and diversity is by taking advantage of the "catalytic effect" referred to earlier. In many areas, single-species stands may be the intention, but natural regeneration of other species is inevitable and adds to diversity (Lugo 1992, Parrotta and Turnbull 1997). In these situations, such as in the Douglas-fir region of North America, this natural regeneration could be encouraged during the vegetation control process. Similar biodiversity enhancement also could be achieved favoring a diverse plant understory (Chey et al. 1997, Lamb 1998). Given sufficient time, this understory community may grow up and join the canopy layer. This means it could compete with the original plantation trees and reduce their productivity. Some of the management options are reviewed in Keenan et al. (1997).

Figure 6. A coastal redwood (*Sequoia sempervirens*) plantation thinned heavily with a younger cohort of sprout origin developing in the understory. (Photo courtesy of Kevin O'Hara.)

Even in plantation monocultures there is considerable scope for enhanced variability. Less-uniform site preparation treatments, variations in tree spacing, and thinning treatments also can enhance stand structure variability. Structural complexity of the planted forest is an important determinant of subsequent biodiversity enrichment because of the importance of habitat heterogeneity for attracting seed-dispersing wildlife and microclimatic heterogeneity required for seed germination for a variety of species (Parrotta et al. 1997). This suggests that broadleaf species yield generally better results than conifers, and that mixed-species plantings are preferable to monocultures, because of, in part, to their increased structural complexity. Two-aged stands also may be a viable alternative in situations where clearcutting is esthetically unpopular. Extending rotation length also could benefit biodiversity, particularly favoring diversity of soil biota and species associated with dead wood or leaf litter (Ferris et al. 2000, Magura et al. 2000). Maintaining snags, logs, and other woody debris on site also can enhance habitat values for a range of species, from fungi to cavity-nesting birds. Management practices that increase soil organic matter content (such as spot cultivation, use of amendments, or retention of harvest residues) and decrease soil disturbance during site preparation and harvest are desirable for maintaining the inherent biological capacity of soils and diversity of soil-living organisms, which are essential for nutrient conservation and cycling (Johnston and Crossley 2002). Although management efficiency may be reduced, these more complex stand structures may be as productive, if not more productive, than comparable even-aged plantations (O'Hara 1996). Although the productivity and actual effects on biodiversity of these structures are not well understood, there is additional uncertainty with regard to current tree breeding and the appropriateness of these trees in complex forest structures.

Landscape Level. Forest management needs to consider plantations from a landscape perspective in that they comprise a spatial array of different elements that can be arranged in different ways depending on management goals. The key elements within a plantation forest are individual stands or compartments of different age and species composition; remnants of native ecosystems, including riparian strips; and amenity plantings. Observations suggest that managing plantation densities and creating irregularities within the spatial structures, favoring the proportion of borders and clearings, and preserving natural plant communities along rivers and in swampy areas would logically increase the level of associated plant and animal biodiversity. Retention of broad-leaved species among coniferous plantations (Ferris et al. 2000), or preservation of native remnants, have been proposed as a management tool to enhance biodiversity at the landscape

level (Fisher and Goldney 1998, Norton 1998).

Some of these elements are fixed in the landscape (e.g., native remnants and riparian strips) but others can be arranged in different ways. Humphrey et al. (2000) suggested locating plantations near existing seminatural woodland fragments. In North America, spatial modeling tools have been used to optimize timber harvesting in native forests to meet biodiversity conservation goals (Bettinger et al. 1997). Similar modeling could be used to optimize the arrangement of different-aged plantation forest compartments and different plantation species to maximize timber production, biodiversity conservation, and ecosystem stability. Different spatial arrangements might be needed where the aim is to modify hydrologic processes (e.g., for salinity control). The key feature of this approach is that it considers biodiversity conservation at the landscape scale rather than at the stand scale and thus removes the direct conflict between biodiversity conservation and timber production at any individual site. The major potential difficulty, of course, is that landownership patterns and consequently management decisions often are made at the local rather than landscape scale. Therefore, ways must be found to ensure social outcomes as well as ecological outcomes at the landscape level.

In his analysis of the role of industrial plantations in large-scale restoration of degraded tropical forestlands, Lamb (1998) suggests a number of management approaches by which forest productivity (and profitability) and biodiversity objectives may be harmonized at the landscape level. These include increased use of native rather than exotic species, creation of species mosaics across the landscape by matching species to particular sites, embedding plantation monocultures in a matrix of intact or restored vegetation, using species mixtures rather than monocultures, or modifying silvicultural management practices to encourage development of diverse understories beneath plantation canopies (Figure 7).

A B

Figure 7. Understory management practices can have a profound effect on biodiversity development in plantations, as illustrated in the two young (<10 years old) eucalypt plantations in Vietnam. In the stand on the left, twigs and leaves are regularly swept up for fuel. In the stand on the right, fuel collection is excluded, allowing understory regeneration of native flora. (Photos courtesy of David Lamb.)

Conclusions

There is no single or simple answer to the question of whether planted forests are "good" or "bad" for biodiversity. Plantations can have either positive or negative impacts on biodiversity at the tree, stand, or landscape level depending on the ecological context in which they are found. Objective assessments of the potential or actual impacts of planted forests on interspecific biological diversity at different spatial scales require appropriate reference points. In this regard, it is important to consider in particular the (biodiversity) status of the site (and surrounding landscape) before establishment of planted forests and the likely alternative, land-use options for the site (i.e., would or could a site be managed for biodiversity conservation and other environmental services or be converted to agriculture or other nonforest uses?). For example, the establishment of an industrial plantation on a particular site will clearly have a more negative impact on stand-level biodiversity if it replaces a healthy, diverse, old-growth native forest ecosystem than if it replaces a degraded abandoned pasture system that was the result of earlier forest conversion. Thus, the ecological context of planted forest development, as well as the social and economic context shaping land-use change, must be considered in the evaluation of biodiversity impacts (Romm 1989, Walters 1997, Rudel 1998, Clapp 2001, Rudel et al. 2002, Sayer et al. 2004).

The need to pay more attention to biodiversity issues in plantation design and management is supported by observational, experimental, and theoretical studies that indicate that biodiversity can improve ecosystem functioning, i.e., it is not just the importance of biodiversity per se but its role in improving the overall resilience of the new ecosystem. Although plantation monocultures have economic advantages, the need to ensure their long-term sustainability argues for greater research effort to develop design and management strategies that enhance plantation understory and soil biodiversity as well as their functional benefits. Many plantations are being established for the contribution they can make to overcome ecological degradation (e.g., soil salinity, erosion) and improve the long-term sustainability of land uses such as agriculture. Faced with the unpredictable, enhancing species diversity may improve adaptability of all managed forest ecosystems to changing environmental conditions (Hooper et al. 2002).

The primary management objective of most plantation forests traditionally has been to optimize timber production. This will continue to be the primary objective in most (although perhaps not all) industrial plantation programs but it will not necessarily be the case in many smaller-scale plantations owned by farmers and other nonindustrial groups. In these circumstances the management objectives may place greater weight on the provision of nontimber products and ecological services such as biodiversity. This will require the development of a new range of silvicultural tools to establish and manage these plantations.

Where managers are seeking to produce goods as well as ecological services, there are, invariably, difficulties in making the necessary tradeoffs. These tradeoffs operate at *all* levels of biological diversity. In the case of genetic diversity, e.g., a balance must be struck between the need to identify the most productive FRM to plant at a particular site and the desire to reestablish the biodiversity represented in the original genotypes. Should a manager use highly productive planting material with a narrow genetic base that has been developed from an intensive selection program, clonal material, or even GM varieties? Or, should one rely instead on natural seed sources with a wider genetic di-

versity because these may confer greater resilience to the plantation, enabling it to cope better with future environmental changes such as insect attacks or climatic events? Judicious use of relevant, well-known tree-breeding strategies and gene conservation strategies can greatly facilitate efforts by managers to maintain genetic variability of plantation species over several generations and thus achieve better balance between economic and environmental benefits and risks.

Likewise, at the species level, should managers establish plantation monocultures or should they give greater emphasis to multispecies plantations? There are, of course, no simple answers to questions such as these because much depends on the fertility of the soils being planted (are they still able to support the original native species and the soil biota required for maintaining soil fertility and nutrient cycling processes?) and on the present objectives of the landowner. Usually, some compromise between the two extremes is chosen.

A critical issue for the future of plantation forests is how to combine biodiversity maintenance and wood production at various spatial scales, i.e., at stand, forest, and landscape levels (Spellerberg and Sawyer 1996). One way to achieve a balance between biodiversity and productivity/profitability is through improved practices at the stand level or alternative silvicultural regimes (species mixture at different scales from individual trees to compartments of different sizes, age, and clone mosaic) combined with biodiversity management at landscape level. This would include, e.g., modification of extensive clearcut practices to reduce group or patch sizes (i.e., plan for smaller compartments of same-aged stands that are dispersed within the plantation landscape) to achieve a better balance between economic and environmental objectives. Thus, it may be possible to achieve a degree of biodiversity at the landscape scale through diversification of plantation landscapes to create mosaics of different planted forest and natural vegetation habitats, even if each of the individual plantation stands within that landscape are established as simple monocultures. In many parts of the world, this will require a reorientation of current practices and, in particular, a shift from a stand-level to a forest- or landscape-level approach to the planning of all aspects of plantation management.

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Jean-Michel Carnus (carnus@pierroton.inra.fr) is director, Forest and Wood Research Site, Institut National Recherche Agronomique (INRA), Pierroton, 33610 Cestas, France. John Parrotta (jparrotta@fs.fed.us) is national research program leader for International Science Issues, USDA Forest Service-Research and

Development, 4th floor RP-C, North Kent Street, Arlington, VA 22209 Eckehard Brockerhoff (Eckehard.Brockerhoff@ensisjv.com) is senior scientist in the Forest Health and Biodiversity group at Ensis, University of Canterbury, P.O. Box 29237, Fendalton, Christchurch, New Zealand. Michel Arbez (aquitaine@iefc.net) is honorary president, Institut Européen de la Forêt Cultivée, 33610, Cestas, France. Hervé Jactel (herve.jactel@pierroton.inra.fr), is director, Forest Entomology Laboratory, Institut National Recherche Agronomique (INRA), Pierroton, 33610 Cestas, France. Antoine Kremer (antoine.kremer@pierroton.inra.fr) is director, Biodiversity Research Unit, Institut National Recherche Agronomique (INRA), Pierroton, 33610 Cestas, France. David Lamb (d.lamb@botany.uq.edu.au) is associate professor, School of Integrative Biology, University of Queensland, Brisbane, Queensland 4072, Australia. Kevin O'Hara (ohara@nature.berkeley.edu) is professor of Silviculture, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114. Bradley B. Walters (bwalters@mta.ca) is associate professor of Geography and Environmental Studies, Mount Allison University, Sackville, New Brunswick, Canada E4L 1A7. *An earlier version of this article was presented at UNFF Intersessional Experts Meeting on the Role of Planted Forests in Sustainable Forest Management, Mar. 24–30, 2003, New Zealand. Buck, A., J. Parrotta, and G. Wolfrum (eds.). 2003. P. 33–49 in* Science and technology—building the future or the world's forests and planted forests and biodiversity. *International Union of Forestry Research Organisations (IUFRO) Occasional Paper No. 15. International Union of Forest Research Organizations, Vienna, Austria.*