The Role of Forests in Carbon Cycles, Sequestration, and Storage

Issue 5: Climate Change Mitigation, Forest Management and Effects on Biological Diversity.

T-B. Larsson[1], A. Barbati[2], J. Bauhus[3], J. Van Brusselen[4], M. Lindner[4], M. Marchetti[5], B. Petriccione[6], and H. Petersson[7]

[1]European Environment Agency, Copenhagen, Denmark
[2]Department of Forest Environment and Resources, University of Tuscia, Viterbo, Italy
[3] Institute of Silviculture, Freiburg University, Freiburg, Germany
[4]European Forest Institute, Joensuu, Finland
[5] Department of Science and Technology for the Environment and Territory, University of Molise, Pesche, Italy
[6]CONECOFOR Office, National Forest Service, Roma, Italy
[7] Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umea, Sweden

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Technical editing: Johanna Kohl, Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW)

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Foreword

Forests and forest management have the potential to make substantial contributions to national and global mitigation portfolios designed to reduce the rate of carbon dioxide (CO_2) increases in the global atmosphere. In developing appropriate management strategies involving forests, managers are increasingly expected to consider a wide range on issues and indicators, including the impacts of their actions on the greenhouse gas balance.

The IUFRO Task Force on Forests and Carbon Sequestration was initiated in 2001 and its term renewed in 2006. Its mandate is to address issues related to the potential role of forests in carbon sequestration and to prepare readily accessible synthesis information, including a series of e-Notes.

The first four e-Notes have addressed the role of forests in the global carbon cycle, the impacts of disturbance regimes on forest carbon storage, the economics of forest management, and forest management options to increase carbon storage.

IUFRO is pleased to introduce this fifth e-Note which addresses the effects of forest management on biodiversity. Task Force e-Notes together provide a suite of timely, readily accessible, concise, and informative state of science summaries.

Editor:
Dr. Werner Kurz
Task Force Coordinator
Natural Resources Canada
Canadian Forest Service – Pacific Forestry Centre
Victoria, BC, Canada, wkurz@nrcan.gc.ca

Dr. Robert Jandl
Task Force Deputy Coordinator
Research and Training Centre for Forests, Natural Hazards and Landscape (BFW)
Vienna, Austria, robert.jandl@bfw.gv.at

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Executive summary

Forest management strategies to promote long-term storage of carbon could include mitigation of ecosystem disturbances, such as fire and other hazards creating carbon emissions, afforestation to increase the area of forest land and silvicultural practices which increase carbon sequestration. A significant part of the carbon stock of a forest ecosystem is found in the litter and soil organic matter. Biodiversity in soil as well as above ground should thus be considered.

The general perception of a natural forest is that this is a biodiversity repository as well as a large carbon stock which only needs protection. However, a main issue both for biodiversity and carbon is that forest ecosystems are naturally dynamic and subject to disturbances and succession. Preserving late successional stages by protection and controlling fire will increase carbon stocks and may enhance biodiversity, but may have negative impacts on the species that depend on earlier successional stages.

In most of Europe, the forests are considered to be semi-natural, reflecting the long history of human use and forestry. One of the structural features that has been generally reduced in managed forests is deadwood. Preserving deadwood, as well as promoting big and/or older trees, is thus favourable both for carbon stocks and biodiversity. The current trend towards increased forest volumes is also mainly favourable, however, the plant diversity in the understorey of darker forests is likely to decrease. In addition, promoting forest growth and carbon sequestration by application of nitrogen fertilizer is highly controversial from a biodiversity point of view. It would exacerbate the effect of long-range air pollution (N deposition), further increase the 'eutrophication' of the forest ecosystem and favour a few nitrophilous plant species while overall ground vegetation species diversity decreases.

While planting is a widespread regeneration technique in the semi-natural forests, establishment of 'forest plantations', i.e. uniform stands of exotic or introduced tree species, is under debate from a biodiversity point of view because highly productive trees would be used, often exotic species and/or biotechnologically 'improved' genotypes. The most extreme would be genetically modified trees that even may include genes to increase resistance to diseases or defoliating insects. From a biodiversity viewpoint, this would be a very risky strategy, because such genes might spread into native populations.

1. Introduction

Forest management aimed at increasing the long-term storage of carbon in terrestrial ecosystems is a potential climate change mitigation measure which could also greatly impact the biological diversity of forest ecosystems. Biological diversity, or biodiversity, is defined within the Convention on Biological Diversity (CBD) as 'the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (CBD Article 2).

As a consequence of the wide definition of biological diversity in the CBD, one must more precisely identify the components of biodiversity to assess the 'effects on biodiversity' of different forest management strategies. The next step would be to assess how these components may be affected – ideally in quantitative terms – and then judge if the effects are positive or not. Decision makers, having the task of balancing biodiversity concerns against other societal needs, like mitigation of climate change, will be helped if 'critical levels/thresholds' of biodiversity impact are provided.

Management strategies to promote long-term storage of carbon on forest land may impact on biological diversity - and will also have to take biological diversity into account - as there are several biodiversity links to the amount of accumulated carbon and the processes affecting the carbon flow in ecosystems (cf. e.g. BIODEPTH, 2007). Such management strategies could include mitigation of ecosystem disturbances, such as fire and other hazards creating carbon emissions, afforestation and other measures to increase the area of forest land, stand management practices (silviculture) that increase carbon sequestration, the life cycle of forest products and finally substituting fossil fuels with forest biomass (Obersteiner et al. 2005).

In the following we will, based upon ideas developed within the IUFRO Unit 8.02.01 – 'Key factors and ecological functions for forest biodiversity', identify biodiversity components as a basis for policy and management and try to apply this to potential management strategies aimed at increasing the long-term storage of carbon in the forest landscape. The perspective will be European but we hope our approach is more generally valid.

2. Key factors of forest biological diversity

The tropical, temperate and boreal forests offer diverse sets of habitats for plants, animals and microorganisms. They hold the vast majority of the world's terrestrial species (CBD). Together with the abiotic components of the ecosystem the species create a complex pattern of interactions, which to a larger or smaller extent is influenced by human interventions.

Given the large number of species and ecological interactions, it is difficult to generalize information derived from measurements of biodiversity, such as a set of species from one or a few taxonomic groups. A Euro-

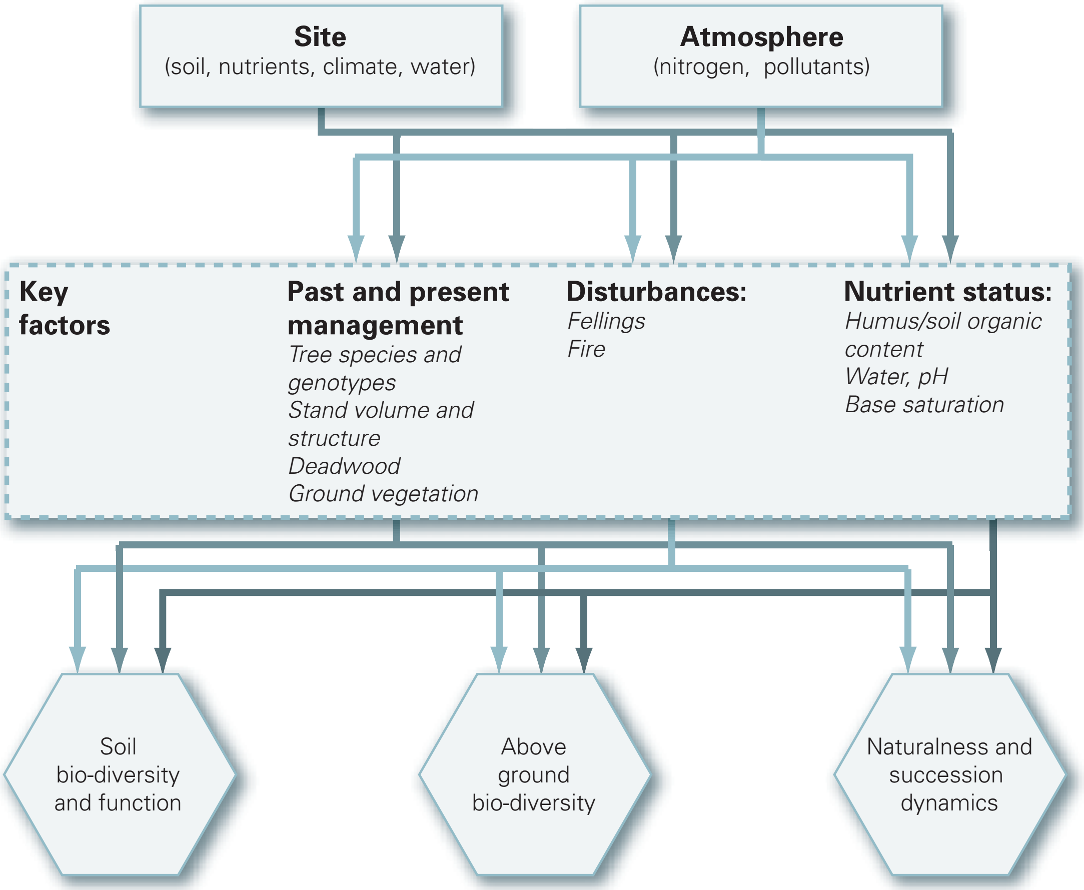

Figure 1.
Some key factors significant for relating biological diversity, carbon stock and processes affecting the carbon flow in the forest ecosystem.

Table 1.
Carbon storage in different forest ecosystems. More than 70% of the carbon was found in the soil organic pool for broadleaved woodland. The corresponding figures for Boreal- and Warm-temperate forest were 38 and 21%, respectively.

Carbon pool estimates in forest ecosystems

C [t ha^{-1}] Carbon pool	Boreal forests, Sweden[1]	Broad-leaved woodlands, UK[2]	Warm-temperate Beech forest, New Zealand[3]
Aboveground living biomass	35	100	193
Belowground living biomass	10	28	47
Dead wood	0.85	2.0	25
Litter	31[4]	3.3	7.3
Soil organic carbon	45[4]	335	71
Total	122	468	344

Note:
Definitions of carbon pools are not perfectly harmonized. E.g., soil organic carbon refers to 0-500 mm depth for Boreal- and Broad-leaved forests, and to 0-600 mm depth for Warm-temperate forests
Sources:
[1] Ranneby et al., 1987, [2] Patenaude et al., 2003, [3] Hart et al., 2003 and [4] Karltun, personal communication.

pean research network has presented a model to assess forest biological diversity based upon the components 'composition', 'structure' and 'function' further specified by 'key factors' (Larsson 2001). Key factors have a major influence or directly reflect the variation in forest biodiversity. There are both practical and theoretical advantages of the 'key factor approach' to assessing forest biodiversity; e.g. it has been shown that key factors to a large extent may be assessed by existing forestry data, e.g. in national forest inventories. Furthermore this approach is well suited to assess biodiversity in 'the wider landscape' and thus should be applicable in discussing forest landscape management for climate change mitigation. The key factors relevant to forest management for climate mitigation should reflect the biodiversity components and related functions linked to carbon accumulation and flow, but also widely reflect the effects of different climate management options on forest biological diversity. Figure 1 shows the conceptual model that will be used as a basis for further discussion. The figure highlights a number of important aspects to consider when planning the management of forest landscapes for climate change mitigation:

- Biodiversity in soil as well as above ground should be considered. A significant part of the carbon stock of a forest ecosystem is found in the litter and soil organic matter pool (cf. Table 1); the preservation of forest vegetation and its diversity is

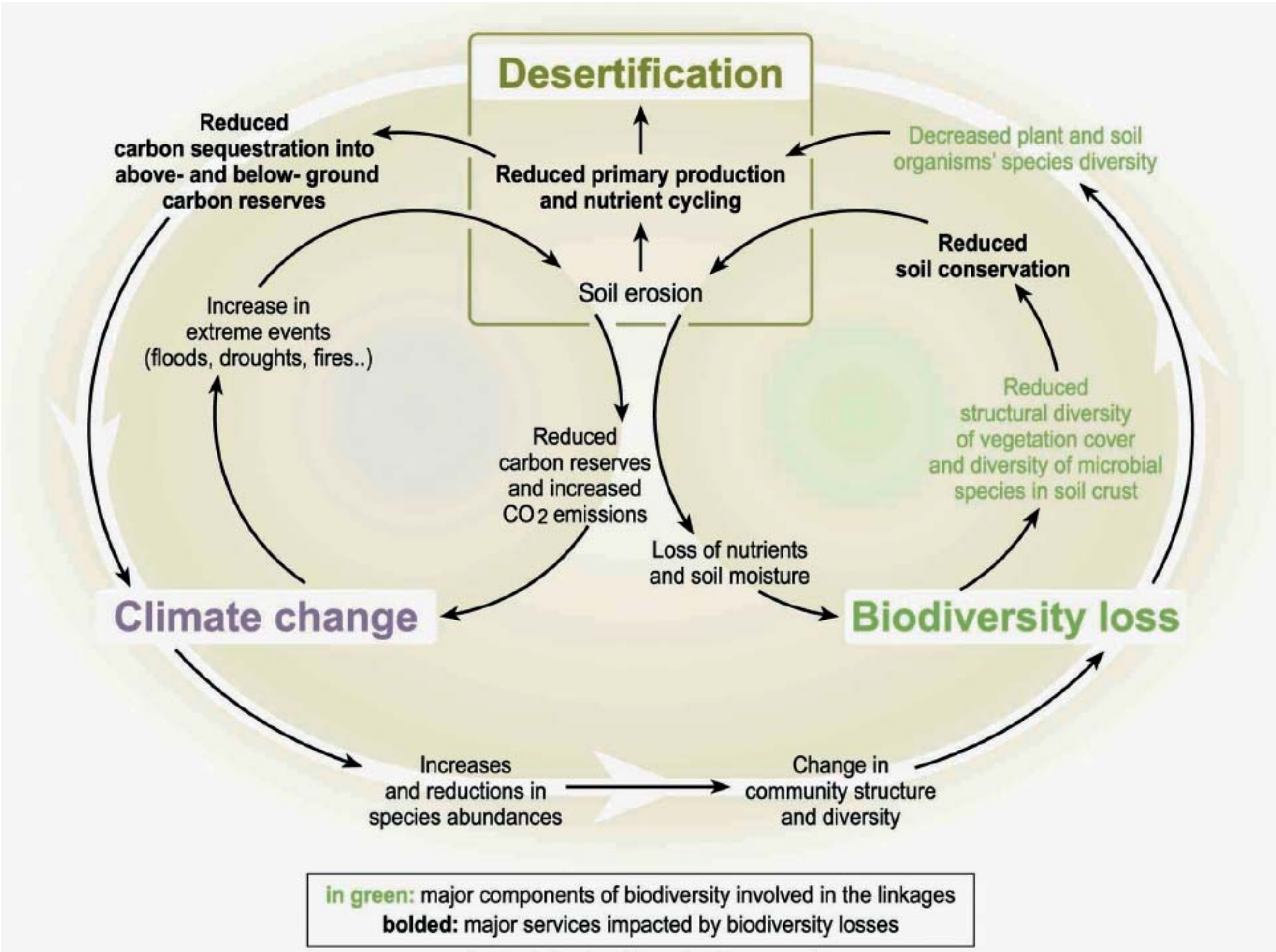

Figure 2.
Linkages and feedback loops among biodiversity loss, climate change and desertification.
Source: Millenium Ecosystem Assessment, 2005

therefore instrumental to the conservation of below-ground carbon reserves, though there are functional links to a number of ecological and biodiversity factors. E.g. in dryland forests biodiversity loss can contribute to reduced carbon stocks and desertification (Figure 2).

- 'Naturalness' and successional dynamics are crucial to consider when discussing management of forest landscapes for biodiversity and carbon stocks.
- Disturbances, from e.g. forestry practices (e.g. felling) or natural (e.g. fire) impact on biodiversity.

Although a common set of key factors is generally valid to characterize the biodiversity of European forests, and may serve as a basis for ecological assessments, there are large bio-geographical and site differences in the relative importance of key factors (Marchetti, 2004). An example is deadwood, which is an important feature both as carbon stock and to secure important components of biodiversity in some forests, but may be considered a problem in other forests, because of increased risk of anthropogenic fires.

Any forest biodiversity assessments must therfore be adapted to specific forest types. Barbati *et al.* (2006) identify 14 main forest categories as the highest aggregation level in a proposed European forest type scheme. These main categories of the European forests need to be identified in international reporting and assessments.

3. A landscape approach to forest management for carbon sequestration

As mentioned in the previous section, 'naturalness' may be a starting point for discussing strategic management of forest landscapes for biodiversity. Taking the example of Europe, most land area (mainly except high mountain, wetlands and some dry grassland areas) would be forest. Today this is only the case in northern Europe. The intense and long human landuse is reflected in forest fragmentation and reduction in forest area in many European countries.

The following text considers the impact of different forest management strategies on carbon storage in

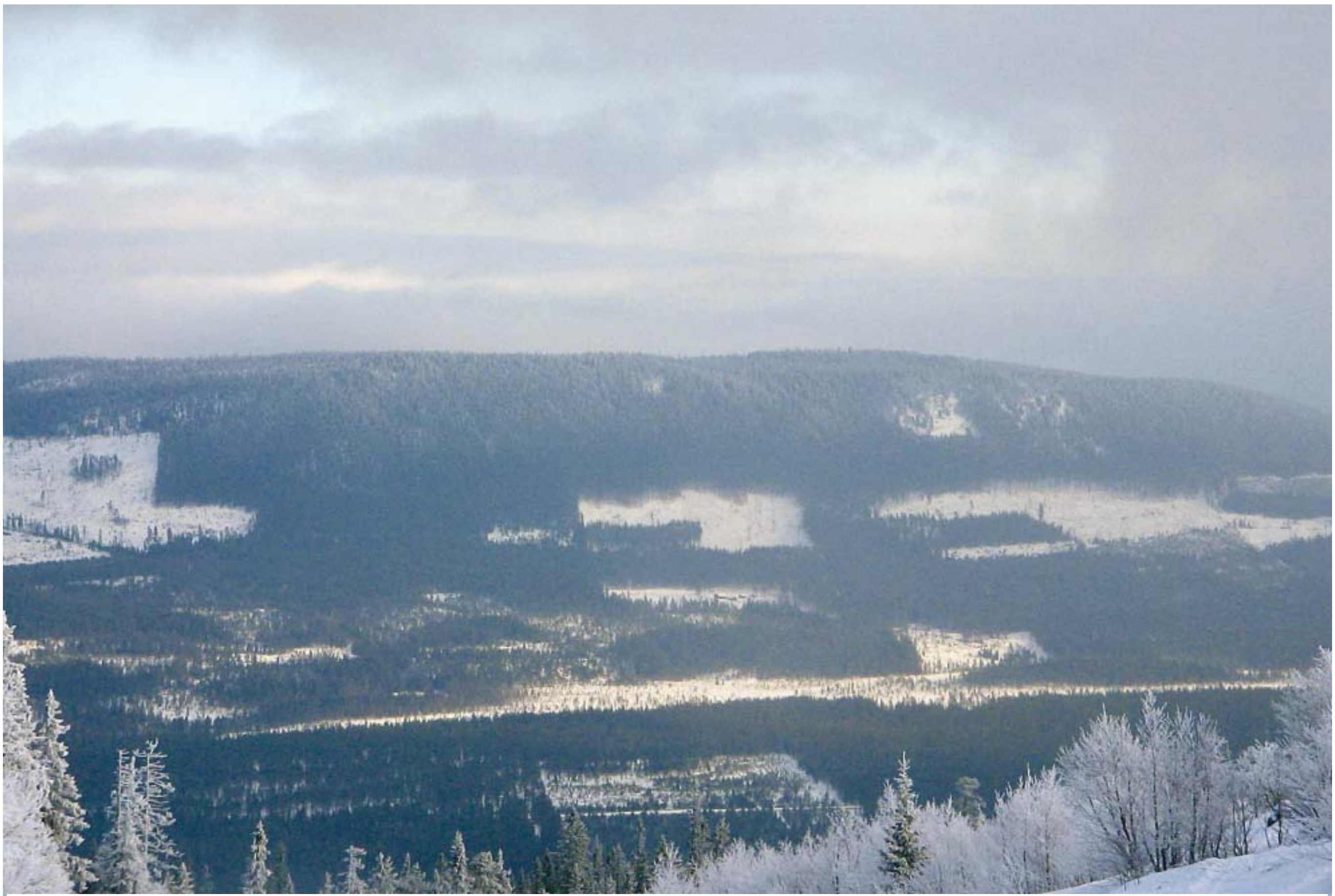

Figure 3. Boreal forest landscape; landscape mosaic is reflected by clear-cut areas *Photo: Tor-Björn Larsson*

primary forests including modified natural forests, in semi-natural forests, and in forest plantations. The impact of such strategies is presented and linked to the extent of the forests in their respective naturalness categories.

Taking into account the vast forest resources of the Russian Federation (including Siberia), about one quarter of Europe's forests can be considered primary forest without clearly visible indications of human activities (UNECE/FAO, 2005). Another 50% are modified natural forests with little human influence. These forests mainly belong to the boreal forest category (Barbati et al., 2006). The main part of forests in Western Europe is considered as semi-natural owing to intense management. In the Czech Republic, Finland, Germany, Netherlands, Norway, Poland, Serbia Montenegro and Switzerland, the share of seminatural forests exceeds 90% of the total forest area. The majority of the European forest types are thus to be classified as semi-natural (cf. Barbati et al., 2006).

Plantations are generally not dominating in Europe; in West Europe the share is only about 6% of the total forest area. However, the proportion of plantations is quite considerable in the forests of the following countries: Belgium (41%), Denmark (63%), Hungary (28%), Ireland (87%), Portugal (33%) and the United Kingdom (68%). In the south eastern European countries the proportion of plantations is overall higher – with a significant part having protective functions.

Primary forests and modified natural forests

It may seem counter intuitive that primary forests should be managed for biodiversity. The general perception of a natural forest is that this is indeed a biodiversity repository as well as a large carbon stock which only needs protection. However, a main issue both for biodiversity and carbon is that forest ecosystems are naturally dynamic and subject to disturbances and succession. Although these disturbances are not always perceived positively they may, from a biodiversity point of view, be crucial to preserve species adapted to specific successional stages.

Two major categories of forest dynamics are often identified by ecologists: large scale stand-replacing disturbances and small-scale (within-stand) gap dynamics (Hansson 1992). A typical example of large-scale stand dynamics is the mosaic of relatively homogenous forest stands of different ages that can be found in boreal forests, created by natural forest fires or maintained by clear-felling practices (Figure 3).

The main biodiversity management problem of primary and modified natural boreal forests, at least in Fennoscandia, is that forest fire is effectively controlled and largely eliminated. This favours later successional stages and increases carbon stocks but the increase in accumulated litter will favour more intense forest fires and thus may, in the long run make fire control more difficult. This is notably the case also in Mediterranean countries. From a biodiversity point

Figure 4.
Gap dynamics of Central European lowland beech forest
Photo: Tor-Björn Larsson

of view, it is important to maintain a balance of both early and late successional stages, each of which provides habitat for a number of different species. Although clear-felling practices re-create early successional stages, some species will not survive under the conditions created by clear felling because they require residual structures like burnt wood or standing dead trees, which would typically be found following natural disturbances. This concern would decrease if management techniques like e.g. prescribed burning (of felled areas) find more practical and political support – a model should be sought to allow more close-to-nature fire dynamics, while overall maintaining and enhancing carbon stocks as well as biodiversity.

Small-scale dynamics created by trees falling individually or in small groups due to wind, snow or other factors occur in all forests. In some forest types this is the dominating pattern of dynamics (Figure 4). Regeneration of the forest takes place in these gaps; in principle the stand will contain all age classes. Dying trees and dead wood are also important features because many species are specialised on specific decomposition stages of deadwood. Preserving the natural state of these types of forest and/or letting stands develop without human interference will increase carbon stocks. Here we have a clear synergy between biodiversity conservation and carbon sequestration; from a biodiversity point of view, a main concern is to preserve large enough areas connected to each other to secure that those species specialised on a specific successional stage, (e.g. deadwood of a certain dimension and decomposition stages) get continuous access to enough habitat to maintain their populations.

Semi-natural forests

Most European forests are considered to be semi-natural, reflecting a long history of human use and forestry. However, the human impact modified the natural conditions only to some extent. This creates a good starting point for maintaining and enhancing forest biodiversity. The challenge for management to enhance carbon stocks is to avoid measures that significantly decrease the biodiversity values of the forest but that instead maintain – or increase – the state of biodiversity.

For example in the boreal forests clear-felling and evenaged stand management are the preferred forestry practises. Late successional stages and deadwood, two important forest features generally decline as a result of these practices, yet both are of importance to carbon stocks as well as biodiversity.

In Europe only ca. 2/3 of the annual increment in forests are presently harvested (UNECE/FAO, 2005). As a consequence wood volumes and carbon stocks are increasing.

One factor contributing to the increase in wood volume is that forest growth rates have increased in many forest types in Europe. This is partly because of increased input of nitrogen from fertilizer applications and long-range air pollution (ICP Forests, 2005). From a biodiversity point of view this ‘eutrophication’ of the forest ecosystem is not desirable as it leads e.g. to increases in nitrophilous plant species, while overall ground vegetation species diversity decreases (ICP Forests, 2006, Ferretti et al., 2005). Application of nitrogen fertilizer to increase carbon sequestration may negatively affect biodiversity.

The increase in wood volumes also leads to bigger trees, a feature associated with late successional stages that benefits species dependent on such trees. Some of these species seem to have a low dispersal ability and depending on distance to source areas – rare in the productive forest landscape - biodiversity may not (immediately) improve as much as one might expect. In any case, a carbon sequestration policy favouring bigger (and older) trees is expected to benefit biodiversity.

The increasing standing wood volumes in semi-natural European forests also means that these forests become darker. Where site productivity increases, where single species forests are being converted into mixed stands, and where early successional species such as pines are replaced by other species, canopy density increases and permits less light to the understorey, which in most temperate forests harbours the majority of plant diversity. Thus plant species diversity is commonly low following canopy closure, when leaf area is at its maximum, until the gradual break up of the canopy when forests become mature to overmature (e.g. Halpern and Spiess 1995). Schmidt and Weckesser (2004) found that understorey plant species richness was greater in old, secondary spruce stands than in mixed spruce-beech forests, owing to the greater light availability beneath spruce. In the case of understorey vegetation, we may have an example of antagonistic effects between C sequestration and biodiversity. Management practices that are likely to increase floristic diversity in forests, will have to create heterogenous within-stand light environments, likely to result in reduced stocking of trees.

Management aimed at increasing dead wood provides another opportunity to combine carbon sequestration and biodiversity objectives because several species are dependent on dead wood. It is considered a structural key factor (Larsson, 2001) and a crucial indicator in the assessment of biodiversity and naturalness of forest systems (McComb and Lindenmayer, 1999, Skogsstyrelsen, 2001). A number of vertebrates, including cavity-nesting birds, as well as many species of lichens, bryophytes, fungi and invertebrates - have decreased and/or are threatened in the semi-natural forests of Europe (Marchetti 2004, Jonsson and Kruys 2001).

Deadwood plays an important role in long-term carbon storage. The amount of dead wood per hectare is slightly increasing in most of Europe (Figure 5), to some extent a result of increased management for biodiversity. However, the average amount is far below that in the primary forests of the Russian Federation. Policies to further increase the amount of dead wood will benefit both carbon stocks and biodiversity. It should be noted that increasing dead wood content in most forest types is a long-term process (Figure 5). In some forest types dead wood accumulation is not desirable; this is particularly the case in Mediterranean conifer forests in which woody debris must be removed to reduce the fire risk.

In this brief overview we will only consider one more aspect of forestry in the semi-natural forest category: genetic improvement of forest trees. In Europe considerable long-term efforts have been made to increase forest production by moving seeds and seedlings and narrowing the genetic variation to high production genotypes. Moving seed material to the north (in the northern hemisphere) may not as such be a problem in a climate change context. If the genetic variation is maintained – which is seldom the case – the same should apply from a biodiversity point of view. To narrow the genetic basis of a tree population in favour of high production genotypes when collecting seeds in nature or through breeding programmes is by definition in conflict with preserving biodiversity. Generally the genetic variation in a population is important to enable evolution to adapt to new conditions – such as climate change. The use of 'improved' forest regeneration material to increase volume production may be tempting in a strategy to increase carbon sequestration but this is not a safe management strategy for the European semi-natural forests because it may lower the ability to adapt to future climate change.

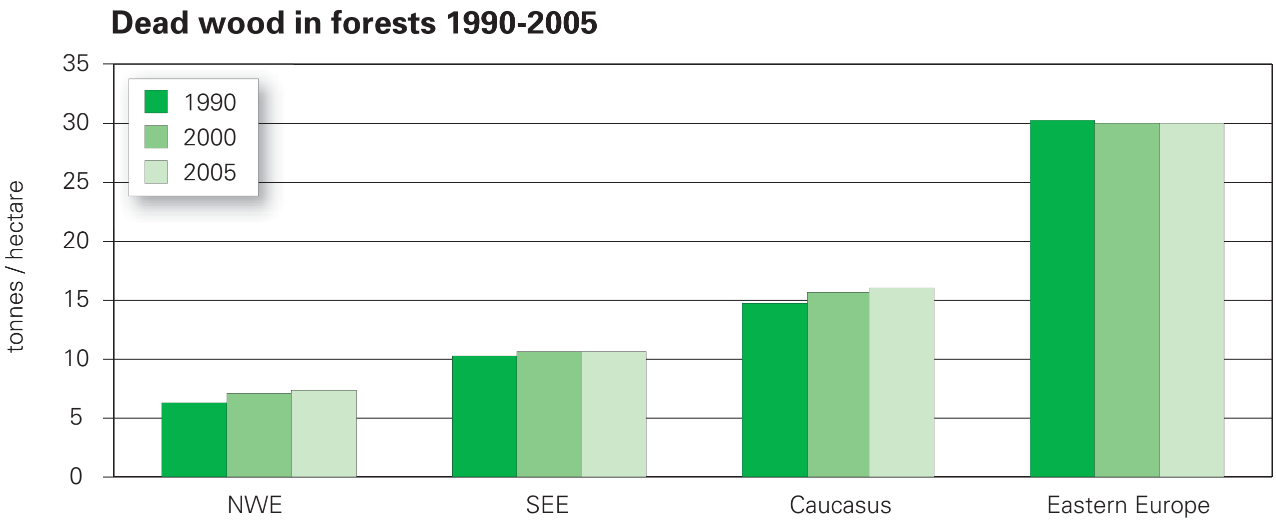

Figure 5. Development of dead wood in forests pan-Europe.

Note: Country groupings:
NWE: Austria , Belgium, Cyprus, Czech Republic, Denmark , Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, Netherlands, Poland, Portugal, Slovakia, Slovenia, Spain, Sweden, United Kingdom, Iceland, Liechtenstein, Norway & Switzerland.
SEE: Albania, Bulgaria, Bosnia-Herzegovina, Croatia, The Former Yugoslav Republic of Macedonia, Romania, Serbia and Montenegro & Turkey.
Caucasus: Armenia, Azerbadjan & Georgia.
Eastern Europe: Belarus, Republic of Moldova, Russian Federation & Ukraine.
Source: UNECE/FAO, 2005

Forest plantations

Planting is a preferred forest regeneration technique in several forest types in Europe, largely considered to belong to the semi-natural category. The internationally agreed definition of forest plantation (FAO, 2005) has created a lot of discussion because it focuses on structurally very uniform planted forest often comprised of exotic tree species. In the context of carbon management the focus is on afforestation, i.e. plantations on land that is transferred from non-forest to forest use. The forest area is currently increasing in Europe (ca 5% per decade, UNECE/FAO, 2005) which reflects abandonment of agricultural areas. About half of this, in particular on extensively grazed land in the Mediterranean, is re-growing spontaneously. This creates a forest with high species and structural diversity, dominated by native species, which is attractive from a biodiversity point of view. Creating a forest by spontaneous re-growth does not require the long-term investment in establishing new forest by planting or sowing, but the increment in wood volume can be expected to be lower.

Planting trees, afforestation, in Europe on the other hand has almost exclusively relied on exotics, like Eucalyptus or North American coniferous species, or on native trees outside their natural range. Use of exotics, apart from creating stands with different biodiversity compared to native trees, is also connected with the risk that the introduced species spread and become invasive. In several European countries (Ireland, France, Spain) afforestation by exotic or species not native to the site has successfully created a basis for wood-based industries, but the ecological and biodiversity states of these plantations are under debate, in Europe and elsewhere (cf. IUFRO, 2005).

Beneficial effects of plantations on biodiversity can be achieved in three ways: At the stand level a modified ecosystem is created, however it has been shown e.g. in the large Irish BIOFOREST study that surprisingly much of native biodiversity can be retained by a set of feasible considerations in the management (Iremonger et al., 2006). The effects of plantations on biodiversity on the landscape level have been shown in some case studies. Where plantations originate from afforestation, replacing non-forest land use, there should be synergistic effects of increasing C sequestration and biodiversity in the landscape.

Afforestation with the explicit main purpose to increase carbon stocks is likely to rely on highly productive tree material, including biotechnologically 'improved' genotypes. The most extreme will be genetically modified organism (GMO) trees that even may include genes to increase resistence to defoliators or diseases. From a biodiversity viewpoint, this would be a very risky strategy, because such genes might spread into native populations.

4. Future prospects and policy options

The previous section has demonstrated a few main principles for a strategy to increase carbon stocks in forests which is not in conflict with the aim to preserve and enhance forest biodiversity:

1. Primary forests and modified natural forests
   - Controlling large-scale natural disturbances like forest fire in natural forests is one option to increase carbon stocks but is advisable only in a medium-term perspective. A long-term strategy to preserve biodiversity in natural systems should, to a certain degree, re-introduce the successional dynamics of habitats.
   - Forest areas characterised by small-scale gap dynamics will, without interference, over time develop positively both from a carbon stock and biodiversity perspective.
2. Semi-natural forests
   - Extending the rotation period between felling will increase carbon stocks and promote biodiversity dependent on large trees and late successional stages.

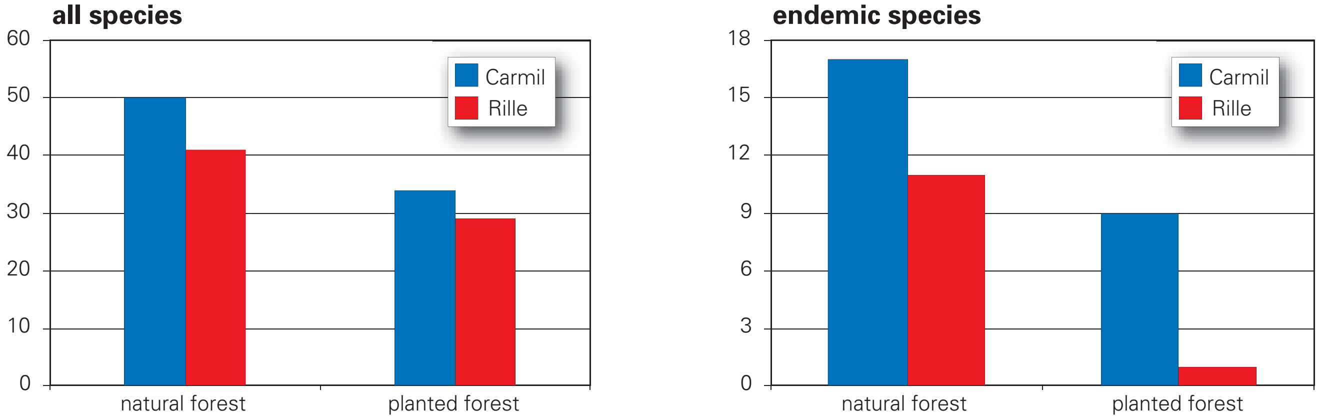

Figure 6. The effects of forest plantations on biodiversity: decrease in soil fauna (number of species)

Note:. Springtails (Order: Collembola) play a major role in breakdown of litter, soil constitution and structure. A study on Collembolan species richness in two areas (Carmil, Rille) in Ariège Pyrenees, France, showed significantly lower richness in conifer plantations than under native beech forests. The difference is even more obvious for the endemic species.

Source: EEA, 2002.

- Promoting dead wood (by not removing damaged or fallen trees) enhances both carbon stocks and biodiversity.
- Applying fertilizers to increase forest production will negatively impact a number of forest species.
- Increasing forest production by tree breeding resulting in a more limited gene pool is a debatable strategy from a biodiversity and climate change adaption point of view.

3. Forest plantations
   - Unassisted regeneration of site-native forest on e.g. abandoned agricultural and grazing land is, from a biodiversity point of view, clearly preferred over afforestation with exotic or non site-native tree species. It may, however, be considered a low-efficiency, but cheap, strategy to increase carbon stocks.
   - Regeneration by planting biotechnologically improved fast-growing trees, including GMO trees, is a high-risk and controversial strategy to increase carbon stocks and/or to create a basis for bioenergy from forest.

These main principles are of major importance in the above main forest naturalness categories but may be more generally applicable depending on the actual situation.

The global forum developing the general biodiversity policy is the UN Convention on Biological Diversity (CBD). At the Conference of the Parties in 2006 (CBD COP-8) issues related to forest biodiversity and potential measures to increase carbon stocks (often as well promoting increased bioenergy potential of forests) were discussed under several themes. The focus was on the issues dealt with under 'Forest plantations' above. The discussion under the forest theme – which will become a major one in the upcoming CBD COP-9 in 2008 – showed an emerging concern about GMO trees (cf. CBD, 2006b). When discussing invasive alien species several countries proposed an explicit statement that afforestation as a measure to mitigate climate change should avoid planting such non-native tree species which could become invasive. It was, however, considered inappropriate to issue a political recommendation in an area regulated by the UN Framework Convention on Climate Change so the CBD just stressed the need to ensure information exchange between the two conventions (CBD, 2006 a). As shown in this brief review balancing biodiversity and climate concerns may result in both win-win strategies and some potential conflicts in need of political compromises. IUFRO can contribute scientific support to this dialogue.

5. Glossary

afforestation: planting of forest on land which for a long time (> 50 years) has not been forested

biodiversity: the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems

biomass: the total dry organic matter contained within living organisms or ecosystems per unit area

Convention on Biological Diversity: http://www.biodiv.org/default.shtml

eutrophication: the process by which an ecosystem becomes enriched in available nutrients, especially N and P

stand: a contiguous group of trees sufficiently homogenous in age- and size-class distribution, species composition and structure and growing on a site of sufficiently uniform quality to be a distinguishable unit, to which the same management practices can be applied.

forest: a collection of stands.

forest plantation: Intensively managed forest stands resulting from afforestation or reforestation through artificial regeneration (planting or sowing). Plantations are commonly even-aged, consist of only one or few tree species (often exotics) that are managed to make full use of the productive capacity of the site. They have a regular shape with fixed and clearly defined boundaries. They may require high inputs of fossil energy and labour.

key factor of biodiversity: factors having a major influence or directly reflecting the variation in forest biodiversity.

naturalness: Area of forest and other wooded land, classified by „undisturbed by man", by „semi-natural" or by „plantations", each by forest type.

nitrophilous species: species that require high levels of nitrogen availability for optimal growth; favoured by (increased) nitrogen availability in the ecosystem.

sequestration: removal and storage; carbon dioxide taken from the atmosphere into plants by photosynthesis.

sink: a process or mechanism which removes carbon from the atmosphere.

soil biodiversity: organisms in the soil; functionally commonly divided into mesofauna (several taxa e.g. mites, nematodes, collembolan etc.) and microorganisms (fungi, bacteria).

source: opposite of a sink.

succession: development of an ecosystem and its biodiversity composition over time, e.g. in response to a disturbance factor. A typical succession occurs in natural forest after forest fire, starting with pioneer organisms establishing themselves on newly burnt areas, followed by the community of closed forest stand and ending with the species specialized to/dominating in the old-growth forest.

6. Further reading

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