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Nilsson, Sven; Niklasson, Mats

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Sustainable Forestry in Temperate Regions

Proceedings of the SUFOR International Workshop
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Editor-in-Chief:
Harald Sverdrup
Professor of Chemical Engineering
Chemical Engineering II, Lund University
Box 124, S-221 00 Lund, Sweden

This issue:

Sustainable Forestry in Temperate Regions
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Editor:
Lena Björk
Information officer, SUFOR
Department of Ecology, Ecology building
Lund University, S-223 62 Lund, Sweden

Scientific committee:
Prof Bengt Nihlgård, Lund University
Prof Ola Sallnäs, Swedish University of Agricultural Sciences
Prof Harald Sverdrup, Lund University

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Preface

By Bengt Nihlgård

SUFOR stands for Sustainable Forestry in Southern Sweden and is an eight years programme funded by MISTRA, the Environmental Strategic Foundation based in Stockholm. All MISTRA programmes are long-term directed integrated research programmes, with the aim to find solutions of importance for society; for its economy, for people and for the environment. SUFOR embraces three universities and some separate institutes. The programme has engaged about 40 scientists and will bring forward in total about 15 PhD-students.

SUFOR has finished its fifth year, and we have come up with a number of results that caused intensive debate among scientists and also some hesitation among foresters about what is the optimal solution for forestry in Southern Sweden. One important theme for SUFOR is to understand the long-term effects on soil, water and productivity, including economy, by the continuous deposition of acid rain and nitrogen in combination with harvests, and to recommend measures and solutions for forest owners. If nature should be considered stabile in a long-term perspective, then the forest soils principally should retain their chemistry in order to produce runoff water with acceptable quality. Negative variables counteracting this goal are sulphur and nitrogen deposition, and a high production followed by harvest. Within SUFOR we consider the today situation not sustainable, and ask ourselves whether forest productivity will decrease or forest damage increase due to this instability in the long run. Will recreation desires from society take over in importance for the South Swedish forests? How can the economy be solved for forest owners?

The international goal about retaining biodiversity of each country has caused discussion on solutions especially in Southern Sweden, where mostly private forest owners are managing the forests. This is another central theme in SUFOR, with the aim to identify solutions that can meet the demands on biodiversity, simultaneously as an economic output is realistic for the landowner. All these aspects have been in focus for models and field research during the five years of SUFOR. At an international workshop held during April 7-9, 2002, we collected constructive aspects which can be found in the following contributions.

Acknowledgements:

I want to acknowledge the support from the following scientists, who have been involved in the planning of the scientific contributions of the workshop as well as in organizing referees for this report: Sven G Nilsson, Leif Mattsson, Mats Niklasson, Kristina Blennow, Ulrika Rosengren, Magnus Lindén, Ola Sallnäs and Harald Sverdrup.

Workshop contributions – an overview

ABSTRACTS OF ORAL PRESENTATIONS

Nutrient sustainability

Restoration of biodiversity

Forest resource management

ABSTRACTS OF POSTER PRESENTATIONS

Some challenging results of SUFOR

By Bengt Nihlgård

Forest soil acidification results

If we do not fulfil the long-term goal of soil and water stability, then productivity may decrease due to imbalances among nutrients, fungi or insect attacks that may increase forest damage, and biodiversity will change. The SUFOR modelling has clearly shown to us that if we want to retain forest soil base saturation, and preferably improve it in order to reach the goals for soil, water and biodiversity, then we do not have so many options to choose among.

1. We can increase the amount of deciduous trees, which will improve sustainability if we assume a deeper root system on the deciduous trees. Then the weathering rate may come into balance with the uptake losses, especially as the deciduous trees usually grow a little slower than conifer plantations on the same soil. However, if we harvest deciduous stands also for bioenergy during e.g. summer or autumn with leaves, then the mineral losses will counteract these positive effects, and we will not improve sustainability.

2. We can lower the harvests of forest trees and bioenergy with about 30% and leave a number of trees for dying, and we will see increasing biodiversity. There will be a net return of base cations from dead and decomposing trees instead, and an improved water quality will slowly appear, according to models after several decades. This will, however, decrease the economic income for the landowners and is not considered a good option for them.

3. We can add nutrients to the forest soils in order to improve the soil and water situation relatively quickly (20-30 years) in the productive stands. This is an option accepted by the Forestry Board in Sweden for soils in Southwestern parts with the most acid situation, or for soils where bioenergy is also harvested.

In addition to these measures we have demands on a decrease of the deposition of sulphur and nitrogen down to at least the ‘critical levels’. This may be reached for sulphur during the coming years, but the nitrogen goal is still far away. This will affect not only productivity and nutrient imbalances but also biodiversity of the forests.

Biodiversity results

We have identified a number of things needed to be done on a large scale in Southern Sweden in order to retain biodiversity. We have to increase the number of standing dead trees in most forests and also increase the number of old and preferably big deciduous trees in all forest stands. The last item is especially important in South Sweden, where oak trees show extremely high potential for reaching high biodiversity, in and on, as well as around them.

We also argue that due to the expected climate change, as well as thinking on biodiversity, it is better to have several different tree species on each property than only one for a landowner.

Finally we argue that it is better to try to increase protected areas around specific central cores with high biodiversity, than to split up protected areas on several smaller plots on each property.

Conclusions

The conclusions drawn from the above results are

- a forest landowner cannot be sure that introduction of deciduous forests quickly will improve forest soils or water quality, especially if harvests will be performed as usual
- it is better for a landowner to add nutrients to productive forest stands if he wants a water runoff with high water quality within 2-3 decades, and to obtain an insurance for the soil productivity in the long-term perspective
- we should have a law that demands addition of wood ash after bioenergy harvesting
- society should increase the efforts to reach sulphur and nitrogen critical levels in deposition

All forest scientists in Sweden did not yet adopt all the above principles.

Decision support for risk management

Kristina Blennow and Ola Sallnäs
Southern Swedish Forest Research Centre
Swedish University of Agricultural Sciences, Alnarp
Kristina.Blennow@ess.slu.se

Abstract

Risk management is about handling uncertainty. Forestry decisions are made in relation to processes over close and distant time spans as well as in space. In a decision situation, the decision maker always has to make an assessment of outcome for each available alternative. It may be difficult to make such assessments in relation to uncertain events such as windfalls or outbreaks of insect attacks as well as for features previously not experienced such as effects of a changing climate. Computer models could, however, provide decision makers with more reliable assessments than can be made without the models. This paper presents how computer tools can be used for providing decision support for risk management in forestry.

Introduction

Risk management is about handling uncertainty. In any undertaking we have a set of objectives we want to attain. To do this we have to make decisions along the way. As part of the implementation of sustainable management of natural resources, the Rio Declaration acts on how we make the decisions:

> In order to protect the environment,
> the precautionary approach shall be
> widely applied by States according
> to their capabilities. Where there are
> threats of serious or irreversible damage,
> lack of full scientific certainty shall not
> be used as a reason for postponing
> cost-effective measures to prevent
> environmental degradation.
> Rio Declaration §15 (1992)

This means that the Rio Convention urges us to be precautious and avoid taking risk in order to protect the environment. In each decision situation, the decision maker chooses between different alternatives. While a risk neutral decision maker would choose the alternative for which he or she expects the utility of the outcome to be the greatest, a risk aversive decision maker would take into account an interval of possible utilities for the outcome of each alternative, i.e. he or she would take uncertainty into account. To avoid a seriously adverse outcome, he or she would choose the alternative with the largest minimum possible utility. Furthermore, a risk aversive decision maker would consider more alternatives to attain a specific objective than would a risk-loving or risk-neutral decision maker (Gärdenfors & Sahlin, 1982).

In this paper we present a systems analysis approach to providing decision support for the production component of sustainable forestry. The procedure consists of analysis within a theoretical framework centred on the decision situation and the development of computer tools for providing answers to specific questions.

Uncertainty

When dealing with decision support, it is of interest to consider the two different types of uncertainty that exist. First, there is the epistemic, or knowledge related, uncertainty. Since we have always more or less incomplete knowledge of the system in which we operate, this type of uncertainty is always present. In decision theory, this type of uncertainty constitutes risk. Secondly, there is the aleatory, or stochastic, uncertainty. This type of uncertainty we cannot reduce by learning more but it may sometimes be affected by actions taken. In forestry such actions correspond to different planning options and silvicultural treatments. In pragmatic usage of the term, risk means the aleatory uncertainty times the extent of negative outcome. The aleatory uncertainty may be expressed in terms of probability.

Decision support

Decision support is meant to help the decision maker attain the objectives. According to Lönnstedt & Svensson (2000), NIPF owners are risk aversive, at least when larger monetary values are at stake. In a decision situation, the decision maker has to make assessments of outcome for each available alternative. Such assessments are based on the decision maker’s experience and his or her information gained from various sources. The forestry system is a complex system where processes over time as well as in space need to be handled, at both large and small scales. Furthermore, this has to be done simultaneously. It may therefore be difficult to make assessments of outcome in ones head. Assessments of outcome that are more reliable than those that can be made in ones head could therefore become useful decision support. Such decision support typically puts pieces of information together to form a whole, thus reducing the epistemic uncertainty. We believe that a decision maker would find estimates of the remaining epistemic uncertainty important determinants of the reliability of the information provided. Separating the aleatory from the epistemic uncertainty, furthermore, makes it possible to evaluate if, how and at what cost the probability of adverse outcome can be reduced. Providing estimates of both types of uncertainty helps the decision maker make rational decisions in correspondence with his or her attitude towards risk taking. It is important to note that the decision maker’s attitude and perception of risk guide in the decision-making process.

Systems analysis — an example

Systems analysis is one approach to helping the decision maker identify a better course of action and make a better decision than he or she might otherwise have made. By defining and using a theoretical framework cantered on the decision situation, as described above, we believe that the chances increase that the information we provide will become useful decision support. In the end, this is, however, up to the decision maker.

We concentrate on providing decision support to southern Swedish non-industrial private owners who own 77% of the south-Swedish forest land (Anon. 2000). Furthermore, we concentrate on providing decision support in relation to hazards, e.g. events of negative outcome that may or may not occur (aleatory uncertainty). Our approach involves three steps: hazard identification, characterization and communication.

Hazard identification

Based on an enquiry, Blennow & Sallnäs (in press) identified the hazards that non-industrial private forest (NIPF) owners perceived as most risky in a forest production perspective. The forest owners were asked to pick out hazards from a given set and rank them according to their recent experience of costly damage, and their willingness to invest money in risk-reducing measures. They were, furthermore, asked to assess the risk associated with each hazard in four classes ranging from very high to negligible risk. The results show that the same six hazards were considered most problematic in all three aspects. These were browsing by large herbivores on plants in regeneration, falling timber prices, damage by wind, spruce bark beetle, root rot and pine-weevil. A majority of the respondents, furthermore, claimed to take action to reduce risk. But, only 33–60% of the respondents claimed to take action to reduce the risk associated with the six hazards for which the respondents were the most willing to invest capital to reduce risk. One explanation for this could be that the decision maker has forestry objectives in addition to production (Ask & Carlsson 2000). Another explanation could be that the optimum choice of action in relation to one hazard is perceived to increase the risk in relation to another hazard. Furthermore, it could also indicate a need for information on existing risk-reducing methods and/or that new efficient methods are needed. Indeed, there was a substantial lack of knowledge in relation to risk reducing measures. Four to thirteen percent of the respondents claimed not to know whether they took risk-reducing action in relation to the top-ranked most problematic hazards. Even if this possibly can be explained by the forest owners managing their forests based on recommendations for which the effects are not explicitly described in relation to each hazard, information about risk-reducing measures could help reduce risk. The level of ignorance was highest for the hazard damage by wind. It was concluded that the need of decision support was largest in relation to the hazard damage by wind due to a combination of perceived high risk and high level of ignorance in relation to whether risk-reducing action was taken.

Hazard characterization

Several models for estimating effects of strong winds on forests have been presented (e.g. Lohmander & Helles 1987; Valinger & Fridman 1997; Fridman & Valinger 1998; Thorsen & Helles 1998 Peltola et al. 1999; Gardiner et al. 2000). These models have in common that the probability of windthrow is affected by silvicultural treatments and forestry planning activities. Consequently, the probability of windthrow differs between forest management alternatives available to a forest owner. We have developed a computer model that calculates the probability of windthrow at a landscape level (Figure 1). By a landscape we mean an area of a few km^2 to a few tens of km^2.

The computer model is built for assessing the probability of windthrow under conditions such as those found in the south of Sweden. In the south of Sweden, the topography is levelled and the forest stands are small (a few to some tens of ha). Norway spruce, Scots pine and birch are the main species for production of forest raw material. Strong winds mainly occur in association with the passage of cyclones, i.e. in association with large-scale weather systems. Within such a landscape, we assume the weather to be the same, i.e. caused by the same weather system. Our approach to model the risk of windthrow makes it possible to assess the probability of windthrow under a different climate than that of today.

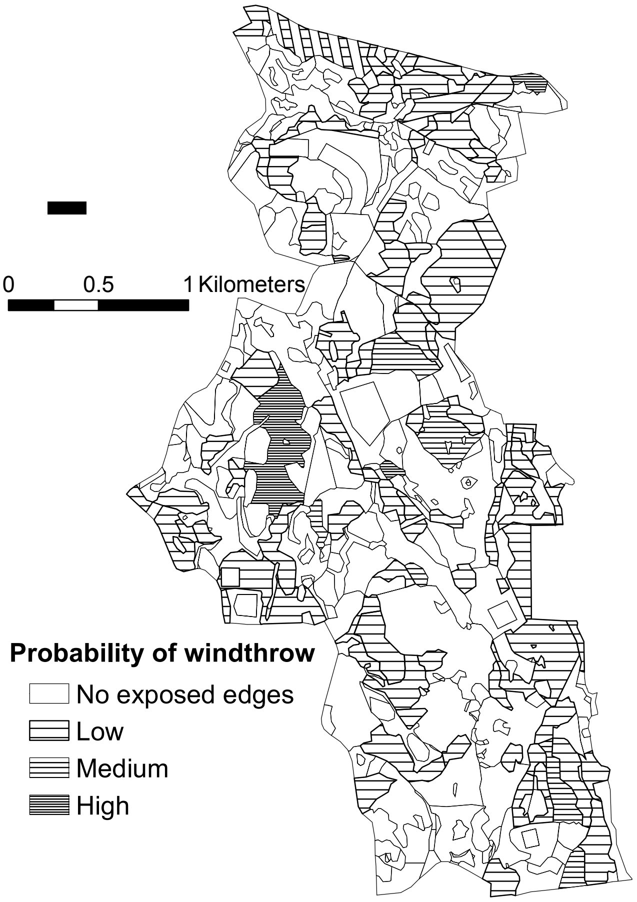

Figure 1. The classified stand wise probability of windthrow calculated for Asa Experimental Forest, Sweden.

Input data to the system are forest inventory data and a digital terrain model (DEM) stored in a geographical information system (GIS) for the area of interest and surroundings, and wind climate data from a nearby meteorological observing station.

The Finnish model HWIND is used to calculate the stability of the forest stands (Peltola et al. 1999). This model calculates the critical wind speed for stem breakage and up-rooting at the stand edge.

Topographic variation and variation in land-use and forest development stages make the surroundings differ between forest stands in a landscape. In combination with effects of the wind direction, this results in a large variation in wind exposure to different stands in a landscape. HWIND has been modified to handle as variables the parameterised aerodynamic properties (roughness length and zero plane displacement height) of the terrain up-wind exposed forest edges. Furthermore, to make it possible to use HWIND for all stands in such a heterogeneous landscape, a model has been constructed that identifies wind exposed forest edges, and calculates parameter values for aerodynamic properties of forest stands and areas up-wind exposed edges. In its present configuration, the system of models calculates the probability of windthrow at wind exposed forest edges of at least 10 m in height. The calculation of aerodynamic parameter values is based on the GALES model presented in Gardiner et al. (2000). In addition, the height above the ground for which the critical wind speeds are calculated has been made into a variable in HWIND to make it possible to compare the calculated critical windspeeds with the results of the wind exposure model.

Our system of models includes the Danish model *Wind Atlas Analysis and Application Program* (WA^{S}P) (Mortensen et al. 1998) for distributing the wind climate over the terrain. This exposure model is fed with wind climate data from a nearby meteorological observing station, information about the topography and the aerodynamic properties of the study area and its surroundings (Figure 2). For the area

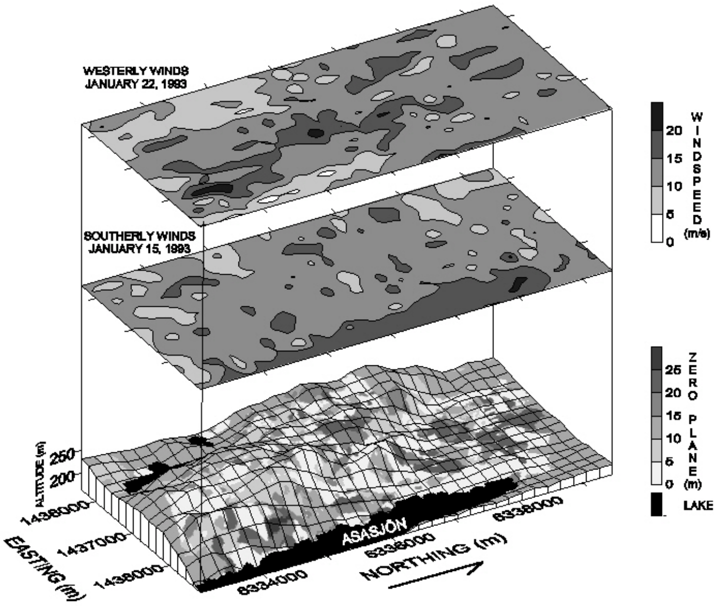

Figure 2:Bottom: Block diagram of the terrain in Asa Experimental Forest, Sweden, and immediate surroundings, draped with modelled values of the zero plane displacement height, d is used as a zero plane for modelling of the wind field over rough surfaces, such as the forest terrain, and is dependent on the aerodynamical properties of the ground. Stacked on top of the block diagram: Two contour maps of the generalised modelled windspeed at 10 m above d for two windthrow occurrences in January, 1993. (From Blennow & Sallnäs 2000.)

of interest and for each stand, the aerodynamic properties are parameterised as described above. After estimating the regional wind, the model gives correction factors that enable the calculated critical windspeed at a specific point in the landscape to be linked to a corresponding regional wind. Calculated using extreme-value statistics, the probability of windthrow is the calculated critical regional windspeed being exceeded.

Communication

Model output in terms of probability values for a particular outcome can be useful in a decision situation. However, both technical and communicative criteria need to be fulfilled for a probability assessment to be reliable thus useful (Thompson & Bloom 2000). The decision maker needs estimates of the epistemic uncertainty and

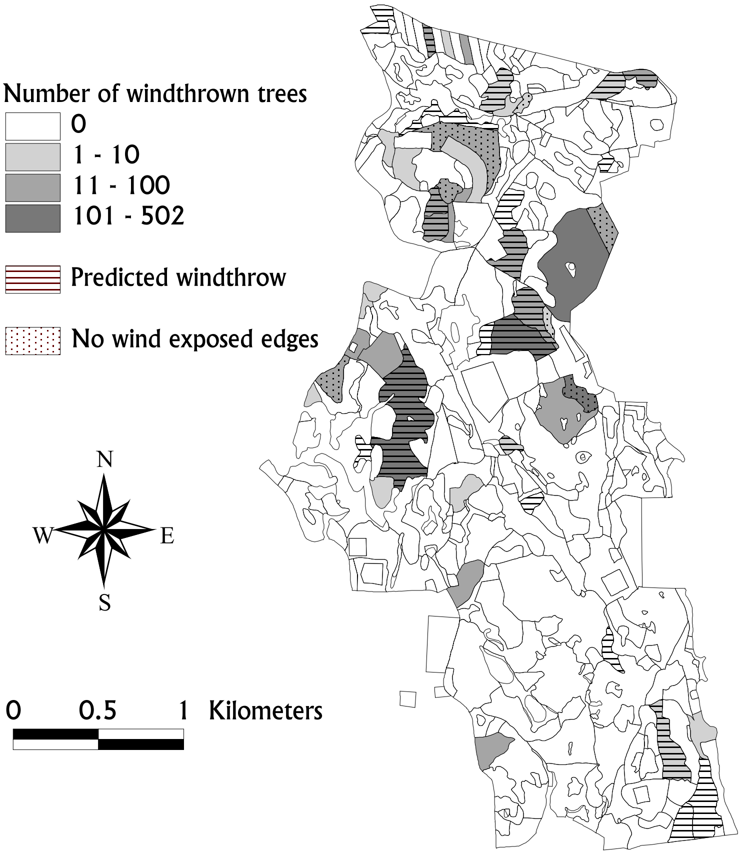

Figure 3: Preliminary results of evaluation of the system of models for the hazard windthrow. Distribution of forest stands in Asa Experimental Forest, Sweden, with the number of windthrown trees marked, as observed in a ground-based field survey after two windthrow events in January, 1993. Additionaly, those forest stands are marked out for which windthrow was predicted by the system of models, as are those with no wind exposed edges identified. (From Blennow & Sallnäs 2000.)

information on what the assessment is based on to be able to estimate its reliability. Here it is important to show in what ways the model has been evaluated (Figure 3). Furthermore, information on potential changes (internal or external such a changed climate), and information about the relevant management options, their cost and effect on the probability are also requested (Thompson & Bloom 2000). To achieve this, the computer model above, together with a landscape projection model, will be used for simulations in relation to the hazard windthrow in order to evaluate silvicultural programmes and other planning options over time and in space under present and changed climate.

Conclusions

The Rio Declaration urges us to make decisions under precaution in order to protect the environment. To provide useful decision support, the research community should, as always, help reduce epistemic uncertainty but it should also provide reliable assessments of outcome. These assessments of outcome should cover not only the expected outcome but also possible seriously adverse outcomes. In this way precautious (risk aversive) decisions can be made. To further facilitate the decision making, the assessments can be used to answer specific questions such as possible effects of climate change and explore if, how and at what cost the probability of seriously adverse outcomes can be reduced.

Acknowledgements

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Characterizing forest spatial structure and diversity

K. von Gadow and G.Y. Hui

Institute of Forest Management, Georg-August-University Göttingen,
Büsgenweg 5, D-37077 Göttingen, Germany

Abstract

The „structure“ and “diversity” of a forest may be defined by the spatial distribution of the tree positions, by the particular mingling patterns of the different tree species which occur in the forest and by the spatial arrangement of the tree dimensions. The paper present a coherent system for assessment and description of three levels of diversity referring to position, species and size. The proposed parameters can be used to provide a comprehensive description of the spatial structure of a forest. The *n* nearest neighbours of a given reference tree or sample point may be regularly or irregularly positioned around the reference tree or point. The *n* trees may include one or several species and their dimensions may be similar or different. Examples are used to illustrate the application of the approach. The main practical advantage of using the proposed neighbourhood parameters is the fact that assessment of the spatial structure does not require measurement of distances between neighbouring trees. Tree positions need not be known and the three levels of spatial pattern, - tree position, tree species and tree size, - can be assessed with very little effort as part of a normal forest inventory.

Key words: forest spatial structure; mingling; dominance; winkelmass; uniform angle index

1. Introduction

The „structure“ of a forest may be defined by the spatial distribution of the tree positions, by the particular mingling patterns of the different tree species and by the spatial arrangement of their dimensions. Several tree species may occur in a given forest, each with its own diameter distribution. The different species and tree sizes may be found in close proximity to each other and thus exhibit a high degree of “mingling”, or they may be spatially segregated (Fig. 1). Structural diversity is often seen as an indicator of ecological diversity. This is a debatable assumption. However, a forest’s spatial structure is one of its chraracteristic attributes. The problem which presents itself is how to characterize and describe forests with different species compositions and size distributions more accurately, using affordable assessment techniques.

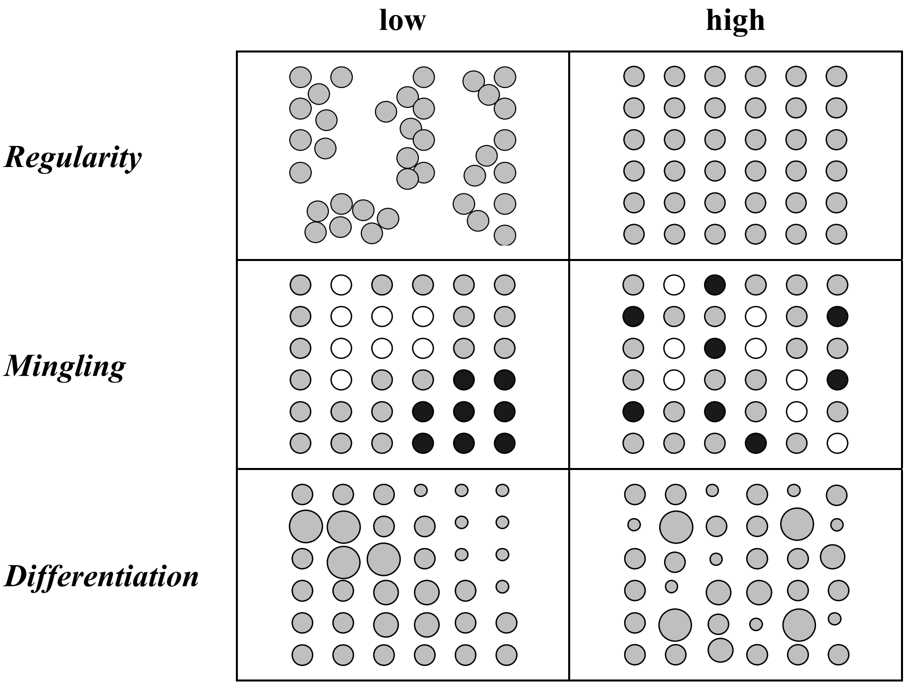


Figure 1. The main elements of forest spatial structure are ***regularity*** *of tree locations species* ***mingling*** *and size* ***differentiation****.*

The variables used to describe forest structure may be assigned to one of three different types (Albert; 1999):

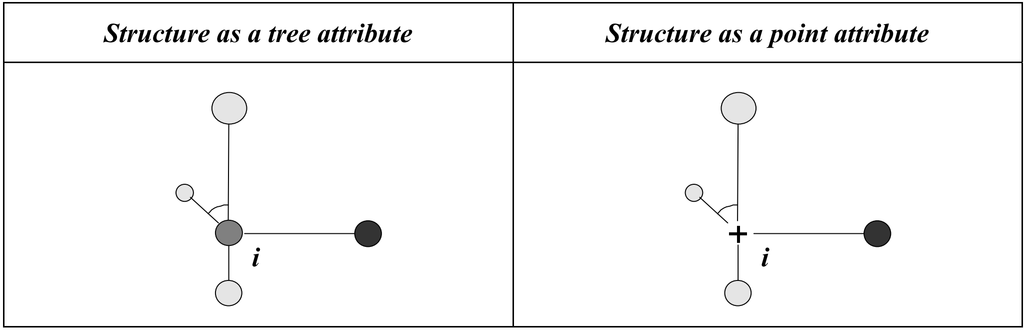
Distance independent variables for characterizing forest structure as a whole
Distance dependent variables for characterizing forest structure as a whole
Neighbourhood-based variables for describing small-scale structural characteristics.

L- und Pair correlation functions are useful for describing forest structures, but they require datasets with known tree positions (Stoyan and Stoyan, 1992). Such data are hardly ever available in practice and this precludes the use of these otherwise elegant methods. Aggregate indices, such as the spatial index proposed by Clark and Evans (1954), can provide a first general impression of the structure of a particular forest, but they cannot be used to describe the great variety of spatial arrangements. This deficit is especially serious in very irregular forests where small-scale structural characteristics are highly variable. An exact description of small-scale structural attributes is considered to be increasingly important as a basis for silvicultural decision-making in regions where selective harvesting and continuous cover forest management is practiced (Spellmann, 1995; Albert, 1999).

For this reason a set of three types of neighbourhood-based parameters is presented. The parameters can be used to provide a comprehensive description of the spatial structure of a forest. The *n* nearest neighbours of a given reference tree or sample point may be regularly or irregularly positioned around the reference tree or point. The *n* trees may include one or several species and their dimensions may be similar or different. Examples are used to illustrate the practical application of the approach.

2. Definitions

The three neighbourhood-based parameters *regularity*, *mingling* and *differentiation* can be used to provide a comprehensive description of the spatial structure of a forest. Assessment and description may be tree- based or point-based (Fig. 2).



Structure as a tree attribute

Structure as a point attribute

Figure 2. Assessment and description of forest structure may be tree- based (relating a reference tree i to the attributes of its immediate neighbours) or point-based (relating the structural attributes of a neighbourhood group to a sample point).

In the tree-based approach a sample tree closest to a sample point is chosen as reference tree and the attributes of its immediate neighbours (size, species) and the regularity of their positions are related to the reference tree. In the point-based approach the structural attributes of a neighbourhood group of trees (variation of tree species and sizes; regularity of tree positions) is assessed at each sample point.

2.1 Regularity

A number of methods have been proposed for characterizing the spatial distribution of the tree positions in a forest (Clark and Evans, 1954; Cox, 1971; Upton and Fingleton, 1985, 1989; Smaltschinski, 1998). A new parameter, the so-called *Winkelmass* (Gadow et al., 1998), offers certain advantages when compared with other methods[1].

2. 11 *Regularity* as a tree attribute

The *Winkelmass* describes the regularity or irregularity of the spatial distribution of the *n* trees nearest to a reference tree *i*. The concept is based on the classification of the angles α_j ($j = 1..n$) between the immediate neighbours of the *n* trees with reference to a sample tree. An immediate neighbour is the next tree following a given clockwise (or anticlockwise) direction. A special case is a constellation in which the angle between two trees exceeds 180 degrees. Between such two trees the angle measurement is taken in the opposite direction, thus α_j is always ≤ 180 degrees (see Fig. 1).

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[1] An appropriate English expression for the *winkelmass* is *uniform angle index*

The *Winkelmass* W_i describes the degree of regularity of the spatial distribution of the four trees nearest to a reference tree i[2]. An appropriate reference quantity is the standard angle α_0, which would be expected if the distribution would be perfectly regular. In the case of the 4-tree sample α_0 could, for example, assume a value of 360 / 4 = 90 degrees. By comparing all α_j with the standard angle α_0 we can derive the binary random variable v_j (Eq. 1)[3]. W_i is then defined as the fraction of the angles α_j, which are smaller than the standard angle α_0:

$$W_i = \frac{1}{4}\sum_{j=1}^{4} v_j \quad \text{with} \quad v_j = \begin{cases} 1, & \alpha_j < \alpha_0 \\ 0, & \text{otherwise} \end{cases} \quad \text{and} \quad 0 \le W_i \le 1 \qquad (1)$$

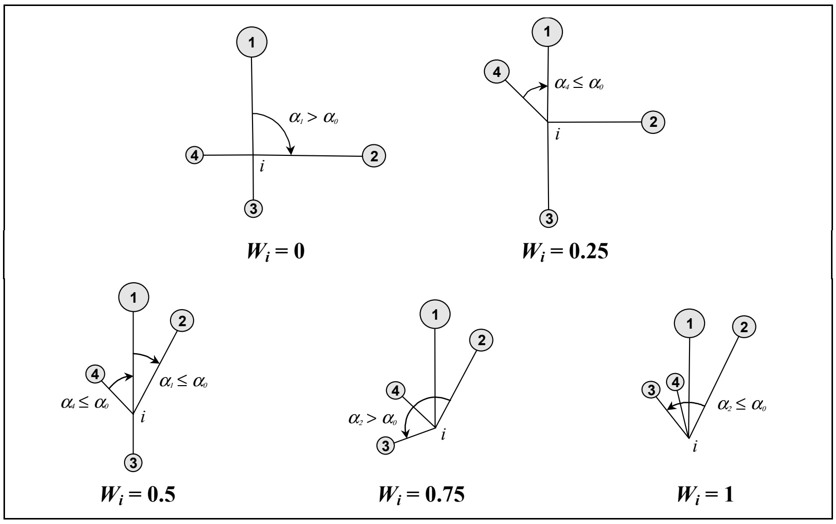

***Figure 1**: Possible values of* W_i *at a sample point* i. *The neighbour of a given tree is indicated by the next higher number (exception is tree No 4: its neighbour is tree No 1). The two graphs below at right show that there are always two angles between two neighbouring trees (clockwise and anti-clockwise; a smaller and a bigger one). When calculating the* Winkelmass *it is always the smaller of the two angles that is used*

W_i=0 indicates that the trees in the vicinity of the reference tree are positioned in a regular manner, whereas W_i=1 points to an irregular or *clumped* distribution. With 4 neighbours, there are 5 possible values that W_i can assume:

W_i	**description**	**category**
0.00	none of the α-angles j is smaller than α_0	very regular
0.25	one of the α- angles j is smaller than α_0	regular
0.50	two of the α- angles j are smaller than α_0	random
0.75	three of the α- angles j are smaller than α_0	irregular
1.00	All four α- angles j are smaller than α_0	very irregular

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[2] Four neighbours have proved to be most suitable based on practical considerations in connection with the field assessment methods (Albert, 1999; Hui and Hu, 2001).

[3] Note that exact measurement of the angle is not required, allowing rapid field assessment of the W_i-value which normally takes less than a minute. A special instrument was developed for this purpose.

The estimator for the *Winkelmass* of a given forest is $\overline{W}$, the arithmetic mean of all W_i -values:

$$\overline{W} = \frac{1}{N}\sum_{i=1}^{N} W_i \qquad (2)$$

with W_i = *Winkelmass* of the *i*-th reference tree
N = number of reference trees

Although the *Winkelmass* mean value $\overline{W}$ is quite revealing for characterizing a point distribution, it is often advisable to study the distribution of the W_i-values which describes the structural variability in a given forest.

2. 12 *Regularity* as a group attribute

Staupendahl (2001) used the point-based *Winkelmass* which is defined as the proportion of angles α_j between the n trees closest to the i'th sample point, which are smaller than the *standard angle* α_0. This index is identical to the one described in the previous section and Eq. (1) applies as well.

2.2 Mingling

Species diversity has become a very important aspect of forest management and a number of parameters are available to describe it. Examples are the *Shannon-Weaver* index which has been used in ecological applications by Pielou (1977, p. 293) or the *species profile index* proposed by Pretzsch (2002). We propose to evaluate the species diversity in the vicinity of a reference tree (*mingling as a tree attribute*) or sample point (*mingling as a group attribute*).

2.21 *Mingling* as a tree attribute

The tree attribute *mingling* describes the species variety in the vicinity of a given reference tree and has been defined as the proportion of the *n* nearest neighbours that do not belong to the same species (Gadow and Füldner,1992):

$$M_i = \frac{1}{4}\sum_{j=1}^{4} v_j \qquad (3)$$

with $v_j = \begin{cases} 0, \text{ neighbour } j \text{ belongs to the same species as reference tree } i \\ 1, \text{ otherwise} \end{cases}$ and $0 \le M_i \le 1$

With four neighbours, M_i can assume the following five values:

M_i	description	category
0.00	all four neighbours belong to the same species as the reference tree	zero mingling
0.25	three of the four neighbours belong to the same species as the reference tree	weak mingling
0.50	two of the four neighbours belong to the same species as the reference tree	moderate mingling
0.75	three of the four neighbours belong to a different species as the reference tree	high mingling
1.00	all four neighbours belong to a different species as the reference tree	very high mingling

An advantage of the method is the ability to describe mingling as a function of a specific tree attribute. Examples are species-specific *mingling or* Z-tree-specific *mingling.*

2.22 *Mingling* as a group attribute

The group attribute *mingling* can be used to assign a proportion of the total forest area to a particular class. A variety of indices for characterizing species diversity have been proposed. Examples are the *Shannon-Weaver* index which has been used in ecological applications by Pielou (1977, p. 293) or the *species profile index* proposed by Pretzsch (2002). In accordance with the approach followed so far, with four neighbours M_i can assume the following five values:

M_i	description	category
0.00	all four neighbours belong to the same species	zero mingling
0.25	three of the four neighbours belong to the same species	weak mingling
0.50	two of the four neighbours belong to the same species	moderate mingling
0.75	three of the four neighbours belong to different species	high mingling
1.00	all four neighbours belong to a different species	maximum mingling

Whereas the tree attribute *mingling* can be used to derive a distribution reflecting proportion of trees that belong to a certain structure class, the group attribute *mingling* represents proportions of the forest area which belong to a certain mingling class.

2.3 Size Differentiation

The diversity of tree dimensions in the vicinity of a reference tree or sample point may be evaluated in a similar way as has been demonstrated in the previous sections. When describing forest structure in terms of the variability of tree dimensions it is often informative to evaluate the relative dominance of a tree with certain attributes, such as the species.

2.31 *Dominance* as a tree attribute

The tree attribute *dominance*[4] was proposed by Hui et al. (1998) to relate the relative dominance of a given tree to its species or silvicultural significance. It is defined as the proportion of the *n* nearest neighbours of a given reference tree which are bigger than the

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[4] The original German designation is *Umgebungsmass.*

reference tree and is calculated in the same way as the previous tree-based structural prameters:

$$U_i = \frac{1}{4}\sum_{j=1}^{4} v_j \tag{4}$$

with $v_j = \begin{cases} 0, \text{ neighbour } j \text{ is smaller than reference tree } i \\ 1, \text{ otherwise} \end{cases}$ and $0 \le U_i \le 1$

With four neighbours, U_i can assume the following five values:

U_i	description	category
0.00	all four neighbours are smaller than the reference tree	very suppressed
0.25	three of the four neighbours are smaller than the reference tree	moderately suppressed
0.50	two of the four neighbours are smaller than the reference tree	co-dominant
0.75	one of the four neighbours is smaller than the reference tree	dominant
1.00	none of the four neighbours is smaller than the reference tree	strongly dominant

The five U_i–values correspond to the social classes developed by Kraft (1884). These social classes are used by silviculturists in Germany.

An advantage of using the *dominance* criterion is the ability to describe the relative dominance as a function of a specific tree attribute. Examples are species-specific *dominance or* Z-tree-specific *dominance*[5].

2.32 *Differentiation* as a group attribute

Differentiation as a group attribute is relatively easy to implement using any quntity that measures the variation of tree dimensions in the neighbourhood of the i'th sample point. A straightforward approach would be to use the diameter coefficient of variation, a quantity which is independent of tree size:

$$T_i = \frac{\text{diameter standard deviation}}{\text{mean diameter}} \tag{5}$$

To make the criterion compatible with the other parameters, T_i can assume the following five values:

T_i	value of diameter coeficient of variation	category
0.00	CV = 0.05	very even
0.25	0.05 < CV < 0.15	even
0.50	0.15 ≤ CV < 0.30	moderately uneven
0.75	0.30 ≤ CV < 0.60	uneven
1.00	0.60 ≤ CV	very uneven

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[5] The term Z-tree is used in Germany and refers to specially selected elite trees which are characterized by their outstanding vigour and stem form.

The symbol T_i is chosen because the interpretation of the differentiation is not directly comparable with the dominance criterion.

3. Application examples

The following examples are used to illustrate the potential of the neighbourhood-based structure variables for describing complex forest structures.

3.1 The Winkelmass mean value

In agreement with the definitions presented above, the optimum standard angle is that which produces an average value of $\overline{W} = 0.5$ for a random distribution. The optimum standard angle was found by means of simulation studies. First, the program *Stochastic Geometry* Version 4.1 (Institut für Stochastik, 1997) was used to generate random, clumped and regular distributions which were then described in more detail with the L- und Pair Correlation function (Stoyan and Stoyan, 1992). Subsequently, using the program *Generate 1.1* (Albert, 1998) the *Winkelmass*-distributions were calculated for the random type, using different standard angles. The optimum standard angle, producing an average value of $\overline{W} = 0.5$ for a random distribution, was found to be 72° (Hui and Gadow, 2002).

1000 random distributions as well as 500 clumped and 500 regular distributions were then generated with a density of 1000 trees per ha each. These distributions were sampled with the aim of calculating the Winkelmass mean value and using a standard angle of 72°. The results for the three spatial types are presented in Tab. 1.

distribution type	**number of simulation runs**	**mean ($\overline{W}$)**	**lower bound of $\overline{W}$**	**upper bound of $\overline{W}$**	**standard-deviation**
random	1000	0.496	0.477	0.520	0.007
regular	500	0.456	0.437	0.479	0.007
clumped	500	0.535	0.509	0.558	0.008

Table 1. Statistics of the Winkelmass mean values using a standard angle of 72°.

The K-S-test revealed that the distribution of the *Winkelmass* mean values follows the Normal Distribution. In the Normal Distribution 99.7 per cent of all values are found within the interval $\mu \pm 3\sigma$ which for the random case is defined by the bounds [0.475, 0.517]. Using a standard angle of 72°, $\overline{W}$-values of less than 0.475 are most likely from a regular distribution and those greater than 0.517 are most likely from a clumped distribution. There are no exact thresholds. However, the two zones of transition between random and regular and between random and clumped are rather narrow.

3.2 Describing complex forest structures

An example from the *Bovenden* forest in Lower Saxony shows the species specific distributions of the tree attribute *mingling* (considering the three nearest neighbours of a given reference tree) for ash and beech (Fig. 3).

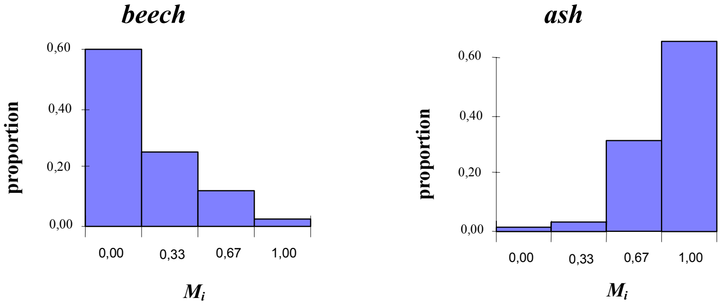
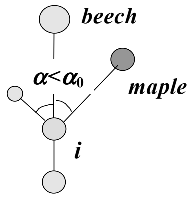


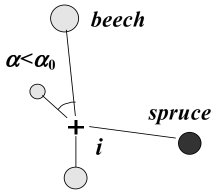
Figure 3. Example of species-specific distributions of the tree attribute mingling *for ash and beech in the* Bovenden *forest in Lower Saxon, Germany.*

Sixty percent of the beech trees are within pure groups of beech whereas most of the ash trees are surrounded by other species. Pure groups of ash are very rare. Such analyses are possible when using *mingling* as a tree attribute.

The following example illustrates the interpretative potential of the structural variables for specific neighbourhood constellations.

	Two of the α-angles are smaller than α_0; one neighbour belongs to a different species as the reference tree and one has a smaller dbh than the reference tree ($W_i = 0.50$; $M_i = 0.25$; $U_i = 0.75$).

Another example illustrates the interpretative potential of the structural variables for a specific point-based group constellation.

	The trees are moderately regularly positioned around the sample point; three of the four trees belong to the same species and the diameter coefficient of variation is equal to 0.23 (W_i=0.25; M_i=0.25; T_i = 0.5).

It is possible, when using certain sampling schemes, such as the continuous forest inventory practiced in Germany, to evaluate both tree- and group-based structural attributes in a complementary way.

Spatial interpretation of thinnings

Structural attributes of trees permit detailed interpretation of a selective thinning. The comparison of the before and after-thinning distributions of the tree attributes *mingling* and/or *dominance*, for example, makes it possible to derive removal preferences based on spatial characteristics. Tab. 2 shows the relative frequencies of the *mingling* attribute for spruce and beech trees of the total (before thinning) and removed trees. The three nearest neighbours of a given reference tree were considered in this example.

	spruce				***beech***			
M_i	**0.00**	**0.33**	**0.67**	**1.00**	**0.00**	**0.33**	**0.67**	**1.00**
total	0.04	0.53	0.35	0.08	0.43	0.28	0.23	0.06
removed	0.00	1.00	0.00	0.00	0.40	0.40	0.20	0.00
preference	0	1.89	0	0	0.93	1.43	0.87	0

Table 2. Relative frequencies of the mingling attribute for spruce and beech trees in a mixed forest of the total (before thinning) and removed trees.

The removal preference was calculated as the *total* proportion in a particular mingling class divided by the *removed* proportion in that mingling class. The results show that all the removed spruce trees had exactly one beech tree among their three nearest neighbours (M_i = 0.33). Beech trees were predominantly removed in pure or almost pure beech groups.

4. Conclusions

The variables presented in this paper can be assessed with relatively little effort as a “by-product” during a normal field sampling. The additional measurements are minimal. The main practical advantage of using the proposed neighbourhood parameters is the fact that assessment of the spatial structure does not require measurement of distances between neighbouring trees. Tree positions need not be known and the three levels of spatial pattern, - position diversity, species diversity and size diversity, - can be assessed with very little effort as part of a normal forest inventory. Interpretation of the results is straightforward. For this reason, some of the parameters like the tree-based *mingling* or the *Winkelmass* are already being used in standard forestry software (e.g. in the growth simulator *BWINPRO 6.0* - Nagel et al., 2001 – and in the forest sampling software *WALDSIM 3.0* – Pommerening and Lewandowski, 2000).

There are advantages of being able to relate certain neighbourhood-based structural attributes to a particular tree. For example, the degree of mingling may be different for different tree species (as shown in Fig. 3); size differentiation may be related to trees identified for a particular silvicultural use (e.g. Z-tree). The point- or group-based approach, on the other hand, allows a more precise evaluation of the variation of tree sizes and tree dimensions within a group of trees. Both tree- and point-based structural variables offer complementary interpretations.

Simulation studies allow comparison of observed structural variables and those which can be expected in a random forest. A test criterion for evaluating significant differences between observed and expected size differentiations was developed, for example, using random permutations of 1000 forests. These differences were rather large in some German uneven-aged managed forests (Pommerening, 1997), but surprisingly small in a South African natural forest (Schröder, 1998).

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Restoration of Biodiversity

Prof. Jari Niemelä
Department of Ecology and Systematics,
P.O. Box 65, FIN-00014 University of Helsinki, Finland
Telephone: +358-9-19157849
Fax: +358-9-19157847
e-mail jari.niemela@helsinki.fi

Abstract

Ecological restoration is the process of re-establishing to the extent possible the structure, function, and integrity of indigenous ecosystems and the sustaining habitats that they provide. Establishement of protected areas should be supplemented by restoration efforts especially in forests where human influence has been strong and long-lasting, such as hemiboreal and temperate forests. What are the principles of restoration of forest biodiversity? Restoration should be conducted at several spatio-temporal scales and be focussed on important elements which have suffered from human actions. Many of the restoration methods are related to allowing disturbance to take place and mimicking natural disturbance regimes. For instance, increasing the amount of dead wood is an important method for recreating habitat for species requiring coarse woody debris. However, restoration is not a simple undertaking. First, our knowledge about species or habitats that we would like to restore is rather poor. Thus, we do not necessarily know how to go about to reach the desired goals. Second, for altered ecosystems it is not always obvious what the desired ecosystem state should be. Third, restoration is expensive, and the question arises whether or not restoration is the ecologically most efficient way of trying to maintain populations of indigenous species and ecosystems. Ecological research is a vital part of restoration, and through adaptive management scientists and the public can be involved in the efforts. The SUFOR programme is in a good position to produce the needed ecological information for guiding restoration efforts.

Keywords: restoration, forest biodiversity, conservation

1. Introduction and definition of restoration

Humans have used forests for a long time. This has resulted in profound changes in forested environments. Consequently, for ensuring the maintenance of forest species in Sweden forest restoration is required as there is not enough forests to be set aside as reserves any more (Angelstam & Andersson 2001). Restoration of habitat elements, structures and processes that have disappeared or weakened is especially important in forests where human influence has been strong and long-lasting, such as hemiboreal and temperate forests.

Restoration is a concept encompassing a myriad of approaches and methods of recreating nature. In brief, ecological restoration is the process of re-establishing to the extent possible the structure, function, and integrity of indigenous ecosystems and the sustaining habitats that they provide (Soc. for Ecological Restoration 1993). There are other, related concepts which may cause confusion. The goal of rehabilitation is not as an original or healthy state as in the case of restoration. The idea of remediation is to rectify or to make good emphasising the process rather than the endpoint. The aim of reclamation is to bring back to a ‘proper state’, but there is no implication of returning to an original state but rather to a useful one (Bradshaw 2000).

Restoration needs ecology as its backbone, but we may not have enough ecological knowledge to guide restoration or the knowledge that we have may be hard to apply. Thus, ecological research is needed and ecologists can greatly contribute to the success of restoration efforts, as restoration presents almost the ultimate challenge to ecologists in the application of their science (Webb 2000).

Although restoration is a desirable way to ’help nature heal’ the approach is not without problems. First, as stated above, our knowledge about habitats or the ecological requirements of species that we would like to restore is rather poor. Thus, we do not necessarily know how to go about to reach the desired goals. Second, for altered ecosystems it is not always obvious what the desired ecosystem state should be (Bradshaw 2000). It is hard to find out what nature looked like and how it functioned before humans started to change it, if the pre-human state is our goal. Third, restoration is expensive, and the question arises whether or not restoration is the most efficient way of trying to maintain populations of indigenous species and ecosystems (Bradshaw 2000).

With this background, the aim of this paper is to discuss the meaning of the concept of restoration, to provide some food for conceptual thinking regarding restoration and the role of ecology in it, and to provide a few examples of restoration activities.

2. Restoration of forest ecosystems

What are the goals as regards forest restoration? According to a working group on forest restoration of the Finnish Ministry of the Environment there are two levels of goals for forest restoration. First, in the short term the goal is to improve conditions for threatened species as threatened species require immediate action, if we want to maintain them in our forests. As many as 37% of the threatened species in Finland occur in forests (Rassi et al. 2001). The long-term goal of forest restoration is to create such a mosaic of habitats and successional stages that maintains viable populations of indigenous species. The short and long-term goals support each other, although the long-term goals do not consider only threatened species but all indigenous species. More specifically, the aim is to restore (1) the natural tree species composition and their proportions, (2) structural elements of the trees (e.g. dead wood), (3) succession processes, and (4) as regards bog ecosystems to restore them by raising the ground water level and by restoring the original runoff properties and hydrology.

In more detail, the methods, intermediate goals and final goals of forest restoration are given in Table 1 (Tukia et al. 2001). The overall goal is the restoration of natural forest. There may be several intermediate goals of varying detail that support the overall goals. For instance, the intermediate goals may include creating more dead wood, and diversifying the age and size structure of trees. Some of the many restoration methods are given in Table 1. Many methods are related to allowing disturbance to take place and to mimicking natural disturbance regimes.

What are then the needs of forest restoration? This is difficult to estimate, but some guidelines can be obtained from restoration plans. In practice, most restoration efforts will focus on national parks and other protected areas. In Finland, 14-71% of the area of 8 national parks or other protected areas will be restored (Tukia et al. 2001). In each case restoration encompasses hundreds of hectares. In managed forests, the proportions are much lower, although the needs for restoration are more urgent. For instance, the proportion of forest land to be restored in the landscape ecological planning system of the Finnish Forest and Park Service is very low. About 0.1% of forest land is classified as 'biodiversity enhancement areas' that include restoration sites, but also other, valuable sites for biodiversity. Thus, it appears that restoration in managed forests will remain negligible.

There are some estimates of how much forest should be restored at the national level. If the goal is to maintain populations of forest species in Sweden, forest area requiring restoration ranges from about 3% in the northern boreal zone to ca. 11% in the nemoral zone (Angelstam & Andersson 2001). The calculations are based on the assumption that species require 20% of suitable habitat to survive, i.e. this is the habitat threshold value.

3. Restoring wooded meadows: an example from the Åland Islands

In Finland, there are no nemoral forests. The closest to it are hemiboreal forests along the southern coast and in the archipelago. Wooded meadows occur in the hemiboreal zone in the south-western part of the country, typically on the Åland Islands. The habitat is maintained by human activity (hay-making) and cattle or sheep grazing. These meadows are rather open, but have some scattered trees, often hazel, ash and birch. The habitat overgrows easily if left unmanaged. Due to lack of management most wooded meadows on the Åland Islands have overgrown by spruce and other trees, and have lost their characteristic vegetation and insect fauna (Niemelä 1990).

In addition to plants, insects are useful indicators of the success of restoration efforts (Williams 2000). We studied the success of a restoration project on the island of Nåtö some 7 km south of the town of Mariehamn by collecting carabid beetles and estimating abundances of vascular plants in (1) managed wooded meadow ('control'), (2) an adjacent, overgrown part of the same wooded meadow, and (3) an adjacent, restored part of the overgrown meadow. Our study was conducted in 1998, the second summer after the restoration in early 1997.

In terms of carabid beetles, the species richness was clearly higher in the managed wooded meadow (22 species) than in the overgrown part of the meadow (9 species) (Hari 1999) (Table 2). The restored section had an intermediate species richness (18 species) approaching that of the managed wooded meadow. In beetle abundance the pattern was the same (Table 2). In particular, open habitat species were missing from the overgrown part of the wooded meadow. Furthermore, the number of *Formica* ants was much higher in the overgrown section than in the restored section or in the managed wooded meadow (Table 2).

Three main conclusions can be made of this study. First, overgrowing of the wooded meadow impoverishes the carabid fauna. Second, carabid beetle assemblages responded very rapidly to restoration activities. Just one year after the removal of spruces and excess of other trees from the overgrown section, the carabid community resembled closely that of the managed wooded meadow (similarity 78%). Third, wood ants appear to respond rapidly to the restoration activities, but their response is reverse as compared to carabids. Ants decrease after the removal of trees. The high number of wood ants in the overgrown section may contribute to the low number of carabids there, as there may be a competitive interaction between wood ants and carabids (Niemelä et al. 1992).

Plants responded in a similar way to restoration as did carabids (Table 2) (Reinikainen 1999). Number of plant species was higher in the managed wooded meadow, intermediate in the restored section and lowest in the overgrown section. As regards canopy cover of trees the overgrwon section had highest cover percentage, while the wooded meadow and the restored sections had much lower but equal coverages.

This example teaches us that the flora and fauna may respond rapidly to restoration efforts. Another lesson is that in this case the establishment of the desired restoration goal as regards habitat state was easy. However, in many other cases it is not as easy, and even here it could be questioned whether the strongly human-impacted wooded meadow really is a desirable state of the ecosystem. Should not the overgrown wooded meadow that is approaching the natural state be the goal of restoration?

4. Restoration: problems and challenges

Restoration is often based on the assumption that nature is unchanging (Parker & Pickett 2000), but in reality, ecosystems are not static, and as a consequence, the aim of restoration may be a moving target (Bradshaw 2000). Threfore, function may be more important to restore than precise structure. Furthermore, it is important to ensure that the processes maintaing the inherent variability are maintained or restored. Here, the concept of biodiversity is of importance. Biodiversity refers to the overall variability in nature, and it is also the capacity of nature to buffer itself against disturbances and the flexibility to adapt to changes (Haila & Kouki 1994). Thus, the maintenance of biodiversity through maintenance or restoration of the processes maintaining biodiversity is of outmost importance for the functioning of nature. Such processes include the natural disturbance.

Ecological understanding of what are the internal and external factors, on the one hand, and biotic and abiotic, on the other hand, that affect ecosystems can guide our restoration efforts. This requires knowledge of ecological patterns and processes. It is therefore evident that ecological research can provide valuable insights to be used in restoration. However, not all ecological research is of immediate use to the manager interested in restoration. Ecology has general principles and models that are articulated at higher, more general levels of hierarchy. For instance, interspecific interactions between species can be described in general terms and studied using models. This kind of information is of limited value to a manager who needs place-specific information to guide restoration of a particular site (Parker & Pickett 2000). Thus, ecological knowledge most useful to those practicing restoration is species, habitat and place-specific. General ecological understanding is of importance for understanding what is possible, feasible and desirable from an ecological point of view. SUFOR is in an excellent position to provide ecological understanding needed for restoration. And the project is doing this.

One way of resolving the dilemma of ecological complexity making it difficult to predict the outcome of restoration actions is adaptive management (Walters & Holling 1990). Adaptive management is “a continuing process of action-based planning, monitoring, researching, evaluating and adjusting with the objective of improving the implementation and achieving the goals" of management standards and guidelines (Covington et al. 1998). The idea is that managers and scientists learn from experience, and use this knowledge to improve subsequent actions (Niemelä et al. 2001). Silvicultural activities in late-successional reserves provide a good example. Initially, existing knowledge of silviculture is reviewed and synthesised as a basis for development of a prescription. During and after implementation, a scientifically credible monitoring and evaluation programme determines whether goals have been achieved, and, finally, new knowledge is incorporated into new prescriptions (Covington et al. 1998, Niemelä et al. 2001).

In addition to ecological complexity, another problem associated with restoration is to determine what the desired state of an ecosystem should be, as discussed above (Bradshaw 2000). Often, 'natural state' is the goal of restoration, but how do we know what this state has been? And how do we know if we have reached the goal? To remedy these problems, Covington et al. (1998) have developed a stepwise systems analytic approach to the design of ecosystem restoration experiments.

1. Diagnose the symptoms and causes of the ecosystem health problem. What are the symptoms that suggest the ecological system has been degraded and what are the underlying mechanisms?
2. Determine reference conditions. What was the condition of the ecosystem before degradation?
3. Set measurable ecological restoration goals. How close to reference conditions do you intend to get? How will you know if you are moving in the right direction?
4. What factors are most limiting to the restoration process?
5. Develop alternative ecosystem restoration hypotheses, and design restoration treatments that will allow you to test the alternative hypotheses.
6. Monitor ecosystem conditions and evaluate hypotheses, and feed the results back into the design and implementation of ecological restoration – adapting management based on results and changing goals.

In these steps, adaptive restoration involves a variety of practices for designing and testing ecological restoration. Systematic ecological techniques, retrospective ecological analysis, and dendrochronology, along with other techniques, are used to determine the natural structure and function of the ecological system to be restored. Goals and performance measures must be defined in measurable terms. Assumptions about ecosystem dysfunction must be stated. A specific set of scientifically-based alternative treatments for restoring ecosystems to the desired condition must be developed. Finally, monitoring and evaluation procedures are used to determine where the restoration worked. A central assessment is whether the ecosystem being restored has been set on a trajectory such that structural and functional equivalency to the reference system will be attained. This information is then fed back into the body of scientific and managerial knowledge for future ecosystem management decisions.

So far, I have considered restoration in the countryside in areas where few people live. In such cases we do not expect any major conflicts between humans and the restoration activities. However, in urban areas, where restoration activities are often needed because of severe habitat degradation, the situation may be different. Although restoration efforts may be supported by local residents, there are often many opinions among them making it difficult to reach a consensus on what to do. As an increasing number of people live in cities, restoration of habitats in urban areas is becoming more important. The stepwise procedure including adaptive management may be a way to alleviate the potential problems associated with restoration in urban areas.

To conclude, restoration is a demanding task of re-creating something that has disappeared. Ecological research is a vital part of restoration, and through adaptive management scientists and the public can be involved in the effort. Although restoration is difficult, we must look ahead: "Once we restore, we are no longer retreating, trying only to slow the wave of destruction. We begin to actually advance, to regain lost ground. Can we really do it, or is the idea only hubris, human arrogance rearing its head one more time? … The short answer is: yes, we can really do it – to some degree. At worst we can produce something that mimics the real thing and that, given enough time, could become the real thing ...‘ (J. P. Wiley, Jr., 1989, cited by Covington, 1998).

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Table 1. The main goal, examples of intermediate goals and methods of forest restoration (modified from Tukia et al. 2001).

Goal	Intermediate goal 1	Intermediate goal 2	Intermediate goals 3	Methods
Restoration of natural forest (including overall biodiversity, natural state, threatened species)	Restoration of the structure and processes of natural forest or allowing the structures and process to exist	Restoration of the diversity of live and dead trees	Tree species composition	Allowance and mimicking of disturbances (e.g. prescribed burning, small openings, damaging of trees, wind and snow damage, herbivore damage)
			Age and size structure of trees	
			Dead wood	
		Increasing size, optimising delimitation of the area	Fragmentation	Removal of forest roads, restoration of gravel pits
			Buffer zones	
		Restoring hydrology	Ditching	Damming of ditches

Table 2. Number of carabids, *Formica* ants and plants in a wooded meadow, an orvergrown part of it and a restored part it on the Åland Islands (invertebrates: Hari 1999, plants: Reinikainen 1999).

	Wooded meadow	overgrown part	restored
Size (ha)	30	10	2
No. of carabid species	22	9	18
No. of car. individuals	1378	221	766
No. of open hab indiv.	36	0	14
No. of *Formica*-ants	227	4558	1648
No. of plant species	66	29	56
Canopy cover of trees (%)	48	120	50
Coverage of bushes (%)	1	7	3

An approach to quantitatively estimate biodiversity preservation potential at forest stand level

Sven G Nilsson[1] & Mats Niklasson[2]
[1]Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
[2]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, S-230 53 Alnarp, Sweden
Corresponding author: Sven G Nilsson, e-mail: sven.nilsson@zooekol.lu.se

Abstract

For efficient biodiversity preservation planning in forestry we need estimates of the actual and potential conservation value of individual stands. Our approach is based on a relatively good knowledge of the habitat requirements of regionally red-listed and threatened species. The estimation requires also knowledge of habitat availability in the surrounding landscape and the distance and species composition at biodiversity hot-spots nearby. The effects of long-time forest continuity on presumed dispersal-restricted organisms are built into our estimates. We argue that a broad taxonomic knowledge is necessary for an efficient planning of biodiversity preservation. Using only vascular plants and/or vertebrates as guidance will inevitably lead to biased estimates of conservational value at stand level.

Introduction

Sustainable forestry includes preservation of biodiversity as an important component (eg. Hunter 1999). The very definition of sustainability contains the concept that the possibility of coming generations of man shall not be constrained by more limited possibilities than our generation. The future values of different species in the forests are unknown, which means that we have to preserve all species although it may be in different proportions compared to the present situation. Species preservation means maintaining viable populations of all indigenous organisms. In Sweden forest living organisms constitute about half of the species (Nilsson et al. 2001). Out of the species that can be assessed based on present knowledge (34% of 58 000), currently 21% are red-listed in Sweden and more than 2000 of these species occur in forests (Gärdenfors 2000). Thus, the present use of the forests of Sweden cannot be considered sustainable from a species preservation point of view. The need for restoration of more natural forest types suitable as habitat for threatened species among others is especially urgent in southern Sweden compared to northern Sweden where still relatively large seminatural forest areas remain (Angelstam & Andersson 2001). An important question is where and how such restoration should be carried out.

The approach presented here aims at guiding forest management in selecting stands for the most cost-efficient habitat restoration in terms of preservation of biodiversity. Here we define biodiversity as the genetic variation within species, species richness and variation of forest types/forest ecosystems with an emphasis on species richness. In this paper we do not consider genetic variation within species and species richness of microorganisms.

The model we are developing (one part in Fig. 1) can both be used in forest stands as well as in any habitat with trees such as wooded pastures and meadows. Recent research has shown that wooded pastures are especially important to include for species conservation since they contain more than 2/3 of the populations of threatened tree-dependent species in southern Sweden (Nilsson et al. 1994, S.G. Nilsson unpubl.). Thus, in landscape planning it is very important to include all habitats with trees. This is rarely acknowledged in similar research. Here we present an outline of our model, while a full version with a quantitative example will be presented elsewhere.

The model

The aim of our model is to get an estimate of the biodiversity preservation potential of a plot with trees (usually a forest stand) for an efficient biodiversity preservation in a landscape. Each region in Niklasson and Nilsson (2002) have their own model, although the general approach is similar in the different regions. The scientific background to our model is presented in several recent reviews (Berg et al. 1994, Nilsson 1997, Nilsson et al. 2001, 2002a, 2002b, Nilsson & Ericson 1997, Jonsell et al. 1998). It should be stressed that in our approach as many organism groups as possible is considered. In contrast to many other countries, this is possible in Sweden due to a relatively detailed natural history information about forest living organisms dating back to the era of Linnaeus. However, for several species-rich groups of insects, e.g. Diptera and Hymenoptera, our present knowledge is still incomplete. Thus, those groups cannot be considered further in our model. In other parts of the world vertebrates (several papers in Hunter 1999) or vascular plants (e.g. Peterken 1996) are used as guides for sustainable forestry planning.

Our model can be run with different amount of input data. If only traditional variables (eg. tree species, dbh, basal area, tree height, site index, mean age) used in forest planning are included, less useful estimates are obtained. The reason is that the connection between such variables and biodiversity preservation potential is weak according to our experience. If a few additional variables are added (Table 1), much can be gained in terms of cost-efficient biodiversity preservation in habitats with trees. We stress that the field estimation of these additional variables are not expensive compared to the costs of setting aside stands for biodiversity preservation. Therefore, much can be gained by including these additional variables in the planning process.

Two types of variables are included in our model, landscape data and tree stand data (Table 1). Planning at the landscape level, often 1000 to 25000 ha, is necessary since many species depend on the forest composition at larger scales (references in Nilsson et al. 2001). For restoration of biodiversity the value of a stand is higher if it is present in a landscape with many threatened species than in a species-poor landscape (e.g. Hanski 2000), especially if dispersal sources are within a reasonable dispersal distance. Threatened species with low dispersal propensity is especially important to consider in the planning since they have the lowest probability to recolonize suitable habitats (e.g. Nilsson & Baranowski 1997). How urgent the need is to restore a given habitat for preservation of species depends on the previous landscape history. For example in southern Sweden, a rapid decrease of old sun-exposed oaks over the last 200 years (Eliasson & Nilsson 1999, 2002) means that a rapid increase of this important component for biodiversity is a cost-efficient measure (Nilsson & Eliasson 2000). However, some of the species dependent on old oak have a very low dispersal rate (Ranius & Hedin 2000), which means that efforts to increase the number of old oaks should mainly be carried out near dispersal sources. This consideration is built into our model.

In accordance to the reasoning above, presently known “hot-spots” with many threatened species are explicitly considered in our model. Such hot-spots have been mapped for wood-living beetles and epiphytic lichens in southern Sweden (Nilsson & Niklasson 1999, Nilsson 2001).

Those two taxonomic/ecological groups contain many red-listed species in Sweden (Gärdenfors 2000). When no species information is available from a landscape, our approach is based on the habitat requirement of red-listed species of the region. Thus, if a region contains many species dependent on for example old oak trees, stands with such trees or if they are present nearby implies a high value for species preservation. On the other hand, inventories of indicator species connected to old oaks can be an efficient means of improving the planning for biodiversity preservation. The beetle *Osmoderma eremita* is a species that, due to its large size is difficult to overlook, and that has proven efficient as an indicator of many red-listed species in a stand (Ranius 2002). The lichen *Lobaria pulmonaria* has also been found to be an efficient indicator for red-listed lichens, and also beetles dependent on hollow trees (Nilsson et al. 1995). On the other hand, it is not associated with many red-listed beetles dependent on dead trees (Nilsson et al. 1995). For those species, the beetle *Ceruchus chrysomelinus* has been suggested as a useful indicator species (Nilsson et al. 2000). However, at present this species is much too rare to be used alone. Other indicator species suggested by Nitare (2000) have apparently not been evaluated yet. These and other suggested indicator species dependent on dead trees and with different preferences for sun-exposure ought to be evaluated (Nilsson et al. 2001).

The landscape planning process

The eastern part of southern Sweden originally had a high frequency of forest fires (e.g. Niklasson & Drakenberg 2001). Recent effort to restore and improve conditions for fire-adapted organisms through prescribed burning has however encountered problems. For efficient biodiversity restoration forest fires should occur when the forests are as dry as possible (L. Wikars pers. comm.). At such occasions the risk of having uncontrolled spreading of fire is also the highest.. In addition, most prescribed burnings are done after partial clearcuts or even total clearcuts. This has resulted in burnings that sometimes are of questionable value from a biodiversity point of view. The reason is that burnt wood and fire-scarred trees are the most important component for many species adapted to burnt forests. Thus, we think that forest burning in southern Sweden ought to be planned where there are natural fire-breaks, e.g. lakes and open wetlands, and a low human population density. In such places it is possible to burn when the forest is very dry. Such strategic decisions of landscape planning are however at present outside the scope of our model. Our model set values on stands from a biodiversity preservation perspective. Then follows a strategic planning process based on the value of stands for timber production, biodiversity preservation and other considerations.

Conclusions

Cost-efficient biodiversity preservation in highly transformed landscapes, as in southern Sweden, depends to a high degree on improved knowledge about the remaining hot-spots. If we cannot preserve threatened species in the few remaining hot-spots, there are few possibilities of a sustainable forestry from a species preservation point of view. The hot-spots act as dispersal sources for possibly viable populations in the future, and at present most of surrounding landscapes can be regarded as hostile “sinks” for many of the species found in hot-spots. Habitat restoration in the surrounding landscape therefore should have a higher value if positioned near these hot-spots. Furthermore, even in landscapes lacking threatened species, concentrated efforts when restoration habitats for biodiversity preservation are most efficient when focusing on the regionally most valuable habitats. Our model aims at providing data for efficient planning where to position habitat restoration.

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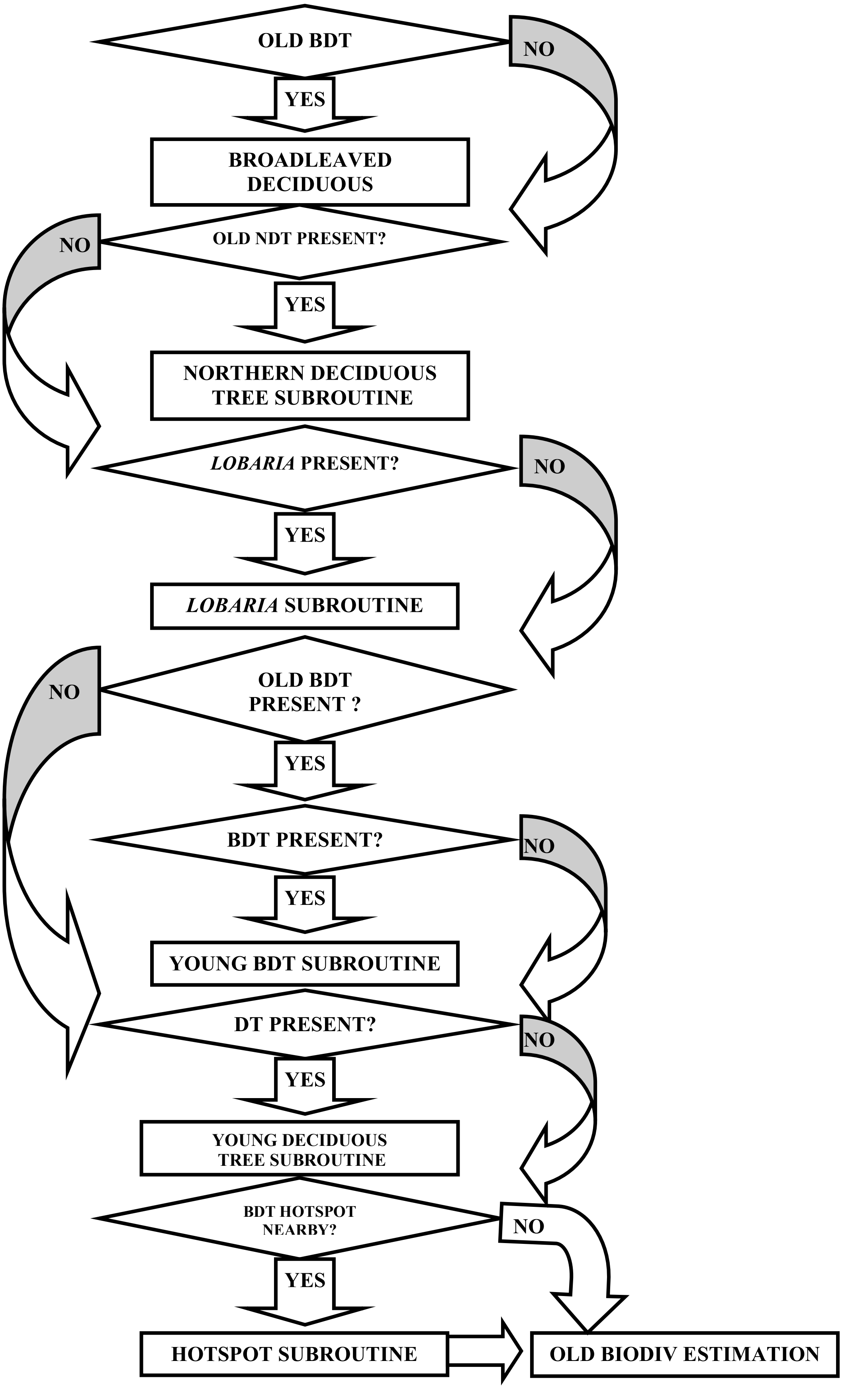
Table 1. Indata to the biodiversity restoration potential estimation. Southern (broad-leaved) deciduous trees include *Quercus, Fagus, Ulmus, Tilia, Acer, Carpinus, Fraxinus* and *Prunus*. Northern deciduous trees include *Betula, Alnus, Populus tremula* and *Sorbus acuparia.*

Landscape data:
Disturbance regime region from Niklasson & Nilsson (2002).
Distance to “hotspots” with information about responsibility species
Number of old trees (hollow trees) of southern deciduous trees in nearby stands
Number of old trees (hollow trees) of northern deciduous trees in nearby stands
Indicator species for dead trees within 2 km
Occurrence of *Lobaria pulmonaria,* or other proven indicator species, in nearby stands
Occurrence of forest plants with low dispersal rate in nearby stands

Tree stand data:
Area of the stand
Age of the stand
Basal area of the stand
Proportion of southern (broadleaved) deciduous trees (oak and beech separated)
Proportion of northern deciduous trees (birch separated)
Proportion of pine and spruce
Proportion of old trees (hollow trees) of southern (broadleaved) deciduous trees
Proportion of old trees (hollow trees) of northern deciduous trees
Occurrence of *Lobaria pulmonaria,* or other in the region proven indicator species
Number of old (> 10 år) large (diam. > 40 cm) dead trees
Number of large (diam. > 40 cm) dead oaks
Number of large (diam. > 40 cm) dead beeches
Number of large (diam. > 40 cm) other dead southern (broadleaved) deciduous trees
Number of dead deciduous trees (diam. > 20 cm)
Number of dead spruces (diam. > 20 cm)
Number of dead pines (diam. > 20 cm)
Occurrence of forest plants with low dispersal rate
Former land use (inmark/utmark, field cleared from larger stones)
Acidity of the upper soil layer (pH)

Fig. 1 (next page). System specification for the biodiversity restoration model, the old deciduous tree component, in the region in central Götaland, southern Sweden. Old trees means trees that are over 150 years old. BDT = southern (broad-leaved) deciduous trees. NDT = northern deciduous trees. DT = deciduous trees.


OLD BDT
NO
YES
BROADLEAVED DECIDUOUS
NO
OLD NDT PRESENT?
YES
NORTHERN DECIDUOUS TREE SUBROUTINE
LOBARIA PRESENT?
NO
YES
LOBARIA SUBROUTINE
NO
OLD BDT PRESENT ?
YES
BDT PRESENT?
NO
YES
YOUNG BDT SUBROUTINE
DT PRESENT?
NO
YES
YOUNG DECIDUOUS TREE SUBROUTINE
BDT HOTSPOT NEARBY?
NO
YES
HOTSPOT SUBROUTINE
OLD BIODIV ESTIMATION

Nutrient Sustainability

Prof. Richard Waring, Dept. of Forest Science, College of Forestry
Oregon State University, Corvallis, OR 97331, USA
E-mail: waring@fsl.orst.edu

Abstract

Fast growing plantations require a sustained supply of nutrients in addition to nitrogen. As nitrogen becomes increasingly available, allocation to growth is shifted proportionally from fine roots and mycorrhizae toward foliage and stems; this shift results in reduced uptake of phosphorus, bases, and micronutrients. For conifers, leaf nitrogen concentrations above 1.5% generally signify that free amino acids are increasing while the concentration of defensive compounds is being reduced. This shift in biochemistry makes plantations more susceptible to outbreaks of diseases and insects.

Over the long term, nitrogen additions, whether obtained through atmospheric deposition, through symbiotic N-fixation, or through commercial application, will tend to make other nutrients less available. Sustainable practices that minimize nutrient imbalances include: (1) favoring a mix of species that recycle bases and (2) imposing practices that reduce the relative availability of nitrogen while increasing the decomposition of woody material rich in bases.

Introduction

The recognition that intensively managed plantations can meet the world's demand for most types of wood products on a few percent of the present forested area is appreciated and applauded by environmental skeptics (Lomborg 2001), foresters (Boyle et al. 1999), and conservationists (Wilson 2002). Yields between 10 to 50 m^3/ha/yr are rarely attained, however, without the application of commercial fertilizer. The exceptions are in areas such as northern Europe, where high levels of atmospheric N deposition are recorded (Schulze 1989, Edfast et al. 1990, Emmett and Reynolds 1995), and in the Pacific Northwest region of the U.S.A., where a wide variety of native symbiotic nitrogen-fixing species abound (Waring and Franklin 1979). The question arises "how sustainable are these yields without application of additional nitrogen and other essential nutrients?"

In this paper, I describe the key role that nitrogen plays in determining wood production, and explain why somewhat less than optimal levels of nitrogen are recommended to reduce the danger from outbreaks of insects and diseases. I also recommend practices for slash disposal and for maintaining a mix of species that should improve nutrient cycling and help maintain growth rates through future rotations.

Key role of nitrogen in determining wood production

Nitrogen influences the growth of wood in three ways:

- By increasing the photosynthetic capacity of leaves
- By shifting the allocation of growth away from fine roots into stem wood
- By increasing the total leaf area, which results in the interception of more light

What is striking about these three responses is that over a wide range in nitrogen availability, the relationships are linear (except for light interception). Photosynthesis may be increased by more than 3-fold in proportion to leaf nitrogen concentrations (Meir et al. 2002). Similarly, through incremental addition of nitrogen, Beets and Whitehead (1996) showed that the fraction of growth allocated to fine-roots was reduced from 0.6 to 0.2, while wood production increased 3-fold from 15 to 45 m^3/ha/yr in *Pinus radiata* plantations in New Zealand. Foliage mass and leaf area showed a similar 3-fold increase with additions of nitrogen (Beets and Madgwick 1988).

Why foliar nitrogen levels should be maintained below optimum for growth

Tamm et al. (1999) provide a comprehensive review and synthesis of a series of major research projects involving optimum balanced and imbalanced additions of fertilizers to Scots pine plantations in Sweden. Linder (1995) provides a similar synthesis for Norway spruce with details on adjusting for seasonal variation in starch reserves. Both studies indicate that the optimum concentration of nitrogen in foliage to obtain maximum tree growth is between 1.4-1.7%. I will argue that it is ill advised to allow conifer foliage to exceed 1.5% N or hardwoods 2.0% N because biochemical changes occur in the proportion of nitrogen associated with the photosynthetic machinery, and that in more soluble forms such as amino acids (Table 1).

Table 1. The amino acid (arginine) increases much more than the foliar nitrogen in Scots pine following additions of N fertilizer (Näsholm and Ericsson 1990).

Foliar N%	0.8-1.2%	1.5-2.0%	2-2.5%
Arginine, % of N	0%	7-16%	10-27%

In deciduous hardwoods, a similar relationship between foliar N% and increasing amounts of amino acids exists (Pahlsson 1992). Along with an increase in soluble forms of nitrogen, there is a decrease in the concentration of defensive compounds such as phenolics. In Scots pine, the concentration of defensive compounds (procyanidins) decrease by 45% while the fraction of arginine in the amino acid pool increases by nearly 400% as foliage N concentrations increase. The problem may be enhanced by air pollution through ozone damage, but occurs in areas without significant pollution, such as Australia (Turner and Lambert 1986) and in the Pacific Northwest of the U.S.A. (Fig. 3).

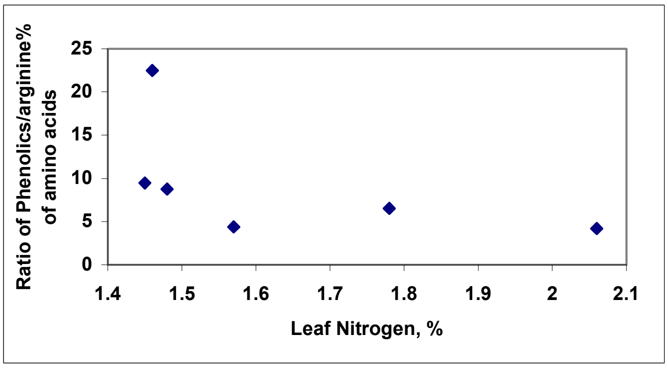


Fig. 2. In Scots pine plantations, the ratio of defensive compounds (procyanidins) to the fraction of total amino acid pool composed of arginine drops significantly at leaf N% ≥1.5% (Kätzel and Löffler 1995, 1997).

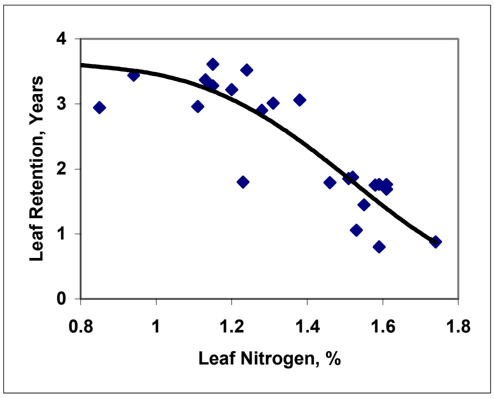


Fig. 3. In Douglas-fir plantations foliar retention is significantly reduced by a needle-cast fungi (Phaeocryptopus gaeumanii) when leaf N% exceed 1.5% (Waring et al. 2000).

Although insect outbreaks are often associated with trees under stress, with very low growth rates (Coyea and Margolis 1992, Christiansen et al. 1998, Waring et al. 1992), insect damage may also increase in stands where growth rates are enhanced through application of fertilizer. For example, spruce stands in British Columbia, when provided incremental increases in available nitrogen and other nutrients, suffered a five-fold increase in weevil shoot damage (Fig. 4).

Silvicultural practices

Slash disposal

In high yielding plantations, thinning is usually practiced. At the time of thinning, the slash produced consists of green foliage and woody material. These two sources of detritus have different C:N and other mineral ratios and require different treatment to meet the goal of maintaining site nutrient balance (Van den Driessche 1984, Ericcson 1994). The foliage, if on sites receiving an excess of the nitrogen, can be piled and later

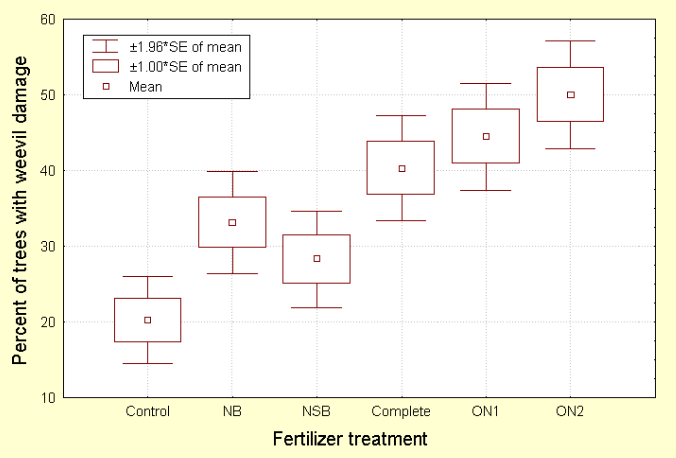


Fig. 4. Additions of fertilizer, even when complete, still lead to increased weevil damage to spruce plantations in British Columbia (Van Akker 2002). ***Control*** *- not fertilized (foliar N concentrations at1.1%;****NB,*** *- fertilize every 6 years with (kg/ha): 200N, 1.5B;* ***NSB*** *- fertilize every 6 years with (kg/ha): 200N, 50S, 1.5B;****Complete*** *- fertilize every 6 years with (kg/ha): 200N, 100P, 100K, 50S, 25Mg, 1.5B;*$\boldsymbol{ON_1}$ *- yearly fertilization to maintain foliar N concentration at 1.3% and other nutrients and nutrient ratios within the "optimum" range;*$\boldsymbol{ON_2}$ *- yearly fertilization to maintain foliar N concentration at 1.6% and other nutrients and nutrient ratios within the "optimum" range (Brockley 1999).*

burned. During ignition, a considerable amount of nitrogen and sulfur will be volatilized, leaving ash rich in bases: Ca^{++}, Mg^{++}, K^{+} (Wan et al. 2001). The woody material, if left on the surface, will decay very slowly. If chipped, however, the woody material is soon incorporated into the soil (Turner 1977). Because the C:N ratio of woody material is high (>200:1), nitrogen will be further immobilized (Paustian et al. 1992), and root growth will increase, along with mycorrhizal activity, which improves uptake of other nutrients. With decomposition of wood, calcium from cell walls is mineralized, and replaces hydrogen on soil cation exchange sites. This raises soil pH, which improves the availability of P and other nutrients (Chandler 1941, Carreira et al. 1997).

Species diversity

R.R. Chandler in 1941 was one of the first Americans to document that mineral concentrations in the foliage of various tree species differed consistently, regardless of the soil on which the trees grew. He noted, for example, that the calcium content in the litter of *Tilia*, *Prunus*, and *Liriodendron* was high, whereas that in the leaf litter from *Fagus*, *Quercus*, and *Acer* was low. Many others have recognized the potential to manage nutrient availability and carbon sequestration in soils through manipulation of species composition (Fyles and Fyles 1993,Vesterdal and Raulund-Rasmussen 1998).

Monitoring Canopy N concentration

With the recognition that nitrogen concentrations in foliage may exceed a critical ratio with defensive compounds that is well below optimum for growth, and that unknown amounts of nitrogen can be provided to ecosystems through atmospheric deposition and symbiotic fixation, it is worth noting that foliar nitrogen concentrations can be monitored and mapped from space using fine-resolution imaging spectrometers (Martin and Aber 1997).

Conclusions

The main points of this paper can be summarized as five recommendations:

- Keep N concentrations below optimum for growth
- Use amino acid assays to indicate nutrient imbalances or other stresses
- Consider burning green slash and chipping woody debris
- Use a mixture of species to provide a balanced litter nutrient content
- Monitor foliar N concentration via remote sensing

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Incorporating nutrient content elasticity in the MAKEDEP model

Alveteg, M.[1], Kurz, D.[2] and Becker, R.[3]
1) Dept. Chemical Engineering II, Lund University, Sweden
2) EKG Geo-Science, Bern, Switzerland
3) ÖKO-DATA,Strausberg, Germany

Abstract

The MAKEDEP model is designed to produce the time series of atmospheric deposition and nutrient uptake and cycling needed by dynamic soil chemistry models such as SAFE.

A range of new features were implemented in the MAKEDEP model including separate treatment of several tree compartments (e.g. root, stem, bark, branch, canopy) and variable nutrient content in the different compartments. The model is designed to produce output that can easily be used as input to the multi-layer soil chemistry model SAFE.

The introduction of variable nutrient content calls for a separate treatment of biomass and stored nutrients and also affects the calibration procedure used in the MAKEDEP model.

Keywords: historic deposition, acidification, dynamic modelling, forest growth, nutrient uptake, SAFE model

1 Introduction

Atmospheric deposition and nutrient uptake and cycling are dominating fluxes in forest ecosystems and are therefore important driving variables for dynamic soil chemistry models such as SAFE (Warfvinge et al. 1993), MAGIC (Cosby et al. 2001) and SMART (de Vries et al. 1989). Atmospheric deposition and nutrient uptake are usually only available as present day values, and there is often no site-specific information available on how deposition and uptake have changed over time. The historic deposition and uptake used as input to dynamic soil chemistry models will, however, influence model calibration as well as validation and forecasts. If a new set of assumptions are used for each new site to which the model is applied, it will therefore be very difficult to distinguish invalid assumptions in the deposition hindcasts from invalid assumptions in model formulation. Serious errors in model formulation may even pass without notice if the deposition and uptake hindcasts are adjusted in order to calibrate model output. If, however, the same set of assumptions is used for the reconstruction of historic deposition and uptake, it is more likely that invalid assumptions in model formulation as well as in the reconstruction scheme will be detected.

To reconstruct historic deposition and nutrient uptake in a general and systematic fashion, the MAKEDEP model was created. The MAKEDEP model quickly became much used in dynamic soil chemistry modelling, both in its original version and as the DEPUPT program(Johansson et al. 1996). Over the years numerous model improvements have been suggested; The original MAKEDEP program as well as DEPUPT considers nutrient contents to be a constant characteristics of the vegetation. In reality, however, nutrient content varies with nutrient availability. Another weakness in the original MAKEDEP model was that deposition of marine salts were always estimated directly from the deposition measurements and treated separately.

The aim of this paper is to describe the current status of the reconstruction model, MAKEDEP which includes optional elasticity in nutrient content and optional separate treatment of marine salt deposition.

2 Atmospheric deposition

The underlying principle behind the reconstruction of deposition in MAKEDEP is to scale deposition and emission trends in the literature to fit measurements of atmospheric deposition at the studied site. To improve the reconstruction temporally and spatially, two important observations regarding deposition are considered: 1) The deposition is higher on a forested area than on a non-forested area and usually increases as the forest grows and decreases as the forest is cut down. This is related to the leaf area index, dry deposition of gases and aerosols, etc. 2) Sites close to the sea usually have different deposition patterns than inland sites, and are likely to have quite different background levels of e. g. SO_4^{2-} deposition.

To include these two observations in the reconstruction strategy there is a need to distinguish between wet and dry deposition, as it is mainly the dry deposition that is affected by changes in vegetation. There is also a need to distinguish between marine and non-marine deposition, since it is the deposition of sea-salts that gives the sites close to the sea their characteristic deposition patterns. We may also need to consider the atmosphere-canopy interactions, i.e., the canopy exchange.

In this study, the input of elements to the forest ecosystem is thus divided into the following five categories:

- Dry marine deposition
- Wet marine deposition
- Dry non-marine deposition
- Wet non-marine deposition
- Canopy exchange

The different deposition categories are reconstructed separately. The categorisation and the reconstruction of each category is summarised in figure 2.

2.1 Categorisation of deposition

The minimum data requirement for this categorisation (see table 1) and reconstruction is current throughfall deposition and wet deposition of major ions, i. e. SO_4^{2-}, Cl^-, NO_3^-, NH_4^+, Ca^{2+}, Mg^{2+}, K^+ and Na^+.

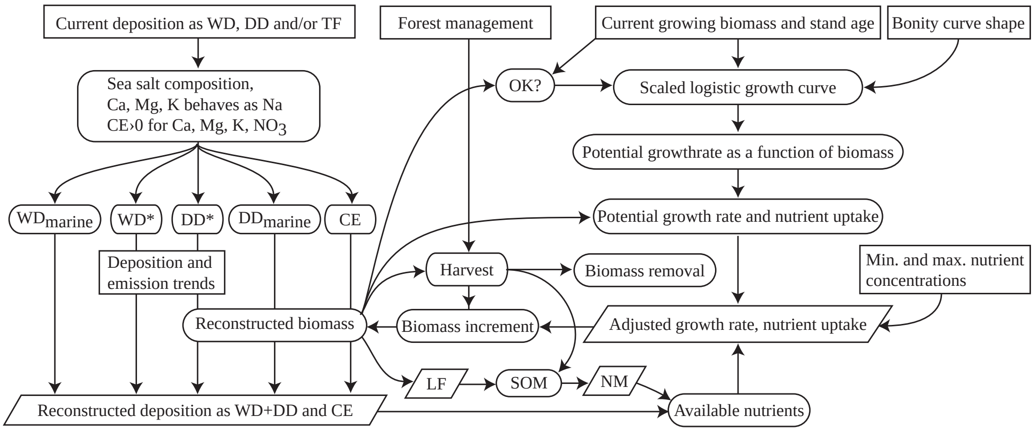

Figure 1: Flowchart for the described reconstruction method. Input are in squares and main output in parallelograms. Starting with measurements of wet deposition and throughfall, the deposition to the ecosystem is divided into five different deposition categories. The deposition categories are scaled using general deposition trends and canopy biomass according to equation 13-18. The parameter w_{max} in the logistic growth-growth rate function is determined iteratively, due to the feedback between canopy biomass and deposition history, until both the present biomass and the present deposition are reconstructed properly.

2.1.1 Use of dry deposition and throughfall measurements

If both dry deposition and throughfall are specified MAKEDEP calculates canopy exchange directly as

$$\mathrm{CE} = \mathrm{TF} - \mathrm{WD} - \mathrm{DD}\ . \tag{1}$$

Any canopy exchange of NO_3^- will be treated as canopy exchange of NH_4^+ while non-zero canopy exchange of SO_4^{2-} or Cl^- causes the MAKEDEP model to reject all input for that site.

2.1.2 Absence of throughfall estimates

If throughfall is not specified MAKEDEP calculates throughfall as

$$\mathrm{TF} = \mathrm{WD} + \mathrm{DD}\ . \tag{2}$$

Canopy exchange is then consequently assumed to be zero for all elements.

2.1.3 Absence of dry deposition estimates

If dry deposition is not specified the MAKEDEP model estimates dry deposition from the input on wet deposition and throughfall deposition. For elements that are not involved in canopy exchange the dry deposition (DD) it is assumed that

Table 1: Summary of equations used to separate atmospheric deposition into different deposition categories starting from site-specific input on wet deposition (WD) and throughfall (TF). DD is the total dry deposition, i.e. $\mathrm{DD}=\mathrm{DD}_\mathrm{j}^{*} + \mathrm{DD}_\mathrm{j,marine}$. It is assumed that $\mathrm{TF_j} \geq \mathrm{WD_j}$ for NO_3^- , SO_4^{2-} , Cl^- , and Na^+

<table>
<tr><th>Deposition category</th><th>SO_4^{2-}</th><th>Cl^-</th><th>Ca^{2+}</th><th>Mg^{2+}</th><th>K^+</th><th>Na^+</th><th>NO_3^-</th><th>NH_4^+</th></tr>
<tr><td>$\mathrm{WD_j}$</td><td colspan="8">Site–specific data</td></tr>
<tr><td>$\mathrm{TF_j}$</td><td colspan="8">Site–specific data or $\mathrm{TF_j}=\mathrm{WD_j}+\mathrm{DD_j}$</td></tr>
<tr><td rowspan="2">$\mathrm{DD_j}$</td><td colspan="8">Site–specific data or</td></tr>
<tr><td colspan="2">$\mathrm{TF_j} - \mathrm{WD_j}$</td><td colspan="3">$\mathrm{WD_j}\frac{\mathrm{TF_{Na}}-\mathrm{WD_{Na}}}{\mathrm{WD_{Na}}}$</td><td colspan="2">$\mathrm{TF_j} - \mathrm{WD_j}$</td><td>$\max(\mathrm{TF_j} - \mathrm{WD_j}, 0)$</td></tr>
<tr><td>$\mathrm{WD_{j,marine}}$</td><td colspan="5">$\min(\mathrm{x_j} \cdot \mathrm{WD_{Na}}, \mathrm{WD_j})$</td><td>$\mathrm{WD_{Na}}$</td><td colspan="2">0</td></tr>
<tr><td>$\mathrm{DD_{j,marine}}$</td><td colspan="5">$\min(\mathrm{x_j} \cdot \mathrm{DD_{Na}}, \mathrm{DD_j})$</td><td>$\mathrm{DD_{Na}}$</td><td colspan="2">0</td></tr>
<tr><td>$\mathrm{WD_j^*}$</td><td colspan="5">$\mathrm{WD_j} - \mathrm{WD_{j,marine}}$</td><td>0</td><td colspan="2">$\mathrm{WD_j}$</td></tr>
<tr><td>$\mathrm{DD_j^*}$</td><td colspan="5">$\mathrm{DD_j} - \mathrm{DD_{j,marine}}$</td><td>0</td><td colspan="2">$\mathrm{DD_j}$</td></tr>
<tr><td>$\mathrm{CE_j}$</td><td colspan="2">0</td><td colspan="3">$\mathrm{TF_j} - \mathrm{WD_j} - \mathrm{DD_j}$</td><td>0</td><td colspan="2">$\min(\mathrm{TF_j} - \mathrm{WD_j}, 0)$</td></tr>
</table>

$$\mathrm{DD} = \mathrm{TF} - \mathrm{WD} \tag{3}$$

where TF is throughfall deposition and WD is wet deposition. Under the assumption that Na^+ is not involved in canopy exchange and that Ca^{2+} Mg^{2+} and K^+ are deposited by the same mechanisms as Na^+ , dry deposition of Ca^{2+} , Mg^{2+} and K^+ can be calculated as:

$$\mathrm{DD}_j = \mathrm{WD}_j \frac{\mathrm{TF_{Na}} - \mathrm{WD_{Na}}}{\mathrm{WD_{Na}}} \tag{4}$$

where j is Ca^{2+} , Mg^{2+} or K^+. This is a simplification of the approach developed by Ulrich (1983) and, if stemflow is neglectable, the same expression as used by Draaijers and Erisman (1995). The remaining input of Ca^{2+} , Mg^{2+} and K^+ , is canopy exchange (CE) defined as positive when elements are excuded from the canopy. CE is calculated as:

$$\mathrm{CE} = \mathrm{TF} - \mathrm{WD} - \mathrm{DD} \tag{5}$$

Canopy exchange may be an important sink or source for NO_3^- and NH_4^+ (Beier et al. 1992) , but our knowledge is too limited to allow a general scheme for deducing canopy exchange from data on throughfall and wet deposition. When the user does not supply estimates of both dry deposition and throughfall, MAKEDEP therefore only assumes canopy exchange to exist when wet deposition of NO_3^- or NH_4^+ is greater than the respective throughfall. Dry deposition of NH_4^+ is then set to zero and canopy exchange to

$$\mathrm{CE} = \mathrm{TF} - \mathrm{WD} \tag{6}$$

As the SAFE model currently does not differentiate between canopy exchange of NO_3^- and NH_4^+, only the sum is reported. Canopy exchange of SO_4^{2-} and Cl^- are assumed to be zero.

2.1.4 Marine deposition

Deposition of marine salts are optionally treated separately, the rationale being that efforts to reduce emissions will not have any direct effects on the emission and deposition of marine salts. For sites where the contribution of marine salts to the total deposition, especially of Na^+ and Cl^-, is considered to be negligable as compared to the deposition caused by anthropogenic emission, it is recommended that the separate treatment of marine deposition is turned of.

Assuming that sea spray is the only source of Na^+ and that there is no fractionation of sea salt elements during transport, wet and dry marine deposition can be calculated as:

$$\mathrm{WD}_{j,marine} = min(x_j\ \mathrm{WD}_{\mathrm{Na}}, \mathrm{WD}_j) \tag{7}$$

$$\mathrm{DD}_{j,marine} = min(x_j\ \mathrm{DD}_{\mathrm{Na}}, \mathrm{DD}_j) \tag{8}$$

where WD_j and DD_j are wet and dry deposition, respectively, for element j and x_j is the relative abundance of element j in sea salt. The disadvantage with this approach is that calculated marine deposition may have a different composition than the sea salt composition and the input data will in that case be inconsistent with the model assumptions. In the new version of MAKEDEP marine deposition for an element is therefore calculated by multiplying the minimum deposition to relative sea salt composition ratio with the relative sea salt composition for that element:

$$\mathrm{WD}_{j,marine} = x_j \cdot min\left[\frac{\mathrm{WD}_{\mathrm{SO}_4^{2-}}}{x_{\mathrm{SO}_4^{2-}}}, \frac{\mathrm{WD}_{\mathrm{Cl}^-}}{x_{\mathrm{Cl}^-}}, \frac{\mathrm{WD}_{\mathrm{Ca}^{2+}}}{x_{\mathrm{Ca}^{2+}}}, \frac{\mathrm{WD}_{\mathrm{Mg}^{2+}}}{x_{\mathrm{Mg}^{2+}}}, \frac{\mathrm{WD}_{\mathrm{K}^+}}{x_{\mathrm{K}^+}}, \frac{\mathrm{WD}_{\mathrm{Na}^+}}{x_{\mathrm{Na}^+}}\right] \tag{9}$$

$$\mathrm{DD}_{j,marine} = x_j \cdot min\left[\frac{\mathrm{DD}_{\mathrm{SO}_4^{2-}}}{x_{\mathrm{SO}_4^{2-}}}, \frac{\mathrm{DD}_{\mathrm{Cl}^-}}{x_{\mathrm{Cl}^-}}, \frac{\mathrm{DD}_{\mathrm{Ca}^{2+}}}{x_{\mathrm{Ca}^{2+}}}, \frac{\mathrm{DD}_{\mathrm{Mg}^{2+}}}{x_{\mathrm{Mg}^{2+}}}, \frac{\mathrm{DD}_{\mathrm{K}^+}}{x_{\mathrm{K}^+}}, \frac{\mathrm{DD}_{\mathrm{Na}^+}}{x_{\mathrm{Na}^+}}\right] \tag{10}$$

where j indicates the elements present in sea salts. Naturally, marine deposition of elements not present in sea salt, i.e. NO_3^- and NH_4^+, is assumed to be zero.

Once the marine deposition has been calculated, the non marine deposition, WD^* and DD^*, is simply (see table 1):

$$\mathrm{WD}_j^* = \mathrm{WD}_j - \mathrm{WD}_{j,marine} \tag{11}$$

$$\mathrm{DD}_j^* = \mathrm{DD}_j - \mathrm{DD}_{j,marine} \tag{12}$$

2.1.5 The reconstruction procedure

The deposition categorisation described above is used only once per site to distribute the measured deposition at year t_{D} into different deposition categories. The deposition categories are then used together with general deposition trends and the reconstructed canopy biomass to estimate the deposition at different years t. Non-marine categories are scaled using general deposition trends, whereas dry deposition categories and canopy exchange are scaled linearly with reconstructed canopy biomass (Alveteg et al. 1998) as

$$\mathrm{WD}_{j_{mar}}(t) = \mathrm{WD}_{j_{mar}}(t_{\mathrm{D}}) \tag{13}$$

$$\mathrm{DD}_{j_{mar}}(t) = \mathrm{DD}_{j_{mar}}(t_{\mathrm{D}})\frac{w_C(t-1)}{w_C(t_{\mathrm{D}}-1)} \tag{14}$$

$$\mathrm{WD}^*_j(t) = \mathrm{WD}^*_j(t_{\mathrm{D}})\frac{S_j(t)}{S_j(t_{\mathrm{D}})} \tag{15}$$

$$\mathrm{DD}^*_j(t) = \mathrm{DD}^*_j(t_{\mathrm{D}})\frac{S_j(t)}{S_j(t_{\mathrm{D}})}\frac{w_C(t-1)}{w_C(t_{\mathrm{D}}-1)} \tag{16}$$

$$-\mathrm{CE}_j(t) = min(-\mathrm{CE}_j(t_{\mathrm{D}})\frac{w_C(t-1)}{w_C(t_{\mathrm{D}}-1)}, \mathrm{WD}_{j_{mar}}(t) + \mathrm{DD}_{j_{mar}}(t) + \mathrm{WD}^*_j(t) + \mathrm{DD}^*_j(t)) \tag{17}$$

$$\mathrm{D}_j = \mathrm{DD}_{j_{mar}} + \mathrm{WD}_{j_{mar}} + \mathrm{DD}^*_j + \mathrm{WD}^*_j \tag{18}$$

where S_j is the general deposition trend for species j and w_C the canopy biomass. It should be noted that while in reality the current canopy biomass is what influences the dry deposition, MAKEDEP uses the canopy biomass of the previous year, corrected for harvesting or thinning if applicable[1]. This is a simplification that reduces the calculations needed considerably: In order to calculate the canopy biomass the current year it is necessary to know the deposition which in turn is dependent on the canopy biomass. A iteration procedure would therefore be necessary if the current canopy biomass was used in the scaling procedure.

Two changes were made compared to the MAKEDEP version described by Alveteg et al. (1998). Firstly all deposited species now have their own general trend curve. It is up to the user to determine if the same data can be used for more than one species, e.g. if all base cations can be scaled with the same general deposition trend. Secondly the separate treatment of marine deposition has been made optional. If marine deposition is not treated separately, division is made into dry deposition, wet deposition and canopy exchange and both dry and wet deposition are scaled using the general deposition trends.

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[1] In the terminology used here, a thinning is a harvest with harvest fraction less than unity.

3 Forest growth and nutrient Uptake

The gross uptake of nutrients from the soil to a forest stand can be defined as

$$\mathrm{GU} = \mathrm{NU} + \mathrm{CE} + \mathrm{LF} \tag{19}$$

where GU is gross uptake, NU is net uptake and LF is litter fall. The dynamic multi-layer soil chemistry model SAFE needs time series of input on NU, CE and LF and calculates the gross uptake from soil using the equation above. Single-layer dynamic soil chemistry models such as the MAGIC and SMART models needs only time series of NU since nutrient cycling (CE and LF) has no effect in single-layer models.

As long as the nutrient content in the tree compartments is constant and there is no severe shortage of nutrients it is pretty straight forward to calculate NU using any kind of logistic growth curve. The MAKEDEP model uses a n:th order Mikaelis-Menten equation for this purpose

$$w_i = w_{i,max} \frac{Y^n}{Y^n + k_i^n} \tag{20}$$

where w is the biomass of compartment i, $w_{i,max}$ a scaling factor representing the maximum possible biomass for the compartment i at that site, Y is the stand age, k_i is the age at which the tree compartment has reached half ot its maximum biomass and finally n is the order of the Mikaelis-Menten equation. The n and k was in previous versions of MAKEDEP fitted to a logistic growth curve for coniferous trees in southern Germany (Assman and Franz 1965, Alveteg et al. 1998). The fitted growth curve was assumed to represent the biomass evolution of all tree compartments except the canopy. For canopy it was assumed that

$$k_C = \frac{k_{\text{tree}}}{3} . \tag{21}$$

The version of MAKEDEP presented here has up to five tree compartments, each with its own k_i and $w_{i,max}$, but all with the same n.

Due to the possibility of N shortage the growth function (equation 20) was transformed to an equation where the potential growth rate for different compartments (r_i) can be calculated from the present biomass:

$$r_i(t) = w_{i,max} \left(\frac{(y_i(t-1)+1)^n}{(y_i(t-1)+1)^n + k_i^n} - \frac{y_i(t-1)^n}{y_i(t-1)^n + k_i^n} \right) \tag{22}$$

where $r_i(t)$ is the potential growth rate of compartment i and y_i is the apparent age of compartment i calculated as

$$y_i(t-1) = k_i \left(\frac{w_i(t-1)}{w_{i,max} - w_i(t-1)} \right)^{\frac{1}{n}} . \tag{23}$$

It should be noted that

$$y(t) \leq y(t-1) + 1 \tag{24}$$

where equality holds if the actual growth equals the potential growth and there is no harvesting.

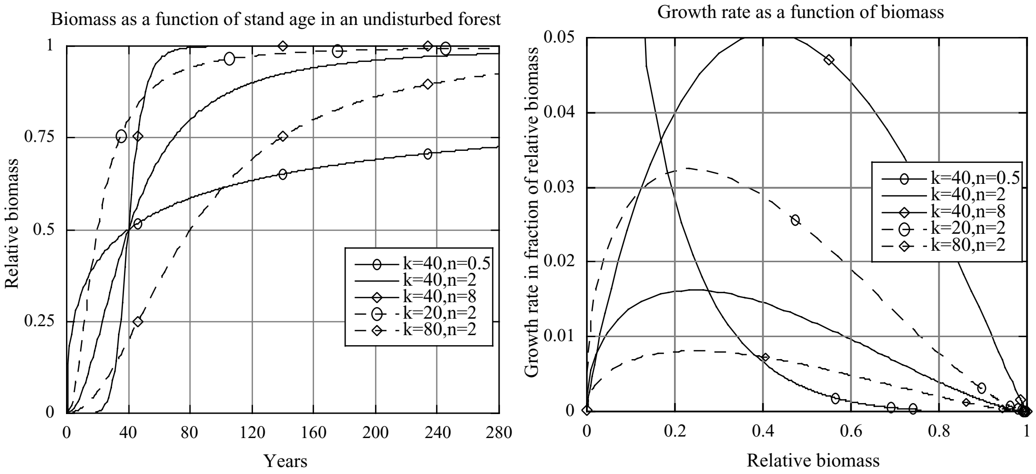

Figure 2: Biomass as a function of age and growth as a function of biomass for different parameters n and k. Note that k is the age at which an undisturbed forest reaches half of the maximum possible biomass at the site. n determines the shape of the growth function, a higher n gives a lower initial growth rate.

3.1 N availability and N uptake

If the nutrient content is constant, the MAKEDEP model only needs to keep track of the biomasses of the different compartments as the amount of nutrients in the different compartments can be calculated easily using the nutrient content. When variable nutrient content in the different tree compartments is taken into account, it is necessary to keep track of the amount of all nutrients in all the compartments as well as the biomass of the different compartments. For sake of simplicity, it is assumed that the nutrient content varies within the compartment and that the nutrient content of a specific part of the compartment was determined by the conditions when this part was created. It was further assumed that replenishment of the canopy biomass has the highest priority during times of nutrient shortage, that growth is reduced by the same factor for both canopy and the rest of the tree and that growth is N-limited.

The new version of the MAKEDEP model assumes that all litter fall goes to the pool of organic material in the soil. The N available for gross root uptake, A_{N}, is thus determined by

$$A_{\mathrm{N}}(t) = \mathrm{WD}_{\mathrm{NO}_3^-}(t) + \mathrm{WD}_{\mathrm{NH}_4^+}(t) + \mathrm{DD}_{\mathrm{NO}_3^-}(t) + \mathrm{DD}_{\mathrm{NH}_4^+}(t) + \mathrm{CE}_{\mathrm{N}}(t) + \mathrm{NM}_{\mathrm{N}}(t) \qquad (25)$$

where NM is net mineralisation.

It should be noted that this assumption is different from the assumption used in the SAFE model. The SAFE model assumes the nutrient in the litter fall to be immediately available for nutrient uptake. Any deviation from this assumption should be specified by adjusting the net mineralisation rate. Thus, in the SAFE model the available N (A_{N}) is calculated as

$$A_{\mathrm{N}}(t) = \mathrm{WD}_{\mathrm{NO}_3^-}(t) + \mathrm{WD}_{\mathrm{NH}_4^+}(t) + \mathrm{DD}_{\mathrm{NO}_3^-}(t) + \mathrm{DD}_{\mathrm{NH}_4^+}(t) + \mathrm{CE}_{\mathrm{N}}(t) + \mathrm{LF}_{\mathrm{N}}(t) + \mathrm{NM}'_{\mathrm{N}}(t) \quad (26)$$

As the MAKEDEP model should produce output that can easily be used as input to the SAFE model, the MAKEDEP model calculates net mineralisation also as

$$\mathrm{NM}'_{\mathrm{N}}(t) = \mathrm{NM}_{\mathrm{N}}(t) - \mathrm{LF}_{\mathrm{N}}(t) \quad (27)$$

The litter fall of nutrients, LF_j in the equation above is calculated as

$$\mathrm{LF}_j(t) = f_{\mathrm{LF}} \cdot m_{C_j}(t-1) \quad (28)$$

where f_{LF} is the litter fraction and m_C the amount of the nutrient in the canopy compartment. As the nutrient content may vary, the canopy biomass that falls to the ground as litter fall can not be deduced from LF but is calculated as

$$w_{\mathrm{LF}}(t) = f_{\mathrm{LF}} \cdot w_C(t-1) \quad (29)$$

Concerning the availability of N and the N demand, there are four different cases to distinguish between

Case 1 If there is enough N available to create biomass of the maximum nutrient content the actual growth will equal the potential growth. Not all N will be taken up, so there will be some leaching.

Case 2 If there is not enough N available to create biomass of the maximum nutrient content, but enough to create biomass with the minimum content there is a need to decrease the nutrient content in the different compartments. For sake of simplicity it is assumed that the nutrient content is reduced by the same relative fraction in all compartments.

Case 3 The growth rate needs to be reduced if there is not enough nitrogen to create the biomass given by the potential growth rate and the canopy replenishment even at the minimum nutrient content, but still enough to replenish the canopy.

Case 4 If there is not enough N to allow replenishment of the canopy, then net uptake is zero for all compartments except for canopy. The net uptake to the canopy compartment will be negative as only a fraction of the litter fall biomass will be replenished and the canopy biomass will decrease.

The equations used to distinguies between the different cases and to determine the gross root uptake, the biomass at the next timestep and the leaching (zero leaching in all cases but case 1) are as follows:

Case 1

$$\left\{\begin{array}{lll}
\text{Condition} & A_{\mathrm{N}}(t) \geq \sum_i \big(r_i(t)\cdot C_{i_{\mathrm{N},max}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},max}} + \mathrm{CE}_{\mathrm{N}}(t) & (30)\\
\sum_i \mathrm{GU}_{i_j}(t) & = \sum_i \big(r_i(t)\cdot C_{i_{j,max}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{j,max}} + \mathrm{CE}_j(t) & (31)\\
w_i(t) & = (w_i(t-1) + r_i(t))\cdot(1-h(t)) & (32)\\
\mathrm{L}_{\mathrm{N}} & = A_{\mathrm{N}} - \mathrm{GU}_{\mathrm{N}} & (33)
\end{array}\right.$$

Case 2

$$\left\{\begin{array}{lll}
\text{Condition} & \sum_i \big(r_i(t)\cdot C_{i_{\mathrm{N},min}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},min}} + \mathrm{CE}_{\mathrm{N}}(t) \leq A_{\mathrm{N}} & \\
 & < \sum_i \big(r_i(t)\cdot C_{i_{\mathrm{N},max}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},max}} + \mathrm{CE}_{\mathrm{N}}(t) & (34)\\
\sum_i \mathrm{GU}_{i_j}(t) & = \sum_i \big(r_i(t)\cdot (C_{i_{j,min}}(1-f_{\mathrm{N}}) + f_{\mathrm{N}}\cdot C_{i_{j,max}})\big) + & \\
 & \quad w_{\mathrm{LF}}(t)\cdot (C_{i_{j,min}}(1-f_{\mathrm{N}}) + f_{\mathrm{N}}\cdot C_{i_{j,max}}) + \mathrm{CE}_j(t) & (35)\\
w_i(t) & = (w_i(t-1) + r_i(t))\cdot(1-h(t)) & (36)
\end{array}\right.$$

Case 3

$$\left\{\begin{array}{lll}
\text{Condition} & w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},min}} + \mathrm{CE}_{\mathrm{N}}(t) \leq A_{\mathrm{N}} < & \\
 & \sum_i \big(r_i(t)\cdot C_{i_{\mathrm{N},min}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},min}} + \mathrm{CE}_{\mathrm{N}}(t) & (37)\\
\sum_i \mathrm{GU}_{i_j}(t) & = \sum_i \big(f_{\mathrm{N}}\cdot r_i(t)\cdot C_{i_{j,min}}\big) + w_{\mathrm{LF}}(t)\cdot C_{C_{j,min}} + \mathrm{CE}_j(t) & (38)\\
w_i(t) & = (w_i(t-1) + f_{\mathrm{N}}\cdot r_i(t))\cdot(1-h(t)) & (39)
\end{array}\right.$$

Case 4

$$\left\{\begin{array}{lll}
\text{Condition} & A_{\mathrm{N}} < w_{\mathrm{LF}}(t)\cdot C_{C_{\mathrm{N},min}} + \mathrm{CE}_{\mathrm{N}}(t) & (40)\\
\mathrm{GU}_{C_j}(t) & = f_{\mathrm{N}}\cdot w_{\mathrm{LF}}(t)\cdot C_{C_{j,min}} + \mathrm{CE}_j(t) & (41)\\
\mathrm{GU}_{i_j}(t) & = 0,\ i \neq C & (42)\\
w_C(t) & = (w_C(t-1) - (1-f_{\mathrm{N}})\cdot w_{\mathrm{LF}}(t))\cdot(1-h(t)) & (43)\\
w_i(t) & = w_i(t-1)\cdot(1-h(t)),\ i \neq C & (44)
\end{array}\right.$$

where h is the harvest fraction described in the next section and C_{i_j} is the concentration of nutrient j in compartment i. The factor f_{N} used in case 2 through 4 above is calculated by setting

$$\sum_i \mathrm{GU}_{i_{\mathrm{N}}} = A_{\mathrm{N}}\ . \tag{45}$$

Net uptake (NU) is calculated as

$$\mathrm{NU}_{i_j}(t)\begin{cases}\mathrm{NU}_{i_j} = \mathrm{GU}_{i_j}(t),\ i \neq C & (46)\\ \mathrm{NU}_{C_j} = \mathrm{GU}_{C_j}(t) - \mathrm{LF}_j(t) - \mathrm{CE}_j(t) & (47)\end{cases}$$

If the nutrient content is constant, these equations simplifies to the equation used in previous versions of the MAKEDEP model (only case 3 and 4 described above apply)

$$\mathrm{NU}_{i_j}(t) = f_{\mathrm{N}} \cdot r_i(t) \cdot C_{i_j}\ . \tag{48}$$

3.2 Harvest, SOM pools and net mineralisation

Forest growth and harvest are separated in time in the version of MAKEDEP described here. For each timestep (year) the forest is first allowed to grow and then a fraction may be harvested. By specifying the stem harvest fraction as 100 % and negative numbers for subsequent years clear cutting with delayed replanting can be simulated.

The harvest is characterised by 1) a harvest fraction (h), i.e. the fraction of the biomass of all compartments that is present on the harvested trees, and 2) the fraction (f_i) of the biomass on harvested trees that is removed from the site. It is assumed that all stem biomass on harvested trees are removed from the site, thus $x_{stem} = 1$. Both the h and the f_i fraction are given as time series and are important input parameters to the MAKEDEP model. The biomass not removed is left on the site for gradual decomposition. The harvested biomass (including what is left on the site to decompose) can be deduced e.g. for case 1 from equation 32 above by replacing $(1-h)$ with h. Thus for case 1 we get

$$w_i(t) = (w_i(t-1) + r_i(t)) \cdot h(t) \tag{49}$$

The harvested amount of nutrients including what is left on the site to decompose is calculated as

$$\mathrm{H}_{i_j}(t) = \left[m_{i_j}(t-1) + \mathrm{NU}_{i_j}(t)\right] h(t) \tag{50}$$

It is thus assumed that the harvest occurs at the end of the timestep and that replanting may occur immediately after harvest. If the harvest fraction is specified as a negative number for the year after clearcut ($h(t+1) < 0, h(t) = 1$) there will be no replanting of forest. The remaining debris after harvest creates a pool of organic matter that is calculated by

$$\mathrm{SOM}_{\mathrm{H}_j}(t) = \mathrm{SOM}_{\mathrm{H}_j}(t-1) \cdot (1 - r_{\mathrm{H}}) + \sum_{i \neq C} H_{i_j}(t) \cdot (1 - x_i(t)) \tag{51}$$

where $\mathrm{SOM}_{j_{\mathrm{H}}}$ is the pool of nutrient j in soil organic matter created by leaving parts of harvested trees at the site, r_{H} is the fraction of the pool that is released every year, t denotes the year, H_{j_i} denotes the the amount of nutrient j in the harvest of compartment i and $x_i(t)$ is the fraction of that biomass that is removed from the site. Note that all compartments except the canopy and stem compartments may contribute to this SOM pool. The stem does not contribute since all stem on harvested trees are assumed to be removed from the site. The canopy does not contribute since the mineralisation rate typically is higher for that compartment. Leaves on harvested trees are therefore, if not removed from the site, considered to contribute to the LF SOM pool. The canopy harvest fraction is assumed to be valid for the canopy on harvested trees as well as for the natural litter fall, thus emulating removal of litter fall from the forest for use e.g. as forage for live stock.

In the first version of MAKEDEP it was assumed that the organic pool on the forest floor is at steady state as long as there is no harvesting. In other words, the same amount of nutrients as the nutrients in the litter fall is released from the organic pool. This may, however, not be a realistic assumptions for all forests and a litter fall mineralisation rate was therefore introduced. Similar to the SOM pool due to harvest there is therefore a SOM pool due to litter fall which is updated according to

$$\mathrm{SOM}_{\mathrm{LF}_j}(t) = \mathrm{SOM}_{\mathrm{LF}_j}(t-1) \cdot (1 - r_{\mathrm{LF}}) + (1 - x_C(t)) \cdot (\mathrm{LF}_j(t) + H_{C_j}(t)) \tag{52}$$

where x_C is the removal of litter fall from the site.

Net mineralisation, i.e. the net release of nutrients from the SOM pools is consequently calculated as

$$\mathrm{NM}_j(t) = \mathrm{SOM}_{\mathrm{H}_j}(t-1) \cdot r_{\mathrm{H}} + \mathrm{SOM}_{\mathrm{LF}_j}(t-1) \cdot r_{\mathrm{LF}} \ . \tag{53}$$

4 Summary of model changes

- Separate treatment of deposition of marine salts is now optional
- Introduced optional nutrient content elasticity based on nitrogen availability
- User specified mineralisation rates for both litter fall and harvest residuals instead of steady-state assumption on SOM content
- Calculated marine deposition is now always internally consistent with relative abundance of different elements in sea salt.
- Individual deposition trends for each element
- Changed number of tree compartments from two to a maximum of five compartments
- Introduced time-variant forest management practices with possibility to specify treatment of all tree compartments.
- Introduced scaling of management practices to simplify running multiple sites with differences in management intensity.
- Dry deposition or Throughfall deposition is optionally estimated by MAKEDEP from user input on wet deposition and dry deposition or throughfall deposition. In the original MAKEDEP program, input on all three were compulsory.

- Introduced possibility for the user to change the Mikaelis-Menten parameters used in the reconstruciton of forest growth/nutrient uptake.
- Introduced delayed replanting after clearcut. A clearcut is specified as a stem harvest fraction of one (1). The forest is replanted the first year after a clearcut for which stem harvest is given as a positive number.

The single-site version of MAKEDEP is identical to what is used within the new PreSAFE regional assessment package except for a slight difference in model input. Whereas the single-site MAKEDEP model takes litter fraction as a model input the PreSAFE package takes the litter fraction of deciduous forests, the litter fraction of coniferous forests and the fraction deciduous trees at the site as input. The PreSAFE package contains the initSAFE, the MAKEDEP model together with some additional routines and is used to create all the necessary input files for running the SAFE model.

5 Discussion

It is important to remember that a model is constructed to answer a set of questions within a certain context. Changing the context or the set of questions to be answered might enforce changes to the model concept or the creation of new model concepts. The usefulness of a model should thus be evaluated with this in mind.

For MAKEDEP the context is the Convention on Long Range Transboundary Air Pollution and the quesions concern the dynamics of soil acidification and recovery. The available data is often very limited, especially on the regional scale, and the available data is not always internally consistent. The possible inconsistencies in the available data calls for careful checking of model results against field data and expert knowledge.

The alternative to using the MAKEDEP model as a means to create input to dynamic soil chemistry models is to either create these files manually, something which increases the risc of inconsistencies in the inter-regional comparison since the calculations for different sites and/or regions are usually done by different people, or to refrain from providing the policy makers with decision support that the assessments of the dynamics of forest soil chemistry constitute.

The MAKEDEP and the DEPUPT models have been used successfully throghout Europe and is likely to find a wider usage with the flexibility introduced in the here presented version. It is our feeling that future enhancements of the MAKEDEP model would require incorporation into a new generation of dynamic soil chemistry models. Such models would need to take the entire ecosystem into account – above-ground as well as below-ground – and incorporate both the carbon and nitrogen cycles through uptake, allocation, litter fall and decomposition.

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Table 2: Summary of temporal notation, subscripts and superscripts.

Symbol	Explanation
Subscripts	
H	associated with harvest (used with SOM, r)
i	denotes tree compartment (e.g. C (canopy), $stem$)
j	denotes nutrient (e.g. N) and other deposited elements (e.g. Cl)
k	denotes pool (LF or H)
LF	associated with litter fall (used with w, f, SOM, r)
$marine$	deposition of sea salts (DD,WD)
min, max	associated with minimum and maximum respectively
Superscripts	
$*$	non-marine deposition (DD,WD)
'	NM' denote net mineralisation as defined by the SAFE model
Temporal notation	
$(t), (t-1)$	Value at this time step and last time step respectively
t_{D}	Value at time of deposition measurement

Table 3: Summary of notation.

Symbol	Explanation	Unit
A_N	N available for nutrient uptake	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
C_{i_j}	Nutrient content of nutrient j in compartment i	$\mathrm{mmol\ kg^{-1}}$
CE_j	Canopy exchange of nutrient j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
DD_j	Dry deposition of element j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
f_LF	Fraction of canopy that falls as litter fall each year	1
f_N	Fraction used to calculate GU during nutrient shortage	1
GU_{i_j}	Gross uptake of nutrient j to compartment i	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
h	Harvest fraction	1
H_{i_j}	Amount of nutrient j in harvested compartment i	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
k_i	Years until compartment i may reach half its max. biomass	$\mathrm{kg\ m^{-2}}$
$\mathrm{L_N}$	Leaching of N	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
LF_j	Litter fall of nutrient j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
m_{i_j}	Amount of nutrient j in compartment i	$\mathrm{mmol\ m^{-2}}$
n	Order for Mikaelis-Menten equation	1
NM_j	Net mineralisation of nutrient j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
NU_{i_j}	Net uptake of nutrient j to compartment i	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
r_i	Potential growth of compartment i	$\mathrm{kg\ m^{-2}\ year^{-1}}$
r_k	Fraction of organic pool k that mineralises every year	1
S_j	General deposition trend for element j	1
SOM_k	Size of soil organic matter pool k	$\mathrm{mmol\ m^{-2}}$
TF_j	Throughfall ofelement j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
w_i	Biomass of compartment i	$\mathrm{kg\ m^{-2}}$
$w_{i,max}$	Maximum biomass of compartment i	$\mathrm{kg\ m^{-2}}$
WD_j	Wet deposition of element j	$\mathrm{mmol_c\ m^{-2}\ yr^{-1}}$
x_i	Fraction of harvested compartment i to be removed from site	1
y_i	Apparent age of compartment i	years
Y	Standage	years

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Managing of game resources in a context of sustainable forestry and biodiversity protection

Olgirda Belova
Dept. of Forest Protection and Game Management
Lithuanian Forest Research Institute, Liepu 1, LT-4312 Girionys, Kaunas District, Lithuania
Fax: +370 37 547446
E-mail: Baltic.Forestry@mi.lt

Abstract

The managing of game resources in sustainable forestry, including biodiversity protection, was studied by implementing a research programme including establishing of a network of permanent belt transects and sample plots for the continuous observation of wildlife. The relation between animals and forest vegetation as integral parts of the forest biota was controlled. It encompassed the qualitative and quantitative assessment of local wildlife populations (census methods, finding concentration sites, identifying the occurrence of animals, places of mating and sites for care of offspring). Studies were made of the management of local game populations, such as the analysis of population dynamics, of hunting and features of harvested animals, of selected technique for hunting as a measure for regulation of the game population, of the arrangement of hunting areas, of optimization of hunting methods and of methods for increasing the carrying capacity of game habitats. The habitat suitability for different game species was ecologically assessed and used as an indicator for the biodiversity conservation on three levels. Based on these estimates the recommendations for foreseeing and controlling local populations of game animals in the context of biodiversity conservation in protected areas were made up. The components and habitat conditions of the forest ecosystem provided the main criteria for biodiversity conservation, among others the animal density, the population age structure, the trophic strategies, competition and predator-prey ratios, stand species composition, state of layers and age structure, canopy density, state of the undergrowth and shelterwood, spatial distribution, forest types and ecotones.

Keywords: game animals, habitat optimization, recreation, sustainability

Introduction

This study provides solutions for an ecologically sound forest and game management in semiprotected areas, with the aim to combine principles for a sustainable use of the game resources with a coexistence of wild animals and forest vegetation, simultaneously with biodiversity conservation. The problem of sustainable use and conservation of wildlife resources including game, is directly related to forest and game management and the demands on environment protection. The managing and use of game resources usually involves four consecutive steps such as: assessing the game population (recent number), ascertaining of the productivity of the game population, ascertaining of environmental factors and definition of their significance, and finally control of factors significant for game and habitats (Leopold 1933). The status of protected areas will dictate the specific conditions for managing of the game populations in accordance with the public opinion and the economic basis. Game resources are indispensable components of the forest ecosystems, important from the standpoints of ecology and science, economy, recreation, aesthetics *etc*. 43% of mammals are forest-dwelling species and 24% belongs to the mixed forest – open land ecotypes. Game animals make up half of all wild mammals and 20% of birds. The vitality and sustainability of living systems, including forest ecosystems, depends on their diversity, and the ecosystems are considered to become more vulnerable due to diminishing of species. The solution to questions of optimisation and sustainability of game management is troublesome due to the collision between consumer's and non-consumer's viewpoints on wildlife resources, a controversy on property and purpose of the commercial hunting, that often want to increase the number of big game animals to maximum levels.

Because of the damage caused by animals, the conflict between foresters and game hunters has become deeper (Sikorski 1990; Bobek 1991). Hunting is one of the main methods for managing and maintaining the renewable wildlife resources at a stable level. However, the sustainable use of wildlife resources is not considering only hunting and maintaining of the permanent level of use (PUL), but also the increase in the endangered, rare and protected species and the decrease in overabundant species which can be harmful to environment and human society. This is a way to protect game and maintain the optimal level of their use and managing their abundance. In all cases, the purposes are implemented by affecting changes in the wildlife populations. The number of game animals decreases not only because of the direct elimination or hunting. Even if game animals are harvested intensively, a comprehensive analysis usually shows that the main reason for the decrease in game number is destruction of their habitats and impoverishment of food supply. It is suggested that 95% of problems of the sustainable use and protection of wildlife resources arise because of the above-mentioned reasons (Caughley 1977; Wollenhaupt 1989). The destruction of habitats and subsequent stronger competition between animals for important and limiting resources may cause deep changes in the relationship between game and their environment. The basis for retaining an ecological equilibrium is balanced by (1) the territorial management by the game habitats and their distribution throughout the area, (2) qualitative regulation of the age and sex structure of game populations, and (3) a quantitative regulation of the number of the population, which must correspond to the carrying capacity.

The issues to be solved, which are illuminated in this overview study, are the sustainable management of animal populations, definition of recent real, permissible and theoretical ecological densities, ascertaining of the interaction between animals and forest vegetation, ascertaining of the damage caused by game to forest, definition and improving of the habitats' natural carrying capacity, restoration and maintaining of the equilibrium between game animals and other environmental resources, the predator to prey ratios. Also, hunting methods and quotas for the game populations, the population ecology and the interactions with forest vegetation and man, as well as delineation of the territories for the game animals must be considered.

Material, Methods and Investigated area

The studies were conducted in October and April 1999 – 2001 in the territory of Zemaitija National Park, Lithuania. A route belt transect method, tracking and sample plot method was applied. A network of permanent route transects and permanent sample plots were established and mapped. The network corresponded to the configuration of the hunting grounds. The unit of the route belt transect was 100 x 4 m. The total length of the route was

18.6 km. The total area made up 21,720 ha including farmlands, pastures and 40% of the forests in the Park. All signs of animal living activities were registered on the belt transects, such as: faecal pellets, signs of feeding as shoot browsing, bark stripping, breaking of tree stems, occurrence of plant species and their abundance, share of the animal diet, footprints of animals, remnants of fur, burrows, lies etc. The main investigated game species were: *Rodentia* (*Castor fiber*, *Ondatra zibethica*), *Lagomorpha* (*Lepus europaeus*, *Lepus timidus*), *Carnivora* (*Vulpes vulpes*, *Nyctereutes procyonoides*, *Canis lupus*, *Felis lynx* and *Mustelidae*), *Artiodactyla* (*Cervidae* such as *Alces alces, Cervus elaphus, Capreolus capreolus* and *Suidae – Sus scrofa*). The list of species involved not only animals that are hunted at present, but also protected and endangered species, the hunting of which is forbidden at present in Lithuania, such as *Lepus timidus*, *Lutra lutra*, *Felis lynx*.

To determine the factors that were significant for animals, natural stressors and their impact, the collected field data was used, as well as data of the official statistics such as forest inventory, land survey, meteorological data, census long-term data. Common environmental factors of importance were the following: the weather; soil fertility, which influenced the species composition, richness and biochemical properties of vegetation; the relief of a territory (*i.e.* very hilly, hilly, downy, plain); forest cover, species composition of forest, age, storey structure and development of the storeys, canopy closure of the overstorey, stem density, forest site type, stand composition and age diversity, size of forest complex, mosaic of the territory; fragmentation of forest complexes; character and diversity of land close to forests; forest edge effects, i.e. ecotones of the different elements of the landscape. The fertility of soil, forest type, species composition of the stands and other plant formations, and other above-mentioned factors were assigned to determine the carrying capacity of the site.

The investigations represented 3,979 ha of the total territory, including 2,416 ha of state mixed spruce-deciduous forests, 240 ha of farmlands and 1,320 ha of the reserve. The investigated territory of the National Park belonged to the mixed spruce-deciduous forest category in the territory of Northwestern Lithuania. The area belonged to the Zemaitija (Samogitia) highland geobotanical complex of the southern taiga of the Baltic province's mixed spruce and deciduous forests, and according to the phytocoenological terminology it was *Picetum – Pinetum – Betuletum – Fraxinetum – myrtillosum and myrtillo-oxalidosum* stands. By the *EUNIS* habitat classification, it was a G4 category. The dominant tree species (*Picea abies* and *Pinus sylvestris*) were mixed with deciduous species. The territory belonged to a climatic sub-region with about 27% of winters with unstable snow cover, 45% of thaws, and the long-term mean depth of snow cover is 20 cm. During strong winters the depth of snow cover sometimes reaches 0.7-1 m. The critical depth of snow cover, making trouble for animal moving and feeding and causing animal migration, is 70 cm for moose and hares, 50 cm for deer, 40 cm for roe deer and 50 cm for the wild boar. The spring is late.

Because of the specific geographical situation there is a surplus of moisture, and the average long-term precipitation is more than 850 mm, while the annual mean reaches 1,012 mm and during the vegetation period 642 mm. The surplus moisture is accompanied by cold weather, with a long-term average temperature of 11°C during the vegetation period. Western and south-western winds prevail, carrying along air masses from the sea.

Results

The average forest cover was 33.5%. The prevailing forest site types were *Myrtillosum* (35.7%), *Myrtillo-oxalidosum* (14.3%), (14.3%), *Oxalidosum* (12%) and forest site types of wetlands (*Myrtillo-sphagnosa*, *Carico-calamagrostis*, *Filipendulosa*, *Caricosa*, *Iridosa*, *Carico-mixtoherbosa*), especially in the western part of the Park where there were many bogs and fens of transitional types. The investigated territory was favourable for wildlife by the carrying capacity with respect to soil fertility, species composition, forest sites, understorey cover and mosaic of habitats. The recreation pressure was high over the year, excluding the most severe winter period. This disturbance factor acted all over the year, also outside the summer season, through gathering mushrooms, fishing, hunting, winter sports *etc*. The existing fragmented forest complexes positively correlated with the frequency of occurrence of wildlife species ($r=0.73\pm0.04$, $p<0.05$). A total of 14 wildlife species were found belonging to the list of game species. Among them there are no game bird species, as this category of game does not attract sufficient hunters' attention. They were therefore not counted and reported for hunting purposes.

The density of *Alces alces*, the moose, increased from 4 individuals per 1000 ha in 1996 to 9 per 1000 ha in 2001, *i.e.* it more than doubled. The density of the red deer (*Cervus elaphus*) increased from 4 to 12, or three times. The density of the roe deer (*Capreolus capreolus)* increased from 14 to 52 per 1000 ha. The census data of the red deer and roe deer based on faecal droppings, and the data collected by the going round method were similar, and showed in both cases that more animals wintered in the reserve (17/1000 and 51/1000 ha, respectively). The analysis of sex and age structure of the deer populations showed that the ratio of males to females of moose and roe deer (1:4) deviated from the optimum (1:1.1 – 1.2 and 1:1.6 – 2.0, respectively), but the sex ratio of red deer was near the optimum and provided for the maximum increment of the local population. The analysis of census data by faecal droppings revealed that the share of kids made up 25.5% of the roe deer population and was near the optimum (30%), while the share of fawns and calves of deer and moose was only 18%, which was far from optimum (22 and 26%, respectively).

The larger complex of forest stands and existing mosaic structure were in general favourable for game species, but unfavorable for *Canis lupus* (L.) and *Felis lynx* (L.). These species were not abundant, and were sensitively responding to further fragmentation. The fragmentation of forest complexes was expressed by the distance between the forest complexes, which should not be more than 400 m for most species, and no more than 100 m for lynx. Most animals preferred the stands with dense understorey, shrubs, habitats with snags, windfalls and thickets for secret moving and foraging, and the mature stands for breeding, and showed a territorial conservatism (cf Belova 2001). Wolf and lynx needed a larger forest complex, and they permanently attended these forests in the studied territory with 1-3 individuals. They all passed the smaller forests and habitats belonging to their hunting area, and intervened between the bigger forests. The reserve and adjacent forest fitted well for the lynx by the age structure and species composition (such as mature stands for the breeding, young stands and thickets for the rest and secret moving).

Vulpes vulpes (L.) occurred everywhere in the territory of the national park. The signs of their occurrence were mostly found in the mixed spruce stands (62% of findings), pine stands (38%) in *Myrtillosum* (53%) and *Myrtillo-oxalidosum* (46%) forest site types, especially near the granges, the crossings of different habitats (76%) as the raccoon dog (100%). The influence of precipitation was not significant ($r = -0.09$, $p<0.10$), but the status of snow density seemed to be important.

The local population of *Nyctereutes procyonoides* (Gray) was comparatively abundant and the number was stable. The present forest fragmentation, ecotones of forest patches, farm lands and granges, the mixture of deciduous species in the coniferous forest stands, open ditches, lake shores and wetlands were all suitable for the raccoon dog.

The density of *Martes martes* (L.) was high in the park, indicating the fitness for foraging and shelter. The findings of the pine marten and polecat mostly occurred in spruce stands with a mixture of deciduous species, in *Myrtillosum* forest sites covered by undergrowth of medium stem density (up to 100% of all findings), in places close to bogs, fens and forest gaps. The trophic carrying capacity and possibilities for shelter were suitable for martens, forming the basis for fitness of their habitats. There was a good possibility for martens to bury themselves in snow in the winter. However, the trophic competitors and antagonists of other *Mustelidae* influenced their abundance. They were all predators and additionally, there was a numbered local population of fox. The *Mustela vison* was a comparatively abundant species. The activities of the beaver fitted for the mink, which actively attended the abandoned beaver sites.

Meles meles (L.) occurred throughout the territory of the national park, and was a comparatively abundant species. The findings of badger were mostly localized in the mixed spruce stands (68% in *Oxalidosa-myrtillosum* forest sites). Abandoned burrows were common, and reasons for moving from the settled burrows could be tourist disturbance factors and felling of spruce stands damaged by pests, as the badgers were cautious animals and often disturbed. They were sensible to forest fragmentation not only because their preference of the large settled territory. If they did not suffer a disturbance and hostile acts for human part (such as destroying of burrows, direct disturbance and so on), badgers could adapt to the human vicinity.

The inhabited locations of *Lutra lutra* (L.) occurred near the rivulets, melioration channels, streams and lakes that were found in a great number in the territory. The carrying capacity of the territory fitted for the otter with respect to the foraging and living space. The water system with abundant main components of the diet suitable for otter was there.

The density of local population of the wild boar increased from 8/1000 ha in 1996, to 29/1000 ha in 2001. It was higher than the recommended density for the mixed spruce – deciduous forest category, i.e. 8-14/1000 ha.

Leporidae mostly occurred in the mixed spruce stands (60% of findings), in the incomplete (with gaps) spruce plantations with a mixture of birch (20%), on the places of *Myrtillo-oxalidosum* (60%) and other (20%) forest sites. The forest fragmentation fitted for them as they were disposed to visit the belt at ±400 m distance from the forest edges to the open land, and at ±200 m distance to the forest direction and within the forest between different inside elements of stand fragmentation such as roads, forest block lines, ditches, rivulet valleys and granges in the forest. A canopy closure of 40-60%, as well as unclosed forest plantations were preferred. The belt mosaic topographical structure of such sites was suitable for the hares that mostly occurred in the reserve, where they were concentrated in the shrubwood and in sites with natural forest regeneration and forest gaps, especially with the insertion of willows. The tendency of declining density was related to recent abiotic factors such as the impact of the changeability and severity of weather for the survival of the first offspring, which is the basic reproductive increment of the local hare population. In addition, there was an impact of an increasing number of predators, especially of foxes. For the maintenance of the hares' density, it was regarded necessary to apply measures for extra care in winter. The ratio of foxes to hares was far from optimal. The present ratio was 1:1.15, while the ecological ratio would be 1:20. Thus the total number of predators was too high compared to the number of preys.

Ondatra zibethica (L.) was missed from 1988 in the investigated territory. It was supposed that the spreading of the American mink (*Mustela vison*) and a great number of other predators and territorial competitors stopped the settling of muskrat. The influence of competitors and antagonists became significant, while the abundance of the main food supply has decreased. Besides, competitors and antagonists had seized the habitats and refuges. The urbanization also influenced, as muskrats lost the building material and become more disturbed by predators.

Castor fiber (L.), a dominant semi-aquatic game species, was widespread throughout the hydrological systems. The demands for habitat and feeding were fulfilled here, with the main food objects being ash, willows, birch, elm, oak and hazel. Most of the beaver sites were dams. In the survey the beaver sites included 40% of the lowlands, abutted on the mixed spruce stands, and in all stands the plant formations and small topographical elements were changed.

Discussion and conclusion

The density of the different game populations revealed the current status of the species, and the population parameters should correspond to the carrying capacity of habitats, to ensure reproduction of the population and protection of the animals' habitats.

A recommended density for deer species was 12 deers/1000 ha in this area, which was occupied by all three deer species. The deer density was 5 times higher, and in the reserve it was 6 times higher than the recommended level. Because the share of winter key habitat for one moose should be 30-40 ha, the recent situation could have disruptive consequences for forest plantations and natural forest regeneration, as well as for the deer populations themselves, for other wildlife species and for biodiversity. This would be true particularly under conditions of severe or changeable winters.

Unstable weather conditions meant that the total climatic situation of the territory was relatively unfavourable for young animals, especially for those without permanent burrows, and whose body temperature depended on age. Nevertheless, weather was not considered critical for the local game populations, as there was no correlation between weather factors and population sizes ($r=-0.12$, $p<0.10$).

The ratio of predators to prey was a significant factor affecting the wildlife resources, and in the same way the biological diversity, although the shelter conditions could be sufficiently fulfilled because of habitat diversity and mosaic structure. Moreover, the hunting press additionally influenced game – preys (e.g. for hares). The share of harvested hares should not be more than the inferior quota limit for use (i.e. 23% or the hare hunting must be limited). It should be underlined that the limits of animal tolerance to shelter conditions became narrower than to other factors, and particularly of importance during the breeding season. During the non-vegetative period the conditions of the foraging suitability for animals became more important and was considered as the limiting factor.

The essential factors for game populations were many, depending esp. on successional stages, forested areas, distribution of the afforestation and natural regeneration and the extent and character of human economic activity and recreation. Logging should principally be done late, only from July to March, and recreation should be restricted in habitats of game species sensitive to disturbance and in sites of offspring care.

Logging, in combination with winter conditions and big carnivores, were cornerstone factors for the game population density and for the impact on forest trees caused by game. Big predators were not typical in the investigated area, because the wolf occurred extensively, and its impact was predominantly episodically on domestic animals. In the forests, where the non-clear cutting prevailed, herbivorous game damaged ash and spruce stands about 9 and 4.5 times more respectively than in forests where clearcutting prevailed. Respectively, in the first case, in the damaged forests the damage on spruce was from 1.5 to 10 times and on ash from 2 to 6 times more than in the second case (Padaiga, Belova 2001). Ash was the most preferred food of *Cervidae*, and the retaining ash stands is today considered problematic without special protective measures. In the deciduous forests it is recommended to fell up to 2% of a total area, and in the coniferous forests up to 1% respectively, and the area of young deciduous stands should be about 15—25% of all deciduous stands, on the condition that clear cuts were not connected, and there were no more than 200 – 400 m distance between the stands.

The problem of damage caused by game to forest vegetation may be solved taking into consideration the conditions of forest growth, by the determination of reasons for damage and foreseeing suitable protective measures including monitoring and managing of game habitats. The biological, mechanical, chemical and forest managing protective measures would be applied. The important measure should be to keep a balance between age and sex structures of the game populations, and their density should correspond to the carrying capacity of the territory. Logging and clear cuts should not be wider than 100 m. This could be coordinated with the mechanic and chemical measures.

The assessment of the status of game species should be based on the three levels of biodiversity conservation and the species recent status (hunted, protected or endangered), its distribution (common, rare or occasional visitor; generalist or specialist), and its sensitiveness to the main factors. Their significance such as key species, cornerstone species should be emphasized. A regular and accurate game census was considered necessary, and should be performed all the year round (Caughley 1977; Sikorski 1990) taking into consideration the species-specific features and ecology. The census of game animals is ascertaining of the non-timber renewable resources, which also indicate the vitality of forest ecosystems. Through the census data the numbers of animals, their densities in certain areas, their relative density or the density of a local population in relation to another, as well as changes in a time perspective can be surveyed.

The total number of animals and birds were considered important for the determination of the population boundaries, and for the solution of problems with wildlife use and protection. Local environmental conditions were important when the number of animals or birds declined, to understand the impoverishment or destruction of habitats. For a sustainable use of wildlife resources, it would be important to ascertain the factors significant both for big and small animals, including birds. In some countries including the Baltic States, game management has developed in an undesirable direction when the number of big game has increased, while small game animals do not attract sufficient attention and their number seems to decline.

The suitability of game census methods was defined above, using a combination of direct and indirect methods. The achieved census data should be mapped and analytical maps prepared with the places of animal gatherings, frequent occurrence, occasional visits, intermediate habitats, local migrations, summer and wintering habitats indicated. Habitats for the offspring care and shelter habitats should be recorded at the site level, as well as habitats of the similar conditions at the stand and landscape level. A special forest management should be applied temporally or permanently, considering key habitats within the part of commercial forest or buffer zones around the key habitats where managing could be permitted or restricted depending on the game species, their ecology and needs.

The animal population density, its changes and dependence of emigration and immigration within the territory should be emphasized and usable indices for the animal species control developed. The carrying capacity of game habitats in context of biodiversity conservation should be evaluated by forest characterization, vertical and age structure of stands, distribution of felling, feeding plots, special forest plantations for the feeding and refuge. The supplemental feeding should be established more remotely (ca. 0.5-1 km) from the places for valuable afforestation and natural regeneration, which could be potentially damaged.

The long-term monitoring of significant factors is needed to take into consideration. The main indicators for game starvation, e.g. for red deer the appearance of white alder, black alder, birch, honeysuckle as well as changes of feeding character, and for roe deer white alder, birch and Norway spruce, should be controlled. An index of food diversity, for the moose including 7 species of woody food, for roe and red deer 12 species, for beaver 4 species and for brown hare *Lepus europaeus* 10 plant species, should be monitored. The predator to prey ratio is important to identify for carnivores.

The management of local game populations should be based on the scientific substantiation of hunting limits, as well as the choice of hunting system as a basic mean for a sustainable use of wildlife resources, on the technological arrangement of hunting areas, for the planning harvests, hunting arrangements, and optimization of hunting. The above given principles would be the background for a combined ecologically sound and sustainable forest and game management especially in protected areas.

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Use of coupled models to predict biodiversity in managed ecosystems

Han van Dobben, Wieger Wamelink, Eric Schouwenberg & Janet Mol
Alterra Green World Research, POB 47, Nederland-6700 AA Wageningen, Netherlands
phone +31-317-477936
e-mail h.f.vandobben@alterra.wag-ur.nl

Abstract

A model chain was used to estimate the feasibility of biodiversity targets for two ecosystem types at three environmental scenarios. The ecosystems studied were pine forest and heathland on oligotrophic dry sandy soil. The scenarios comprised a constant (45 kg ha^{-1} y^{-1} N) and decreasing (from 45 kg ha^{-1} y^{-1} N in 1990 to 10 kg ha^{-1} y^{-1} N in 2090) deposition of nitrogen, and a proportional decrease of acid deposition. Management was assumed to be 'natural' forest management (i.e., removal of 10% of the stemwood each 10 years) and sod-cutting (once each 30 years) in the heathland, combined with grazing in one of the scenarios. The models used were: SMART2 (soil chemistry), SUMO2 (plant growth and competition) and NTM3 / NTM4 (vegetation composition and biodiversity). The models were initialised using field observations from the period 1990 - 2000. Simulation runs were made for the period 1990 - 2090. Results showed that (a) the effect of decreasing nitrogen deposition is limited in the forest because excess nitrogen is only very slowly removed from the ecosystem, and (b) grazing enhances the beneficial effects of decreasing deposition.

Keywords: forest heathland biodiversity competition nitrogen grazing

Introduction

In the past decades both international treaties and local regulations have put an increasing pressure on forest and nature reserve managers to increase or at least maintain local biodiversity (Spence 2001). At the same time, national governments attempt to promote biodiversity by improving environmental quality on a national scale (e.g., Anonymous 1998). Despite such attempts, it is not immediately clear whether the present or expected environmental quality (e.g. in terms of atmospheric deposition or groundwater level) really allows a manager to fulfil certain biodiversity targets. In this paper a set of models is presented to make projections of biodiversity into the future at different environmental scenarios.

A large number of processes are involved in the causal chain leading from environmental quality to biodiversity, operating at different scales in both time and space. For example, an increase in cattle density leads to an increase in emission of ammonia, which through deposition and soil processes leads to an increased availability of nitrogen and hence, increased growth and competition and often to the exclusion of rare species. Dynamic or static models are available to describe all the steps in this chain. Our aim was to couple these models, so that the complete sequence of processes can be evaluated in a single model run, and feedbacks between the various processes can be taken into account. If the model chain is sufficiently flexible, and sufficient data are available, environmental scenarios can be evaluated at various scale levels, from a single stand to a complete country.

Model description

In our models, biodiversity is constrained by atmospheric quality, groundwater level and management. Soil and groundwater pollution (e.g. by heavy metals) are left out of consideration. A complete model chain to evaluate all processes is depicted in Figure 1. Here we present a simplified model chain, consisting of four submodels: SMART2 (soil chemistry, dynamic), SUMO2 (plant competition, dynamic), NTM3 (plant biodiversity, static) and NTM4 (vegetation type, static). Each of these models is shortly described here; the data exchanged between the models can be seen from Figure 1. Feedbacks exist between SMART2 and SUMO2, and information exchange takes place in each timestep (one year).

SMART2

SMART2 (Kros et al. 1995, Kros 2002) is a simple one-compartment soil acidification and nutrient cycling model that includes the major hydrological and biogeochemical processes in the litter and mineral soil. It consists of a set of mass balance equations, describing the soil input-output relationships, and a set of equations describing the rate-limited and equilibrium soil processes. Apart from pH, the model predicts changes in aluminium (Al^{3+}), base cation (BC^{2+}), nitrate (NO_3^-) and sulphate (SO_4^{2-}) concentrations in the soil solution and solid phase. The soil solution chemistry in SMART2 depends solely on the net element input from the atmosphere (deposition) and groundwater (seepage), canopy interactions (foliar uptake, foliar exudation), geochemical interactions in the soil (CO_2 equilibria, weathering of carbonates, silicates and/or Al-hydroxides, SO_4^{2-} sorption and cation exchange) and a complete nutrient cycle (litterfall, mineralization, root uptake, immobilization, nitrification and denitrification) for base cations and N. Litterfall and uptake by the vegetation are provided by SUMO.

Soil interactions are either described by simple rate-limited (zero-order) reactions (silicate weathering) or by equilibrium reactions (carbonate and Al-hydroxide weathering and cation exchange). Influences of environmental factors such as pH and moisture content are included for mineralization, nitrification and denitrification. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and a fixed depth. The time step of the model is one year, so seasonal variations are not considered. De Vries et al. (1998) provide a justification of the various assumptions and simplifications.

SUMO2

SUMO2 (Wamelink et al. 2001) is a dynamic growth and competition model. In SUMO, biomass is partitioned over three organs (root, stem, leaf) and five 'functional types' (herb, dwarfshrub, shrub, pioneer tree, climax tree). This approach allows the simulation of succession in almost all terrestrial vegetation types occurring in The Netherlands. The functional types compete for light and nitrogen. Light extinction follows Lambert-Beer's law, with the extinction coefficient proportional to leaf biomass. The highest functional type catches light first, and functional types with leaves at equal height compete for light according to their leaf biomass. Therefore plant height is also explicitly simulated, dependant on biomass increment. Each functional type has three sources of nitrogen: internal recycling of nitrogen before litterfall, uptake from the atmosphere, and uptake from the soil. In the soil the available nitrogen is partitioned over the functional types according to their root biomass. Biomass increment of each type is proportional to light interception, and is related to nitrogen availability through a Michaelis-Menten equation. The carbon and nitrogen acquired are partitioned over the organs. The uptake of nitrogen is limited by setting a maximum on the nitrogen content of the biomass;

excess nitrogen remains in the soil and may be leached. The vegetation structure type is determined from the distribution of biomass over the functional types. Management is accounted for in SUMO by removing biomass or soil organic matter, and implemented as mowing, thinning, clearcutting, sod-cutting, or grazing. The density of grazers is constant for domestic species, and varies between certain limits according to food availability for wild species. The grazers' faeces are returned to the soil organic matter pool.

Parametrization in SUMO is done for each functional type (e.g. biomass increment as a function of light interception, partitioning of C and N over organs, height increment as a function of biomass increment, etc.). However, for trees (12 species) and for grazers (15 species), parametrization is done per species. The initialization depends upon the available data. In the present example data are available as vegetation relevees on a 10*10 m^2 scale, and the initial tree species can be explicitly imposed. Although SUMO can only simulate competition between two tree species, the number of species can be varied by taking different tree species in different grid cells, or by making the two species equal (i.e., two generations of the same species).

NTM

The philosophy behind NTM is based on the observation that it is very difficult to predict the presence of a given species on the basis of external circumstances (soil, management etc.). On the species level, factors that are not accounted for in our model chain, or on which data are lacking, play a dominant role. Such factors are e.g. seed dispersal or stand history. However, on a higher level there is a relationship between environment and vegetation that can be quantified (Wamelink et al. 2002). NTM uses four dominant factors to characterize the environment: groundwater level, soil pH, soil nitrogen availability, and management. In NTM the relation between vegetation and these environmental factors is determined by regression. The vegetation can be characterized on two levels: generalized 'potential' biodiversity (NTM3), or vegetation type (alliance in the sense of Braun-Blanquet 1951; NTM4).

Parametrization in NTM takes place by means of a training set of vegetation relevés. Ideally, the training set contains relevés of which management, groundwater, pH, and nitrogen availability are known. However, because such data are presently not available on a sufficient scale, we use Ellenberg's (1991) indicator values for F, R and N as a proxy for the soil conditions (Wamelink et al. 2002), and we use the vegetation structure type as a proxy for the management (forest [coniferous or deciduous]: no management or cutting/thinning, heathland: sod-cutting or extensive grazing, and grassland: mowing or intensive grazing). NTM uses different parametrizations for these four vegetation structure types. Per structure type, the response of the vegetation is linked to the abiotic variables using the B-spline approach of Eilers and Marx (1996). In this way, a smooth, nonlinear response surface is fitted to the data, in which the degree of smoothness can be actively controlled. NTM in its present form uses a separate calibration to link Ellenberg's indicators (on an arbitrary scale) to physical units (pH, N mineralization + deposition in kg $N.ha^{-1}.y^{-1}$, groundwaterlevel in cm below soil surface) (Wamelink et al. 1996, Ertsen et al. 1998).

In NTM3, biodiversity is the response variable. In the training set, biodiversity is determined according to the methods of Hertog & Rijken (1992, van Dobben et al. in prep). Its principle is that each plant species is assigned a conservation value depending on its national rarity and temporal trend (the criteria of the red list, Mace and Stuart 1994). The conservation values of the species are used to calculate a biodiversity value per relevé as an abundance weighted sum over the species. The resulting biodiversity value should be considered as a measure for the probability of occurrence of Red List species, rather than as a measure for the total number of species or the actual number of Red List species. In NTM4, the vegetation type is the response variable (Schouwenberg et al. 2002). Each relevé in the calibration set is assigned to an alliance using an automated procedure (van Tongeren 2000), which is linked to the abiotic predictors using a logit transfer function. Thus, the output of NTM4 is the probability of occurrence per alliance at a given combination of vegetation structure and abiotic circumstances.

Example of model runs

Here we present an example of an application of the above model chain to evaluate the effects three simple scenarios at stand level. The scenarios differ in deposition, which is constant at 45 kg N $ha^{-1}.y^{-1}$ in scenario A, and decreasing from 45 kg N $ha^{-1}.y^{-1}$ in 2000 to 10 kg N $ha^{-1}.y^{-1}$ in 2090 in scenarios B and C. Scenario C is equal to scenario B, but includes the presence of grazers. To define the initial state of the models we used data from two reserves on dry, sandy soil in the Netherlands: a Scots pine forest and a heathland. In the forest, management is 10% thinning each 10 years and initial grazing density is 0.1 red deer per ha. In the heathland, management is sod-cutting each 30 years, and grazing at a fixed density of 0.5 sheep per ha.

Figure 2 shows the simulated development of vegetation structure in the pine forest, starting in 1990 at an average age of 67 years, for scenario C. After 2015, the pine reach their maximum age and the stand starts to collapse. Between 2020 and 2040, there is a more open phase with a higher abundance of herbs and dwarfshrubs, but after 2040 oak starts to become dominant. Beach is present from 2040 onward, but oaks remains dominant to the end of the simulation period. Shrubs are present, but steadily decreasing all over the period. The effect of the exclusion of grazing in scenarios A and B (not shown) is mainly a strong increase in the herb biomass during the transition phase, resulting in competitive exclusion of dwarfshrubs. Generally, grazing results in a higher structure diversity, i.e. a more even distribution of biomass over the functional types. The differences between scenarios A and B are very small. Figure 3 shows the simulated development of the biodiversity indicator for the three scenarios. In the forest there is very little change over time, although in the long run the biodiversity tends to increase in scenarios B and C.

Figure 4 presents the simulated development of vegetation structure in the heathland reserve for scenario C. In each management cycle dwarfshrubs steadily increase and remain dominant over the complete cycle, although trees also increase. Herbs are only present at the beginning of each cycle, but are outcompeted towards the end. However, in scenario B (not shown) herbs become dominant in the first cycle, and in scenario A this happens in all cycles. These differences are clearly reflected by the biodiversity indicator, which increases after each cutting event, and decreases thereafter. However, in scenario A there is only this cyclic change, while in scenarios B and C there is an overall increase, and mostly so in C (Figure 3). In scenarios B and C the biomass at the end of the management cycle decreases in each subsequent cycle.

The probability of occurrence of the Calluno-Genistion pilosae; Schaminee et al. 1996) in the heathland for the three scenarios is shown in Figure 5. Generally, this probability reaches a maximum around the middle of each cycle. In scenario A there is a strong decrease towards the end of each cycle (which corresponds with the dominance of grasses at that time), but a return towards the same value at the beginning of the next cycle. In scenarios B and C the amplitude is less, but there is a steady decrease over time, with lower values for scenario C all over.

Discussion

The simulated development of vegetation structure, vegetation type and biodiversity for the two reserves is plausible in the light of present-day knowledge. Especially for heathland there is a vast body of experience with various management types (Bakker & Berendse 1999) which shows that (a) at deposition of > c. 20 kg N $ha^{-1}y^{-1}$ a cutting cycle of 30 years is not sufficient to maintain a constant dominance of *Calluna*, and (b) in heathland, grazing strongly enhances biodiversity (Bokdam & Gleichman 2000). To this may be added the historic records of a transition of heathland to open sand under a regime of grazing, sod-cutting and low deposition (De Smidt 1981). The beginning of this process is seen in the simulation in Figure 4, where total biomass at the end of the last cycle is reduced to c. half the biomass at the end of the first cycle. In this case exhaustion of the nitrogen pool takes places, which may ultimately lead to the complete disappearance of vegetation. At the same time biodiversity steadily increases, which also agrees with historic records of heathland in periods of very low N availability e.g. the 19th century.

In contrast, the effect of decreasing deposition on forest stand structure and ground vegetation seems to be limited. This is surprising as a clear effect of deposition on both tree growth and ground vegetation composition has been demonstrated by several authors, e.g. Brunet et al. (1998) or Tamm et al. (1999). The explanation is that nitrogen, accumulated during the period of high deposition in the 20th century, is only very slowly removed from the system. In the heathland, sod-cutting is a very effective way to remove nitrogen, and under decreasing deposition its availability rapidly decreases. To reach the same effect in forest more drastic measures would be needed, e.g. clearcutting, litter removal (Bartelink et al. 2001) or a more heavy grazing regime (Kuiters & Slim 2002). In the present example a natural collapse of the stand takes place because the reserve is even-aged. During the transition phase to another tree species the nitrogen is partly preserved in the herb and dwarfshrub layer.

Figure 3 shows that the biodiversity of the forest reserve is always lower than the biodiversity of the heathland. This is caused by the fact that in The Netherlands, the vast majority of the red-list species are species of low vegetation (e.g., grassland, heathland, peatbog) (Slim & van Dobben 1997). Therefore the forest biodiversity as determined by NTM3 (i.e., the species diversity) would remain below the value of heathland even if N availability would decrease. In general, if biodiversity is to be increased, the recommendation to politicians would be to decrease deposition, and the recommendation to the reserve manager would be to actively remove nitrogen from the forest, and to decrease grazing pressure or cutting frequency in heathland if deposition really decreases.

The presented examples show that coupled models are able to make plausible predictions of vegetation development in forest and heathland, on which recommendations can be based. A weakness of all predictive models is the lack of validation. The combination of SMART and SUMO has been validated on a stand level on the basis of historic data (Wamelink et al. 2001). But even for a well-validated model, uncertainty in the input may cause considerable uncertainty in the output. In our forest example, the output appeared to be highly sensitive to the initial biomass of oak; if initial oak biomass is slightly increased, succession is strongly accelerated. Therefore there is a strong need for standard procedures of uncertainly analysis (Schouwenberg et al. 2000, Jansen et al. 2000).

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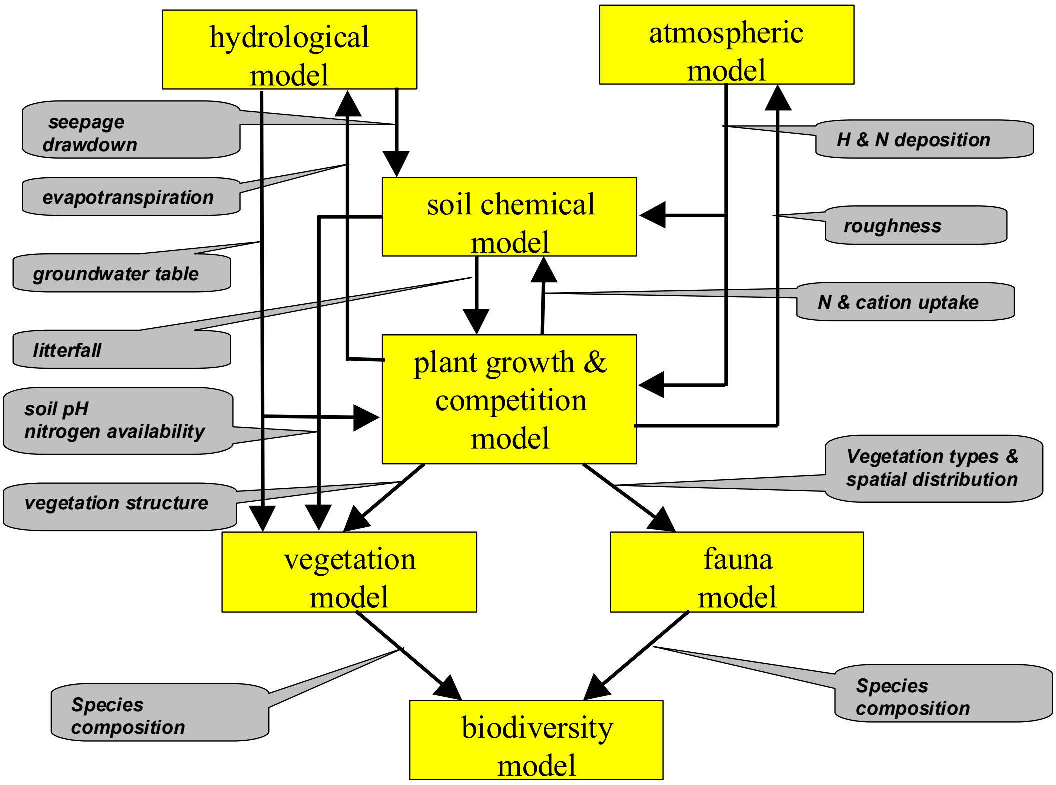

Figure 1: Ecological model chain. Boxes denote models, arrows denote information streams.

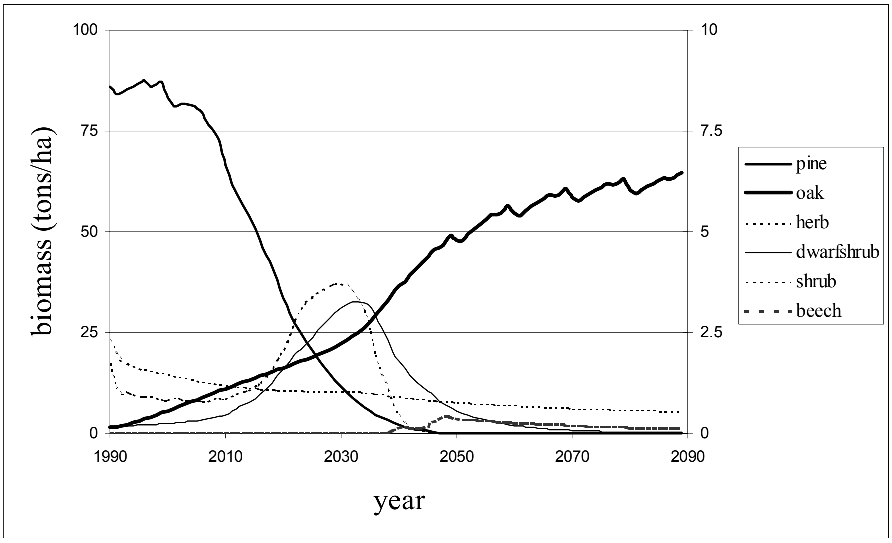

Figure 2: Development of biomass per functional type in the pine forest under scenario C (decreasing deposition + grazing). The left axis give biomass for pine and oak, the right axis for all other types.

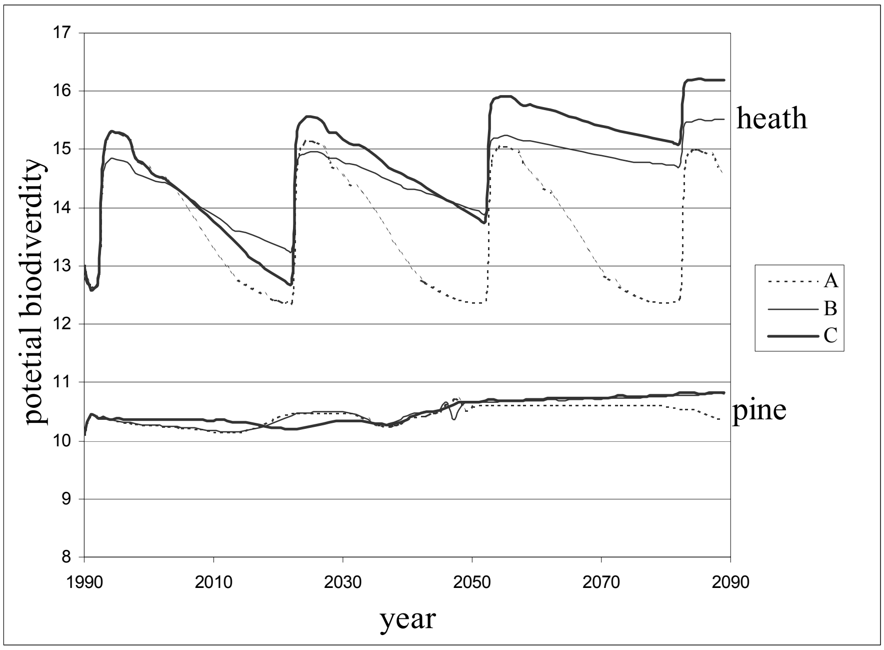

Figure 3: Development of potential plant biodiversity under the three scenarios: A = constant deposition of 45 kg N $ha^{-1} \cdot y^{-1}$, B = deposition decreasing from 45 kg N $ha^{-1} \cdot y^{-1}$ in 2000 to 10 kg N $ha^{-1} \cdot y^{-1}$ in 2090, and C = like B, with 0.1 red deer ha^{-1} initially (pine forest) or 0.5 sheep ha^{-1} (heathland). 'Potential biodiversity' is an index on an arbitraty scale that reflects the suitability of the soil (in terms of pH, N availability and groundwater level) for a vegetation containing rare and declining species (i.e. the criteria of the Red List); a value ≤ c. 10 indicates a low probability of Red List species, a value ≥ c. 15 indicates a high probability of Red List species.

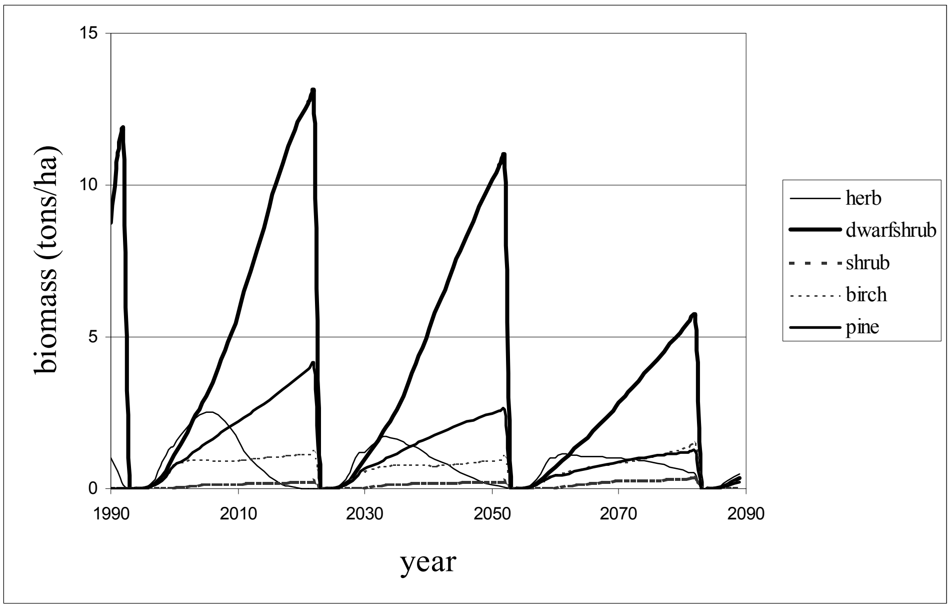

Figure 4: Development of biomass per functional type in the heathland under scenario C (decreasing deposition + grazing).

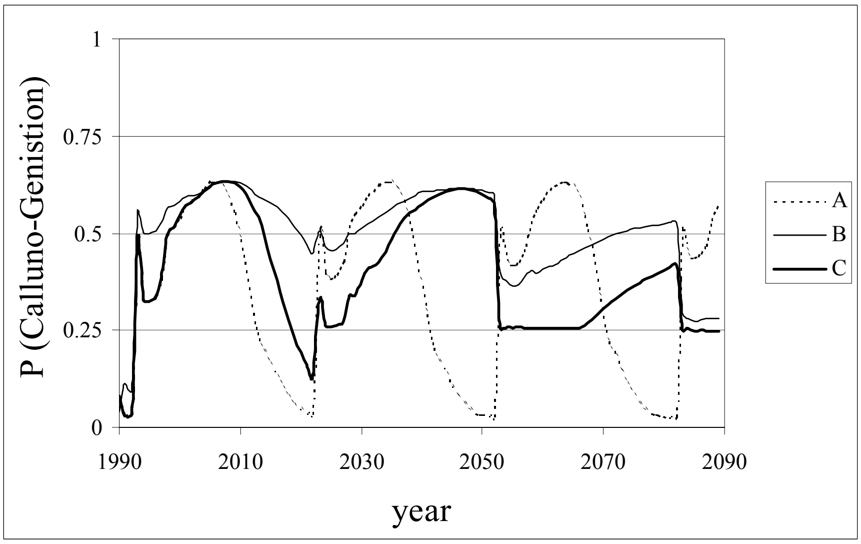

Figure 5: Development of probability of occurrence of Calluno-Genistion pilosae in heathland, under the three scenarios: A = constant deposition of 45 kg N $ha^{-1} y^{-1}$, B = deposition decreasing from 45 kg N $ha^{-1} y^{-1}$ in 2000 to 10 kg N $ha^{-1} y^{-1}$ in 2090, and C = like B, with 0.5 sheep ha^{-1}.

Effects on soil chemistry and nutrient uptake by admixture of birch in Norway spruce stands

Hans Göransson, Ulrika Rosengren, Gunnar Thelin, Bengt Nihlgård
Section of Plant Ecology, Lund University, Ecology building, SE-223 62, Sweden
Corresponding author: Hans Göransson
Tel: +46 46 2223745; E-mail: Hans.Goransson@planteco.lu.se

Abstract

In order to investigate the effects on the soil status of a birch admixture in Norway spruce stands, pure Norway spruce, pure birch and mixed plots of birch and Norway spruce were established in 1984/1985 at four locations in southern and central Sweden. The soil was sampled down to 30cm soil depth in1984 /1986, 1993 and 2001. We report results on soil chemical changes and changes in base cation stores above and below ground. No significant positive effect on soil chemical status of the birch admixture was found even though the uptake of base cations into the trees was smaller in the mixed stands. All treatments showed a decrease in soil chemical status in the mineral soil over time.

Keywords: *Betula pendula Roth*., *Picea abis* (L.) *Karst*, mixed stands, base cations, soil chemical changes, nutrient uptake

Introduction

In southern Sweden the pool of exchangeable base cations in forest soils are known to decrease due to leaching caused by high levels of acid deposition (Falkengren-Grerup and Tyler 1991; Jönsson et al. 2000). Another factor depleting the soil in base cations is intensive forest management. Short rotation times and whole tree harvesting causes a large export of nutrients away from the forest system (Olsson et al. 1996). When practicing whole tree harvesting the growth induced acidification is not neutralised by the decomposition of harvest residues which is futher depleting the base cation storage. This depletion in base cations may lead to nutrient imbalance in the trees and affecting growth and vitality (Thelin 2000). Birch has been said to improve the soil chemical status (Frivold 1991, Frank 1994), while Norway spruce has been reported to deteriorate soils (Liljelund et al. 1986). Three often used explanations for this are (i) that Norway spruce litter contain more recalcitrant chemical components and produces more such components during decomposition in comparison with deciduous litter and thereby is decomposed slower (Johansson 1995, Binkly and Valentine 1991). (ii) Larger leaf area of Norway spruce, especially during wintertime effectively filters acid airborne particles. This leads to a more acid troughfall in spruce stands than in deciduous stands (Lundmark, 1991; Liljelund et al. 1986). (iii) Norway spruce have a more shallow root distribution than birch trees and thereby a smaller uptake zone which makes the soil more acid as there is less minerals that can be weathered (Liljelund et al. 1986). It is confirmed, by many experiments, that growth of deciduous species ledd to a higher pH and base saturation in the soil than growth of conifers (Nihlgård, 1971; Bergkvist, 1986; Liljelund et al. 1986; Binkley and Valentine, 1991). No effect or the opposite has also been found in some reported experiments (France et al., 1989, Rothe and Binkly 2001;). An admixture of birch in Norway spruce stands has been suggested to decrease the acidification and depletion of base cations in the soil (Brandtberg, 2001). Vandermeer (1989) distinguished between two mechanisms explaining the positive effects of a mixture of two different species. (i) The comparative production principle, saying that two species with small niche overlap will use the resources more efficiently due to a weak intraspecific competition and (ii) the facilitative principle, stating that two species alter the environments of one another positively. Thelin (2000) proposed both mechanisms to be valid for spruce/birch mixtures and suggested that birch acts as a cation pump in mixed stands. Birch trees, that usually have deeper roots than Norway spruce (niche separation) (Siren 1955), take up cations from the mineral soil and release them on the surface with the litter / throughfall. The cations released by decomposition are utilized by the more shallow Norway spruce roots as a net contribution to the Norway spruce nutrient cycling. However Brandtberg (2001) did not find any difference in root distribution down to a depth of 10 cm in the mineral soil (2/3 of the A-horizon) between mixed and pure Norway spruce stands at one of the sites used in this study. Thelin et al. (2002) and Brandtberg (2001) both found higher ratios of K/N and P/N in the needles from mixed stands than in needles from pure Norway spruce stands. This indicates a larger access for Norway spruce of K and P in the uptake zone in the mixed stands than in the pure stands. On the other hand if birch trees have a larger uptake of base cations in the mineral soil, birch may deplete these horizons more in mixed stands compared to pure Norway spruce stands (Alban 1978). Similar findings were reported by Nihlgård (1971) that found a difference in pH between Norway spruce and the more deep-rooted beech (*Fagus sylvatica L.*) (Roth and Binkly 2001) was larger in the organic top layer than in the lower mineral soil were beech had only slightly higher pH than Norway spruce.

The depletion of cations in the soil may depend on different cation uptake in the biomass (Alban et al., 1978; Eriksson and Rosen, 1994). Alriksson and Eriksson (1998) found that Norway spruce contained 100% more Ca and 50% more K and P compared to birch in above ground biomass in even aged trees mainly due to that a larger part of the biomass of Norway spruce is nutrient rich foliage and branches. This means that birch is a less intensive competitor for these nutrients compared to Norway spruce. A lower competition for Ca, K, and P in the mixed stands compared to pure Norway spruce monoculture may also be an explanation to the higher P/N and K/N ratio in the needles from the mixed stands (Brandtberg 2001).

This study is based on the hypothesis that a mixed forest stand of Norway spruce and birch leads to a lower harvest of base cations and lower acidification of the soil compared to a pure Norway spruce stand at similar growth rates. For this purpose we used experimental plots consisting of pure Norway spruce (*Picea abis* (L.) Karst), pure birch (B. *Pendula* Roth and B. *pubescens* Ehrh.) and mixed Norway spruce and birch. Here we report data on soil chemical changes and changes in base cation stores above and below ground.

Materials and methods

Site description

Four field experiment sites in southern and central Sweden were used (Fig 1, table 1). The soils were acid forest soils (pH humus < 4,5). The depth of the organic layer ranged between 4 and 10 cm and the humus form was mor. When the experiments were established all stands were young mixed Norway spruce-birch stands.

Three of the sites used in this study, Huseby (Hb), Burhultsnäs (Bn) and Södra Skoga (SS) (se table 1 and 2) were selected from a thinning experiment comprising eight sites, established during the period of 1983-1985 designed to to study the long-term yield in mixed Norway spruce and birch stands (Tham 1987, Mård 1996). The fourth study site, Degeberga (DB), (se table 1 and 2) was established in 1985. At the time of establishment at Huseby, Burhultsnäs and Södra Skoga (approximately 20-30 years after regeneration) the stands consisted of even-aged birch sheltering Norway spruce of approximately the same age. Each plot was 0,075 ha with a 5 m buffer zone.

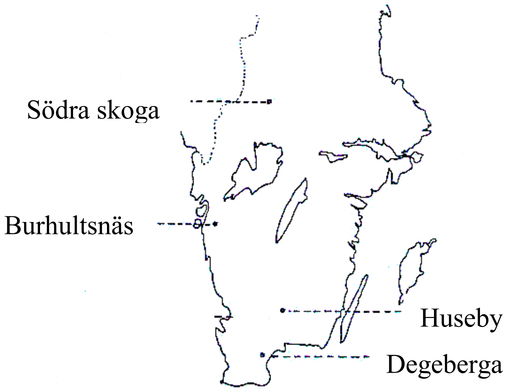

Figure 1. The locations of the test sites in southern Sweden.

Table 1. Description of the four study sites

	Sites			
	Burhultsnäs	Huseby	SödraSkoga	Degeberga
Province	Västergötland	Småland	Värmland	Skåne
Latitude, longitude	57°54’N; 12°15´W	56°49´N; 14°41´W	60°03’N; 13°23´W	55°47’N; 13°57’W
Altitude (m.a.s.l.)	110	170	170	180
Mean Temperature (°C)[a]	+6,3	+6,4	+3,6	+7,2
Mean precipitation (mm/yr)[a]	940	651	671	562
Soil texture	Sandy loam	Loamy	Sandy	Sandy loam
Site Index (H100)[b]	23-29	30-35	30-31	32-35
Stand age (2001)	35	44	Aprox. 38	Aprox. 26
Site history	Planted with spruce in 1967, much natural regenerated birch	Clear cut in 1955, planted with spruce in 1958, much natural regeneration of birch and spruce	Probably planted with spruce in 1964, much natural regeneration of birch and spruce	Probably planted with spruce in mid –70, natural regeneration of birch.
Deposition of N[d]	11,9	14,4	7	7,5
Deposition of S[d]	8,5	7,5	4,6	4,8

[a] Average (1961-1990) yearly mean temperature and precipitation are recorded at nearby climate stations (SMHI, S-601 76 Norrköping)

[b] Height of dominant Norway spruce at 100 years of age

[c] Tham 1987

[d] Deposition over open field in 1999/2000. (IVL <www. ivl.se>)

Table 2. Number of used plots of pure birch, pure Norway spruce and mixed birch and Norway spruce forest at each site, percentage of birch in mixed stand in 2001 and the years during which samples were taken at each site.

	Birch	Norway spruce	Birch and Norway spruce	% Birch in mixed stand 2001	Samples taken
Burhultsnäs	0	1	1	9%	nov-84,nov-86 humus only, sep-88, okt-93, apr-01
Degeberga	1	1	1	8,6%	okt-86, sep-88, okt-93, feb-01
Södra Skoga	1	1	2	21%	nov-84, nov-86 humus only, sep-88 humus only, okt-93, apr-01
Huseby	1	1	1	13%	nov-84, nov-86 humus only, sep-88 humus only, okt-93, mar-01

All birches were felled in the Norway spruce treatment, leaving approximately 4900 Norway spruce stems/ha. In the mixed stands, birch was thinned to a shelter with 500 stems/ha sheltering approximately 4400 Norway spruce stems/ha. This resulted in the mixed stands being comparatively denser, with respect to basal area and volume, than the pure Norway spruce stands (Mård 1996). In 1989 a minor thinning of Norway spruce were done on all plots and in 1997 birch was thinned down to 100 stems/ha in the mixed plots (fig 2) (Brandtberg 2001).

At Huseby and Södra Skoga 0,01 ha pure birch plots without buffer zones were established in 1984 and have not been thinned since then. At Degeberga the plots (birch, Norway spruce and mixed) were 0,01ha without buffering zone. The mixed plots where thinned to 50% birch and 50% Norway spruce based on basal area. None of the plots in Degeberga have been subjected to thinning after the start of the experiment but on the mixed plot self thinning of birch seems to have occurred. On all sites, slash have been removed after thinning from the pure plots and left on the mixed plots (se table 2).

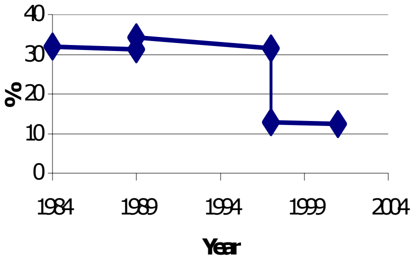

Figure 2. Percent of the basal area in the mixed plots that was birch from 1984 until 2001 Average for the BN, HB and SS sites. Spruce was thinned in 1989 and birch in 1997.

Soil Sampling

Soil samples have been taken from Södra Skoga, Burhultsnäs and Huseby since 1984 and Degeberga since 1986 (See table 2).

In order to attain comparable results the soil samples were taken and analyzed with the same methods each year. At each plot 16 soil samples were taken, 8 on each diagonal, from the Humus, A1, A2, and B-layer. A1 was separated from A2 as it was influenced by black humus particles. The 8 soil samples from each diagonal were put together into one composite sample. The humus layer was taken with a soil corer (12 cm Ø), and the mineral soil samples with a corer (3 cm Ø) reaching down to 30 cm. Al horizons were not reached in all plots. In 2001 four samples were also taken from the B-horizon in one 50-cm deep pit per plot for nitrate and ammonium analysis. Two pits (50x50 cm) were made on each site and the density and stoniness was calculated for each horizon (SS and BN in 1984, DB and HB in 2002)

Chemical analysis

The soil samples were dried at 40°C to constant weight. The humus samples were sieved through a 6 mm sieve and the mineral soil was sieved through a 2 mm sieve. The water content at 105°C, and the loss of ignition at 550°C for two hours was determined. The soil (10g of humus samples and 20g of mineral samples) was extracted in 100 ml of 1M KCl for determination of pH and by titration exchangeable total acidity and exchangeable Al^{3+}. The same amount sieved soil was extracted in 1M NH_4Cl for determination of the mineral elements Na, K, Ca, Mg, B, Fe and Mn on an intercoupled plasma spectrophotometer (ICP-Optima 3000 DV instrument, Perkin Elmer).

Samples taken in 2001 were also analyzed for $pH(H_2O)$, Kjeldahl-N and total-C through ignition on a Leco-Instrument (Carbon determinator CR 12). Two samples from each 50 cm pit were directly frozen when returning from the field. 25 g of the frozen soil samples were extracted in KCl for determination of ammonium and nitrate on a Flow injection analyzer (Perstorp analytical) (Balsberg 1990).

Tree base cation content

Norway spruce stands and the mixed stands at SS, BN and HB base cation uptake into was calculated from the amount of standing biomass plus biomass felled in thinnings. All biomass that been thinned was calculated as removed from the plot. The nutrient content in the biomass per ha has been calculated from diameter, height and number of trees in a nutrient uptake model based on biomass functions in Marklund (1988) and nutrient concentrations of different tree fractions (se below). The trees were measured when thinnings were made in 1984, 1989 and 1997 (pers. com. Per-Olov Brandtberg).Tree growth rate from 1997 to 2001 was assumed to be the same as between 1989 and 1997. The nutrient concentrations of the different tree fractions were chosen from a compilation of tree nutrient concentrations.

Statistics

A two way ANOVA with site and treatment as independent factors was used to test for differences between the treatments. General changes in all treatments from 1984/86 to 2001 were analyzed with a paired t-test. All statistics were carried out according to Sokal and Rohlf (1995).

Results

Effect of treatments

Birch seemed not to have improved the soil status in terms of base cations or acidity neither as a pure stand nor in a mixture with Norway spruce compared to pure Norway spruce stands. Already when the stands where established there where differences between the plots indicating higher levels of base cations in the mixed treatment plots (tab 3). In the humus layer Mg was significantly higher in the mixed treatment compared to the pure treatments and in the A1 horizon Ca and base saturation was higher in the mixed stands than in the pure stands.

In 2001 the mixed plots still had higher concentrations of base cations in the humus layer (Mg and Ca) and higher base saturation in the A1 horizon. In 2001 the mixed plots had developed higher Ca and Mg concentrations in the A2 horizon than the pure plots and in the birch treatment the humus was more acidified and had developed higher Al^{3+} concentration than in the other treatments. In the A2 horizon however the birch treatment had developed lower Al^{3+} concentrations compared to the other treatments (table 3).

The change in base cation stores in the soil did not differ between the pure Norway spruce stands and the mixed stands in SS, HB and BN but the Norway spruce stand took up more base cations into the biomass (fig 3). The total production average, including harvested biomass from 1984 until 2001 was almost similar and was for the mixed stands 102,4 ton/ha^{-1} d.w. (stdev=23,6, n=3) and for the pure Norway spruce stands 105,4 ton/ha^{-1} d.w. (stdev=5,0, n=3).

Table 3. PH KCl, exchangeable acidity, Excahangeable AL3+, Exchangeable organic acids, Ca, K, Mg, Na, Cation exchange capacity and base saturation in 1984 and 2001. Different letters means that there is a significant difference according to a two-way ANOVA test with site and treatment as independent values. No soil samples could be taken in the mixed treatment from HB in Min A2 and HB, SS and DB in the Min B horizon. In the Norway spruce treatment samples are missing from SS in the Min B horizon.

Year	Treatment	Layer	pH KCL	Exch.acid. µekv/g	Exch.Al3+ µekv/g	Exch. H+ µekv/g	Exch.org.A µekv/g	Ca µg/g	K µg/g	Mg µg/g	Na µg/g	CEC µekv/g	Bassat.. %
1984	Birch	Humus	2,95	116,28^{a}	57,59	13,17	45,52	3426,08	513,97^{a}	590,95^{a}	74,23	352,17	68,59
1984	Mixed	Humus	3,02	110,90^{a}	62,86	10,99	37,06	2916,26	668,42^{b}	523,86^{b}	105,14	321,13	64,85
1984	Spruce	Humus	3,08	88,59^{b}	55,14	9,16	24,29	2916,29	574,64	443,28^{c}	76,65	288,56	71,31
				p=0,049					p=0,025	p=0,025			
1984	Birch	MinA1	3,17	56,26^{a}	45,20^{a}	6,95	4,12	523,87^{a}	115,19	89,31	35,83	94,25	39,64^{a}
1984	Mixed	MinA1	3,24	37,80^{b}	28,54^{b}	7,01	0,10	862,47^{b}	160,13	137,02	67,86	97,83	61,26^{b}
1984	Spruce	MinA1	3,39	34,74^{b}	28,76^{b}	5,42	0,58	514,58^{a}	117,62	75,61	50,53	75,20	43,14^{a}
					p=0,077			p=0,029					p=0,057
1984	Birch	MinA2	3,54	22,62	19,84	2,89	-0,10	108,24	23,48	13,96	13,98^{a}	30,38	24,14
1984	Mixed	MinA2	3,61	23,94	19,63	2,57	1,61	187,43	32,45	24,10	22,27^{b}	34,92	38,47
1984	Spruce	MinA2	3,67	22,60	19,87	2,48	0,25	179,65	39,30	24,31	21,75^{b}	35,51	28,38
											p=0,0142		
1984	Birch	MinB	3,51	**27,82**	**23,11**	**3,19^{a}**	**1,52**	**41,15**	**8,26**	**8,13**	**5,21**	**26,96**	**23,43**
1984	Mixed	MinB	,3,91	**16,78**	**11,73**	**1,34^{b}**	**3,72**	**172,28**	**24,48**	**15,90**	**17,71**	**28,17**	**41,34**
1984	Spruce	MinB	3,99	23,38	22,51	1,06^{b}	-0,19	131,67	27,39	14,42	24,72	33,12	21,18
						p=0,001							
2001	Birch	Humus	3,13	102,14^{a}	70,92^{a}	9,08	22,13	1731,45^{a}	481,78^{a}	363,00^{a}	57,18	233,21	56,86
2001	Mixed	Humus	3,01	68,85^{b}	23,74^{b}	11,52	33,59	2412,35^{b}	733,05^{b}	447,75^{b}	73,30	248,00^{a}	71,24
2001	Spruce	Humus	3,10	76,75^{b}	38,34^{b}	9,71	28,69	1737,34^{a}	731,54^{b}	311,41^{a}	71,97	210,90^{b}	64,07
				p=0,022	p=0,002			p=0,029	p=0,0007	p=0,027		p=0,01	
2001	Birch	MinA1	3,53	62,79	56,77^{a}	3,00^{a}	3,03	175,41	60,03^{a}	29,40	12,84	76,06	15,56^{a}
2001	Mixed	MinA1	3,15	47,96	34,41^{b}	7,50^{b}	6,05	299,51	73,61^{a}	52,91	18,34	69,94	30,05^{b}
2001	Spruce	MinA1	3,21	54,29	41,43^{b}	7,46^{b}	5,40	204,46	141,43^{b}	45,19	21,35	72,76	24,12^{c}
					p=0,035	p=0,001			p=0,0012				p=0,0012
2001	Birch	MinA2	3,81	32,58^{a}	25,45^{a}	1,64^{a}	5,50	44,41^{a}	13,19^{a}	7,14^{a}	6,37	36,00^{a}	10,56
2001	Mixed	MinA2	3,50	42,80^{b}	32,10^{b}	3,58^{b}	7,12	82,29^{b}	27,13	17,68^{b}	9,51	49,47^{b}	14,64
2001	Spruce	MinA2	3,53	38,20	32,38^{b}	3,30^{b}	2,52	42,65^{a}	36,00^{b}	11,95^{a}	9,75	42,65	10,69
				p=0,025	p=0,018	0,04		p=0,012	p=0,015	p=0,038		0,01	
2001	Mixed	MinB	4,08	51,66	45,15	0,92	5,59	25,12	27,90	8,63	11,89	54,85	6,34
2001	Spruce	MinB	4,01	45,92	38,71	1,22	5,99	38,01	24,46	9,29	10,74	49,68	7,92
					p=0,058			p=0,061					p=0,058

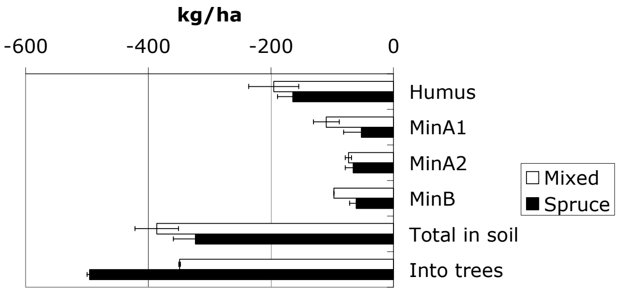

Figure 3. Mean change from 1984 until 2001 in cation pools in soil and tree biomass based on SS, HB and BN. The uptake is higher in the spruce plots (p=0,003) whereas changes of cation stores in the soil do not differ between treatments (p= 0,6). Error bars show standard error. No soil samples could be were taken in the mixed treatment from HB in Min A2 and HB, SS in the Min B horizon. In the Norway spruce treatment samples are missing from SS is in the Min B horizon

General effects over time for all treatments

In the humus layer of all treatments did Mg, Ca, Na and CEC decrease from 1984/1986 to 2001. In the A2 horizon exchangeable acidity, Al3+ and CEC increased from 1984/86 to 2001 whereas Ca, Mg, Na and Base saturation decreased (fig. 4). There were very small amounts of nitrate (0,003±0,0016 mg/g) and ammonium (0,043±0,028mg/g) in the deep mineral soil below 50 cm, and no differences between the treatments could be detected.

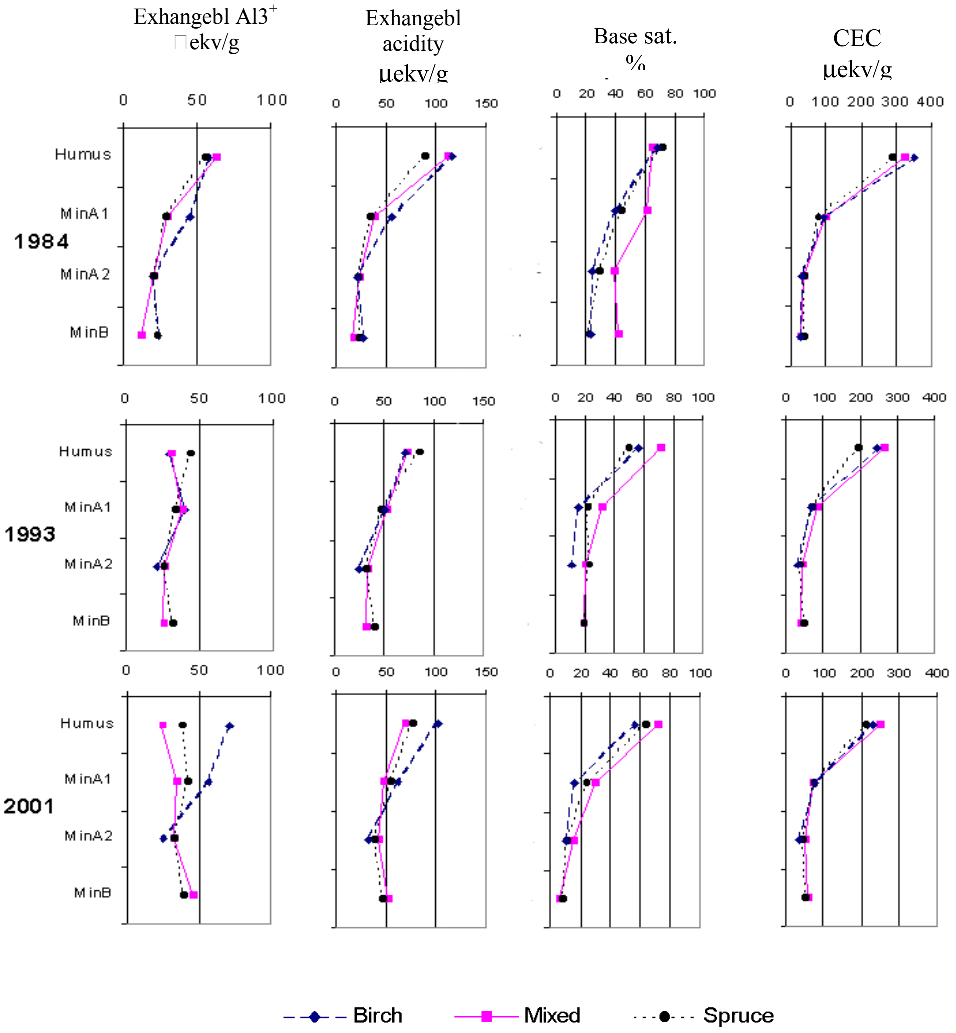

Figure 4. Mean Exchangeable acidity, exchangeable AL3+, CEC and Base saturation in 1984 (Degeberga site 1986), 1993 and 2001. In the humus layer the concentrations have decreased from 1984-2001 for Mg (p= 0,001) Ca (p= 0,001), Na (p= 0,02) and CEC (p=0,001). In the A2 horizon Exchangeable acidity, Al^{3+} and CEC increased (p=0 0,001, p=0,001, P=0,012) whereas Ca, Mg, Na and Base saturation decreased (p=0,001, p=0,029, p=0,001, p=0,001). No soil samples could be taken in the mixed treatment from HB in Min A2 and HB, SS and DB in the Min B horizon. In the Norway spruce treatment samples are missing from SS in the Min B horizon.

Discussion

General trends over time

The general trends for all treatments in the deeper mineral soil (A2 and B-horizons), i.e. decreasing concentrations of base cations and increasing exchangeable acidity ,are similar to trends on monitoring sites in conifer stands in southern Sweden that from 1988-1993 (Jönsson et al. 2000). There have been much growth induced acidification and depletion of base cations as the stands have been in their maximum growth phase. This has contributed to the decrease in base saturation in the mineral soil. The decline in CEC in the humus layer and the increase in the mineral soil may depend on a transport of DOC from the humus layer to the mineral soil (pers.com. Björn Berg) as an increase of DOC increases CEC (Lindroos et al. 1995). This movement of DOC could explain some of the increased acidification and decreased base saturation of the mineral soil. The increased number of exchangeable positions in the mineral soil seem to have been occupied by Al3+ since base cations concentrations have decreased despite an increase of CEC. In the humus layer Al3+ are showing signs of decreasing amounts (mixed and the Norway spruce stands). This indicate that Al3+ may have been transported along with organic matter. The movement of DOC from the humus layer to the mineral soil could depend on climate factors. There was indications on that the humus layer had decreased in depth from 1984 to 2001 which may be a result of that the mild winters during the last decade (SMHI 1990-2001) may have increased the decomposition and increased the percolation.

Effect of tree species and mixture

Brandtberg (2001) found, on partly the same sites as used in this study, in 1991-1993 that the concentration of exchangeable cations in the litter and humus layer was higher in the mixed stands of birch and Norway spruce compared to the pure Norway spruce stands despite a higher production in the mixed stands (Mård, 1997). We cannot confirm Brandtbergs (2001) results as the differences found between the treatments do not indicate that birch in any way would improve the soil chemical status even though slash have been left on the mixed plots. Brandtberg (2001) found ,however, no effect on soil chemistry as a result of the different slash treatments. The soil chemistry have developed more or less in the same way in the different treatments, except the increased acidification in the humus layer in the birch plots, between 1993 and 2001 (fig 4). There may be several reasons for this. (I) The admixture of birch may have been too low since the thinning in 1997 so that differences existing in 1993 has disappeared. Thelin et al. (2002) found indications that a birch admixture of less than 30% basal area did not have any effect on the soil chemistry. This may be the case in this study also (fig. 2). (II) The birch plots (10x10m) without buffering zone, may have been too small and thereby affected by the Norway spruces standing around it. This mean that the birch plots more or less can be regarded as a mixed stands in terms of both root distribution and litter fall. A large area of the birch plots were probably occupied by Norway spruce roots and much of the litter from the birches probably ended up below the surrounding Norway spruces whereas the contribution of needles from the Norway spruces to the birch plot was probably small (Rothe and Binkly 2001). The decreased litterfall and the spruce root occurrence may have overridden the possible positive effects of birch on soil chemistry. The admixture of birch may have been too low even in the pure birch plots. (III) The mild winters in the last decade changing the CEC may have obscured the possible effects of birch. (IV) This study have taken into account the differences that existed already when the plots were established. These differences could however been an effect of that the soil samples were taken up to 2 months after the thinning in 1984/1986. During this time the slash left on the mixed plots may have leashed base cations improving the soil chemistry. (V) There is no difference between mixed and pure spruce plots, on these soils, possible because of no differences in rooting depth as found on one of the sites by Brandtberg (2001).

The larger uptake of base cations into the trees in the pure spruce stands than in the mixed stands depend on the higher uptake of base cations per year for Norway spruce compared to birch in the nutrient uptake model. The changes in the soil base cation pools were however similar in the pure and the mixed stands. This may indicate that the soil in the pure Norway spruce stands have had a higher weathering rate. If so, increased weathering might be a result of a higher density of mycorrhiza which have been found in pure Norway spruce stands compared to mixed spruce-deciduous stands (Wallander pers. com). Direct utilization of the minerals by "rock eating fungi" could possibly also explain the higher uptake by the Norway spruce stands without a larger loss in the soil exchangeable base cation pool (Van Breemen et al. 2000). The growth of the mixed plots from 1997 to 2001 is, however, underestimated as the growth rate of the Norway spruces left after the birch thinning in 1997 probably increased there growth rate compared to the period 1993-1997 but this could hardly compensate totally for the large difference in uptake between the pure Norway spruce and the mixed treatment.

Conclusion

In this study no species induced effects on soil chemistry or base cation pools could be detected. This may depend on that there were to little birch admixture to develop any measurable changes. Climate effects and differences existing between the treatments already in 1984/86, could also, have obscured the possible species effects on soil chemistry. For making firm conclusions on the effects on soil chemistry of mixing birch in Norway spruce stands more studies under a longer time, preferable a rotation, and under more homogeneous conditions are needed.

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Habitat preferences and management of macrofungi on beech CWD in Danish forests

Morten Christensen* & Jacob Heilmann-Clausen**
*Royal Veterinary and Agricultural University, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark, telephone (+45)35282229, fax (+45)35282671, email moc@kvl.dk
**Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, DK-2970 Hørsholm, Denmark, telephone (+45)35282614, fax (+45)35282671, email jhc@kvl.dk

Abstract

Based on extensive field studies in beech forests in Denmark the authors give suggestions on practical management of macro-fungi associated with decaying beech trees. Red-listed species were found to have a strong preference for trees in intermediate to late stages of decay. On this basis it is concluded that a continuous supply of dead wood is essential for the maintenance of populations of these fungi.

Tree size was found to have less importance for red-listed species than expected. When equal cumulative volumes were sampled small trees were even found to host more species than larger trees. Similarly, larger branches (diam >10 cm) were found to be more species rich per volume unit than logs and snags. On this basis it is concluded that managed beech forests might serve as valuable stepping-stones for fungi associated with decaying wood, if larger volumes of logging waste is left for decay. Firewood collecting may appear to have more negative effects on bio-diversity than hitherto expected.

Keywords: Biodiversity, CWD, *Fagus sylvatica*, management, species richness

1. Introduction

An important goal in sustainable forestry is to preserve and restore native biodiversity (e.g. Lindenmayer et al. 2000). In this respect organisms associated with coarse woody debris (CWD) represent an important but problematic group (Samuelsson et al. 1994). The maintenance of these organisms requires that wood, representing a possible economic income, is left for natural decay. This could lead to the conclusion that CWD-associated biodiversity is best protected in forest reserves. Managed forests may, however, represent very important stepping-stones for exchange of genes and species between reserves, and their role in the management of CWD-associated bio-diversity cannot be neglected (e.g. Hansen et al. 1991). Accordingly, it is important to develop CWD management practices, which combine an optimal protection of biodiversity with minimal economic drawbacks.

In Fennoscandia, several studies have focussed on the effects of forestry on CWD-associated organisms (e.g. Andersson & Hytteborn 1992, Bader et al. 1995, Høiland & Bendiksen 1996). A few studies have even made practical suggestions on how to manage CWD in a sustainable way (e.g. Kruys & Jonsson 1999, Martikainen 2001).

In Northwest and Central Europe comparable studies are scarce (e.g. Smith 1997, Ódor & Standovár 2001, Schiegg 2001, Heilmann-Clausen & Christensen 2002), and few authors have to our knowledge published practical advices on the management of CWD, based on field data.

In this paper we investigate how decay phase and size variables affect the diversity of fruiting macrofungi on decaying beech trees. Such variables have earlier been shown to be the most important determinants of fungal diversity on decaying beech tress (Heilmann-Clausen & Christensen 2002). Further, we focus on the importance of various tree parts for diversity. In both cases we intend to develop practical suggestions for CWD management.

2. Material and methods

The data presented in this paper come from two different studies in unmanaged beech forests in Denmark; both carried out jointly by the authors. Study 1, including 110 trees distributed across nine localities, was carried out in 1997 and 1998. Study 2 was carried out in 2000 and 2001 and included 200 trees distributed across five localities, of which two were included in study 1. The twelve sites represent a range of the most common types of beech forests in Denmark.

The diameter at breast height (DBH) of the studied trees varied between 20 and 130 cm. In both studies the trees were selected to represent a range of size and decay classes on each locality. The trees, including snags and branches with a diameter exceeding 10 cm, were inventoried for fungal sporocarps at three separate occasions (late summer, mid-autumn and late autumn). In the second study the funga (fungal flora) was inventoried independently on the snag, the log (as useful for timber) and larger branches (diam >10 cm). Both studies include all groups of macromycetes (sporocarps larger than 1 mm), except fully resupinate corticoid fungi and inoperculate discomycetes with sporocarps regularly smaller than 10 mm.

A number of environmental variables were recorded for each tree, but only the role of decay stage (see Heilmann-Clausen 2001 for definitions) and tree size is covered in detail here.

Wood volumes were estimated using the formula for truncated cones: Volume (cm^3) = $\pi*(((d_1/2)^2 + (d_1/2)*(d_2/2) + (d_2/2)^2)/3)$, where d_1 is the diameter (cm) in one end of an actual wood piece and d_2 is the diameter (cm) in the other end. Diameters were measured at each end of all branches until the 10 cm size limit and in all branching points. The logs were measured at each end and at regular intervals, mostly 2 m, along the length.

In the data analysis the species were divided into two groups, viz. species occurring in the Danish Red Data Book (Stoltze & Pihl 1998), in the following referred to as **red-listed species**, and the remaining species, referred to as **non red-listed species**.

The Utilization Index (Ui) was adopted from Kruys et al. (1999), and is calculated as $Ui = \frac{nij / Ni}{xj / X}$, where *nij* represents the number of records of species group *i* in substrate group j, *Ni* represents the total number of records of species group *i*, xj represents the number of units in substrate group j and X represents the total number of units investigated. *Ui*>1 means that a substrate is utilized more than should be expected from its availability, whereas *Ui*<1 means that it is utilized less than expected.

Curves of cumulative species richness were calculated using PCord4 (McCune & Mefford 1999). Average species numbers and confidence limits were, for each subsample size, calculated on the basis of 500 random subsamples of the full data set. In order to compare equal volumes of different tree parts and tree size classes, average volumes were calculated within each defined group and used to distribute data points along X-axes in figures 2 and 4b.

3. Results

3.1. Relations to tree size and decay stage

348 fungal species were recorded in total, including 22 red-listed species. The number of observed species per tree varied between 1 and 46 with a mean of 17,9. Both overall species richness and richness of red-listed species was found to be significantly affected by DBH and decay stage (linear regression and ANOVA; $p<0,0005$).

According to substrate utilization values, red-listed species utilized trees in intermediate to late stages of decay (DC 3 and 4) more than should be expected, while they were utilizing newly dead trees (DC 1) much less than expected. Non red-listed species appear to be less selective (Fig 1a). With respect to DBH both species groups show a very uniform response, i.e. increasing *Ui* values with increasing diameter (Fig 1b). Despite this, small trees host more species per volume unit, and have significantly higher cumulative overall and red-listed species richness compared to medium or large trees, when equal volumes are sampled (Fig 2).

3.2. Tree part preferences

For 200 trees the snag, log and branches were investigated independently. 127 of the trees possessed snags, on which a total of 109 fungal species were recorded. All trees possessed logs, yielding a total of 209 species. Branches occurred on 178 trees, yielding a total of 214 species.

Both red-listed and non red-listed species were found to utilize branches more than logs and especially snags (Fig 3). When equal numbers of units are sampled, logs and branches have quite similar cumulative species richness, while snags are significantly poorer (Fig 4a). However, when equal volumes are sampled, branches have significantly higher cumulative species richness than logs (Fig 4b). The cumulative richness of red-listed species is not significantly different if equal volumes of logs and branches are sampled, but branches are significantly richer than snags for cumulative volumes exceeding $100m^3$ (result not shown).

4. Discussion

In accordance with several Fennoscandian studies involving coniferous logs (e.g. Renvall 1995, Høiland & Bendiksen 1996, Kruys et al. 1999), we found trees in intermediate to late stage of decay to be especially important for red-listed species (Fig 1a). The reasons behind this tendency are probably complex, but are likely to involve a dependency on certain decay pathways facilitating the establishment of red-listed species (Renvall 1995, Holmer et al. 1997, Heilmann-Clausen & Christensen 2002). The strong preference of red-listed species for trees in a rather narrow range of decay classes, highlights that CWD supply gaps (in time) are critical for these species, and may help explain their scarcity in managed forests and even their status as threatened, red-listed species (see also Stokland 2001).

We did not find large trees to be especially important for red-listed species (Figs 1b & 2). This contrasts with general assumptions and some results from Fennoscandia, supposing red-listed wood inhabiting cryptogams to be dependent on the presence of large diameter logs (e.g. Bader et al. 1995, Renvall 1995, Kruys et al. 1999). Actually, we found small trees to sustain red-listed species significantly better than large trees (Fig 2b).

In accordance with our results, Kruys & Jonsson (1999) found spruce logs with diameter <10 cm to host more cryptogam species per volume unit, than logs with diameter >10 cm. Their study included few red-listed species, but nevertheless they found it unlikely that small logs should be able to sustain red-listed species in a satisfying way. Schiegg (2001) found beech ‘limbs’ with diameter <10 cm to be richer in both common and red-listed saproxylic insect species, compared to beech trunks (diameter >20 cm). Both Kruys & Jonsson (1999) and Schiegg (2001) explained the higher relative species richness in fine woody debris (FWD) with the fact that equal volumes of FWD involve many more separate units, than CWD, and hence represents a more diverse habitat per volume unit. We find it likely that the same explanation applies in our case. Presumably, most of the red-listed species that we encountered are not dependent on features commonly accepted as characterizing large diameter CWD, such as stable temperature and humidity, longer decomposition time etc. (e.g. Renvall 1995, Schiegg 2001). It is, however, quite likely that factors characterizing large logs are important for some rare and red-listed fungi associated with beech CWD. It should therefore not be concluded that log diameter is completely irrelevant in management of wood associated fungi in beech forests.

The results regarding tree part preferences (Figs 3 & 4) show that snags are not optimal for protection of wood inhabiting fungi. But often snags are the only CWD left for natural decay in managed Danish beech forests, as they represent very limited economical values and are well-known to be valuable for hollow breeding birds (e.g. Samuelsson et al. 1994, Smith 1997). The result, that branches are more valuable for fungal bio-diversity than logs (Fig 4) corresponds well with the finding that small trees have higher cumulative species richness than larger trees (Fig 2). Accordingly retaining of whole trees for natural decay is not the only or optimal way of preserving wood inhabiting organisms in managed forests. The results also indicate that firewood collection, withdrawing small diameter CWD from the forests, is more critical for biodiversity than hitherto expected. Firewood collection has increased dramatically in Denmark since the 1970’s, and represents an important source of income in some forests.

5. Conclusion

Because our studies are based in unmanaged forests, caution must be taken when transforming our findings into practical suggestions for CWD management. Tree architecture, mortality patterns and size/age relations differ considerably between managed and unmanaged forests. This may affect fungi depending on special habitat types, infection strategies or old rather than large trees. It is not certain that CWD of smaller dimensions is as important for fungal bio-diversity in managed forests as in unmanaged forests. In near-natural forestry mimicking natural forest dynamics and structures differences are likely to be less evident. However, we find our results significant enough to support the following conclusion on CWD management in beech forests in Denmark and surrounding regions:

- A continuous supply of CWD is important for the maintenance of populations of wood inhabiting fungi in managed forests. Supply gaps may be critical, especially for red-listed species.
- The cumulative CWD volume left for decay is more important for fungal diversity than tree size and wood type. However, snags have rather limited value as habitat for fungi. Further, it must be emphasized that small CWD units decay faster than large CWD units, and accordingly they contribute to the cumulative wood volume for a shorter time.
- Logging waste may serve as an important resource for fungi in managed forest. The negative impact of firewood collection on bio-diversity may be underestimated, and should be investigated in more detail.

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Figure 1a

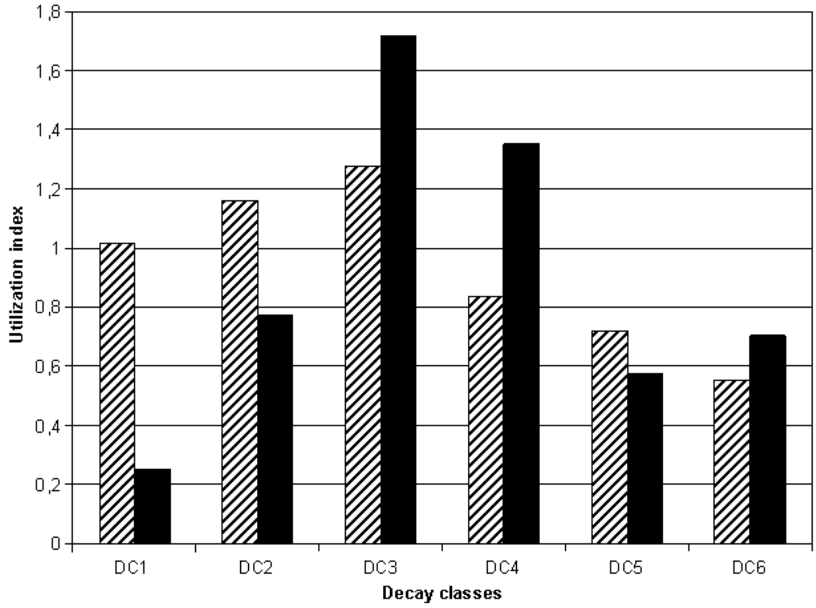

Figure 1b

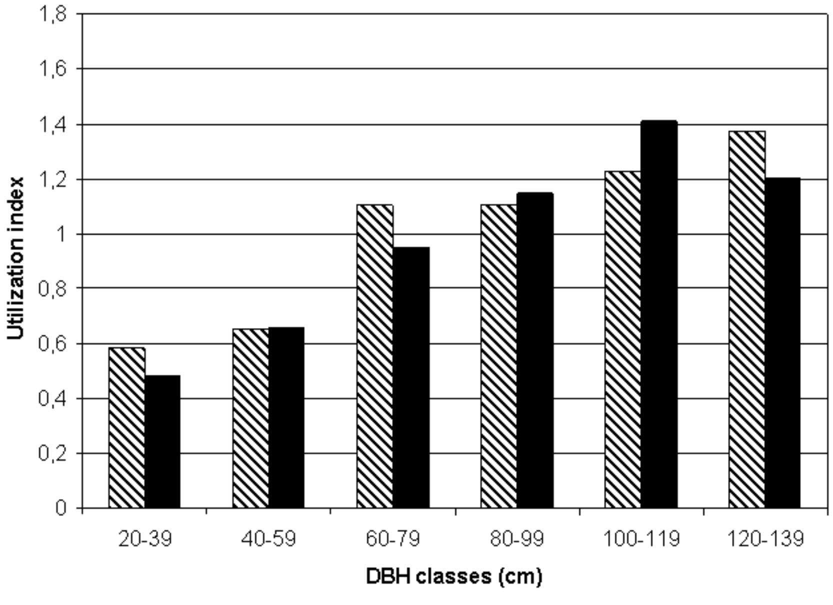

Fig 1. Utilization index values for non red-listed (hatched) and red-listed fungi (black) in relation to decay classes (DC1; newly dead, DC6; strongly decomposed – see Heilmann-Clausen 2001 for details)(a) and DBH classes (b).

Figure 2a

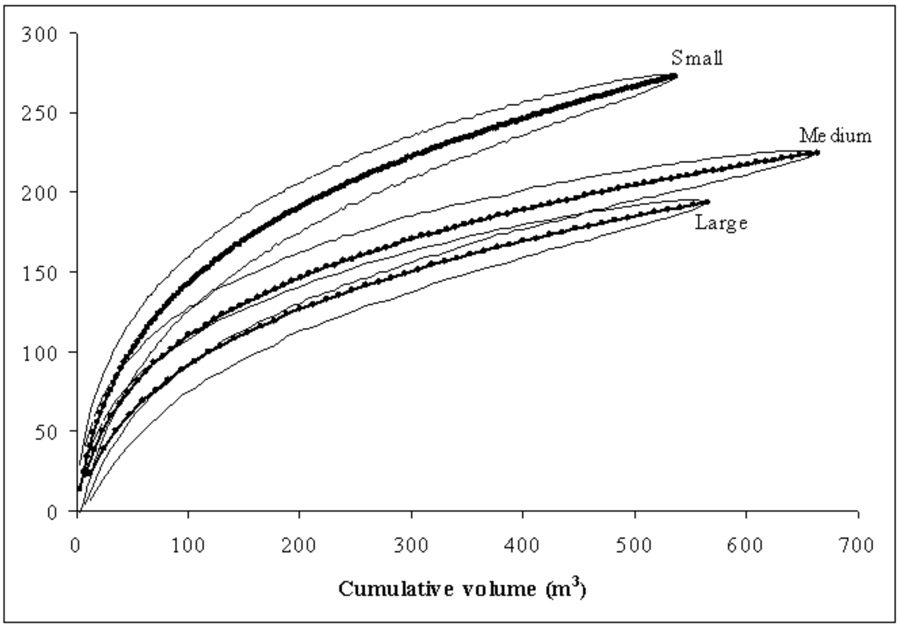

Figure 2b

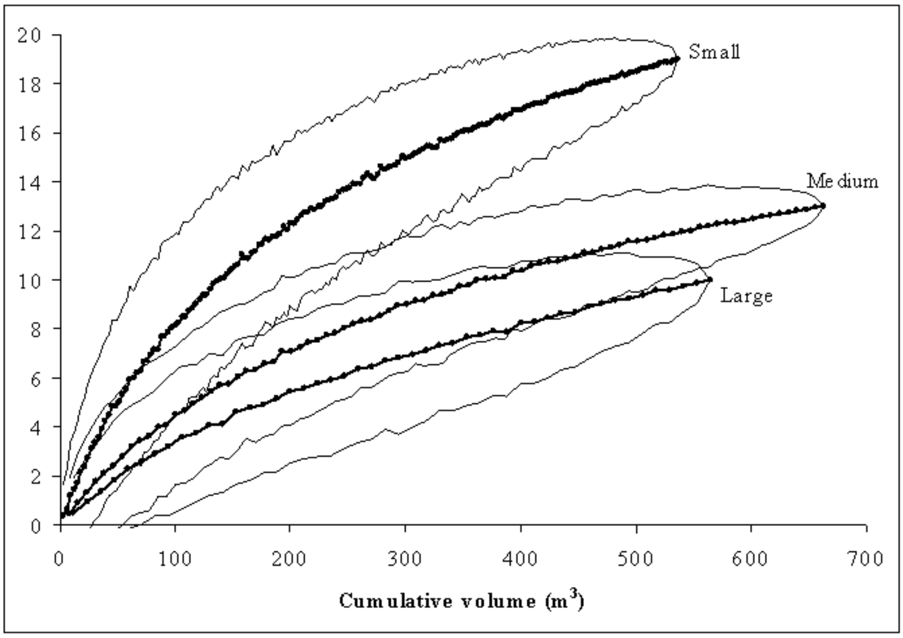

Fig 2. Cumulative total species richness (a) and cumulative richness of red-listed species (b) in relation to cumulative volume of small (DBH 20-84 cm), medium (DBH 85-109 cm) and large (DBH 110-130 cm) trees. Thin lines indicate 95% confidence intervals around the mean values for each size class.

Figure 3

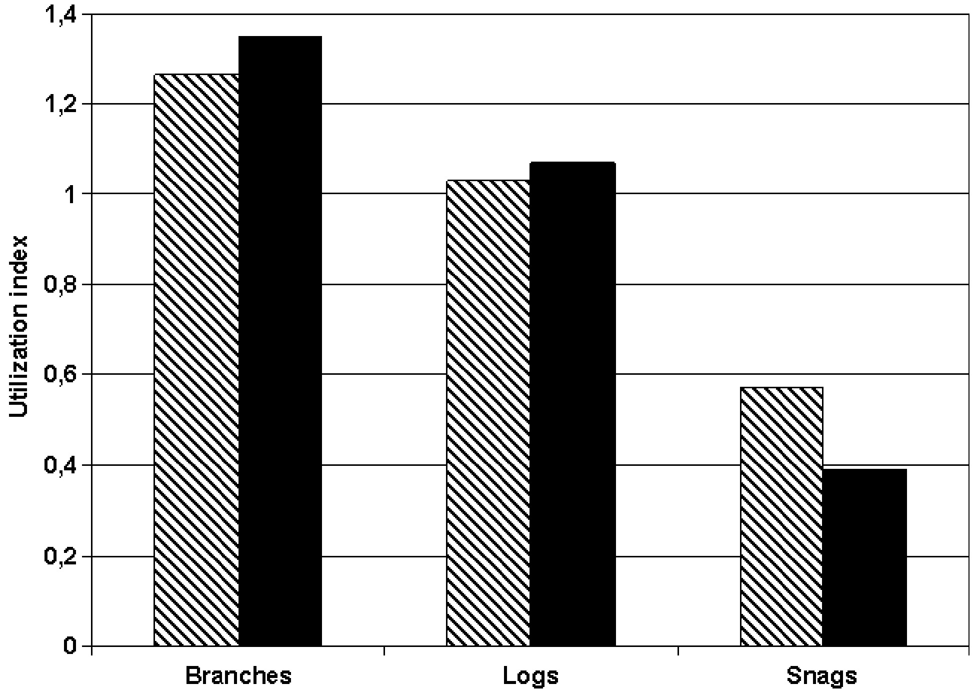

Fig 3. Utilization index values for non red-listed (hatched) and red-listed species (black) in relation to tree parts.

Figure 4a

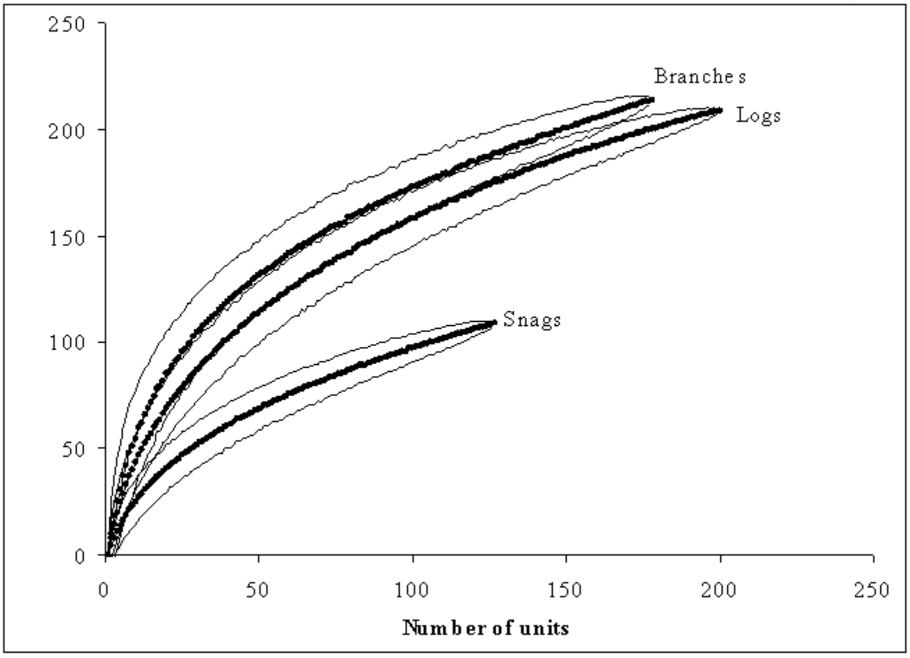

Figure 4b

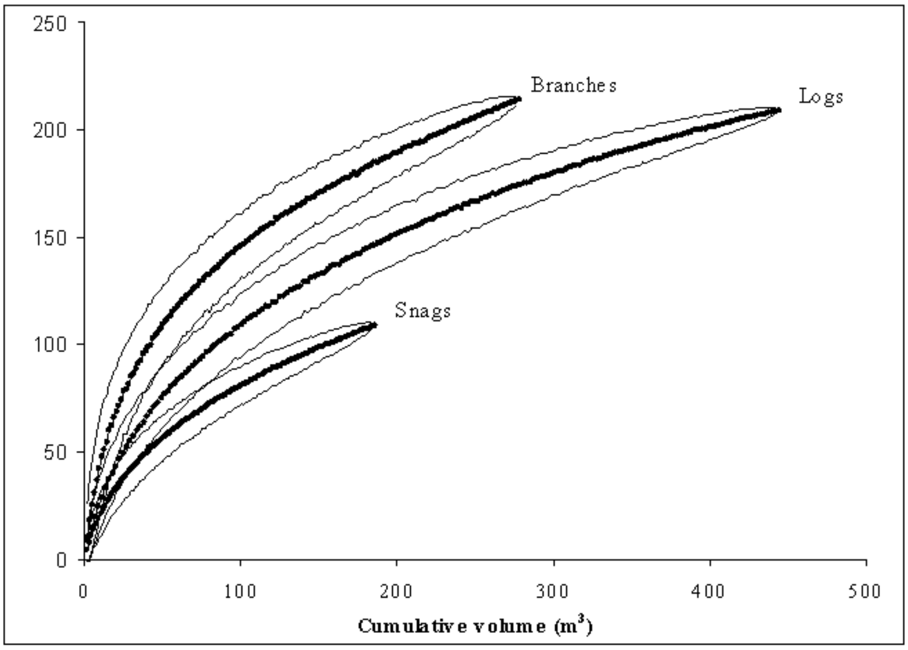

Fig 4. Cumulative total species richness in relation to number of units (a) and cumulative volume (b) of snags, logs and branches. Thin lines indicate 95% confidence intervals around the mean values for each tree part.

Effects of tree species in the riparian zone on brook-water quality

Lars Högbom[1], Sten Nordlund[1] , Per-Erik Lingdell[2], and Hans-Örjan Nohrstedt[1,3]

[1]SkogForsk, Uppsala Science Park, SE-751 83 Uppsala, e-mail: lars.hogbom@skogforsk.se

[2]Limnodata HB, Gunillbo 20C, SE-739 92 Skinnskatteberg

[3]Present adress: Formas, P.O.Box 1206, SE-111 82 Stockholm

Abstract

We have studied effects of tree species in the riparian zone on brook-water quality. The measurements included water chemistry, water temperature, bentic fauna composition and litter-fall into the brook. After four years of reference measurements a 10m wide zone was thinned. Along one of the brooks, all coniferous species were removed while all deciduous species were removed along the other. The reference measurements revealed that the two brooks were rather similar. Most of the studied ions, together with pH, colour and water temperature, showed a statistically significant correlation between the brooks, but other variables e.g. alkalinity, inorganic-N and total-P was not correlated. As for the bentic fauna, the two brooks were more similar to each other than to any other studied Swedish brook measured by the Sørensen similarity index. Up to now, three years after thinning, no detectable changes due to the change in tree species composition has occurred.

Introduction

A riparian forest could best be described as a forest growing in close vicinity of surface waters, and is more or less a permanent area for ground-water discharge (Bergkvist, 1999). The size of the discharge area depends to a large extent on precipitation, at storm events the discharge area increases in size. The water flow in a brook could be regarded as a mixture of water from two sources, rainwater and groundwater. The dynamic in the brook-water chemistry depends on residence time and movements I different soil horizons (which is affected by precipitation, temperature etc.) before reaching the brook (Grip & Rodhe, 1988). The discharge area could potentially have large effects on the runoff chemistry and thus affect the fauna in the brook. For example, studies on runoff-water chemistry following storm events have revealed that a substantial part of the acidity in the brook water originates from the moss-layers in the ground-water discharge area on both sides of the brook channel (Bishop, 1991).

Tree species composition could have a number of potential effects on life in and in the vicinity of the brook (Edenius, 1995). Factors like, litter quality, light, temperature and differences in snow cover patterns could be of vital importance. Deciduous trees are considered to be less acidifying than coniferous species (Liljelund et at, 1986). Since litter falling into the brook is the main food source for the bentic organisms, the quality and amount of litter could be of fundamental importance for the bentic life forms.

Our hypothesis, not previously tested experimentally, is that a riparian forest comprising mainly deciduous tree species, should result in 1) higher pH and 2) increased concentrations of base cations in the water, than a pure coniferous riparian forest, due to direct effects on water via litter input and indirect effects via the soil. Such an influence on water chemistry may by positive for species diversity in the brook. Earlier surveys have indicated that this might be the case (Lingdell & Engblom, 1995). However, in the surveys, other factors (e.g. geology) could interact with tree species composition, thus indirectly affecting the results. The aim of this paper is to form a baseline and a background for future measurements.

Material and methods

At two brooks in the vicinity of Kungsberget (60º45'N; 16º24'E) central Sweden, various aspects of water quality were measured. The two brooks are more or less running in parallel along a weak slope facing NE. The two brooks are 200 m long above the sampling point and are running 200-250 m apart. Each catchment is approx. 4-5 ha. The brooks run through a 15-year-old Scots pine (*Pinus sylvestris L.*) forest with a rather large spontaneous regeneration of birch (*Betula* spp). Reference measurements started in May 1996 and continued until the end of 1998. In late October 1998, a c. 5 m wide strip was thinned at both sides of each brook using two strategies. The thinning was made upstream from the sampling point and along the whole length of the brooks. Along one of the brooks (BIRCH), all coniferous trees were removed and along the other brook (PINE) all deciduous species were removed. Before the species selective thinning started the stand at the BIRCH brook contained 640 conifers ha^{-1} and 1170 birch trees ha^{-1} (calculated as means of 10 test plots with a radius of 5 m close to the brook) and the PINE brook 660 conifers ha^{-1} and 624 birch trees ha^{-1}. The average tree diameter was for the BIRCH brook, 10 cm and 7 cm at breast height for pine and birch trees respectively, and for the PINE brook, 8 cm and 6 cm at breast height for pine and birch trees respectively.

Water samples were taken bimonthly from snowmelt until end of May, once a month during June-August, and again bimonthly from September and onwards until the brooks were frozen (normally in November). The samples were sent frozen and they were analysed by KM Lab AB in Uppsala (1996-97) and by IVL (1998-2000). During the period 1996-1997 brook water was analysed for the following constituents: tot-Al, Ca^{2+}, SO_4^{2-}, alkalinity, pH and colour. For 1998 and onwards the analyses were extended to include the following variables in addition to those mentioned: Mg^{2+}, Na^+, K^+, Mn^{2+}, Fe^{2+}, SO_4^{2-}, Cl^-, NO_3-N, NH_4-N, Kjeldahl-N, total-P and conductivity. The brook-water temperatures were measured manually at each brook-water sampling event, a few cm below surface.

On regular intervals along both brooks, 10 litter collectors were installed, five on each side and as close as possible to the channel. The area of each circular collector was 0.25 m^2. The collectors were established in the field in April each year. At the end of each season in October, after the main leaf litterfall of the birch and pine, the collectors were emptied and the content was separated manually into needle and leaf litter fractions, before drying (24h 50ºC) and subsequent weighing.

Investigations of the faunal composition at the two brooks were made in May 1997 and May 1998. The surveys were made according to a modification of method M42 (Anon., 1996). In short, three bentic samples were taken every 5:th meter, along a 50 m long section of each brook. The samples were taken with a collector (16 cm in diameter) with a 1-mm mesh size. Each sample contained the material emanating from a 0.2 m^2 large area of the brook bottom during a 5 sec. disturbance. The method does not give quantitative results but a good picture of the proportions between the different taxas.

Table 1. *Mean values ± 1 s.e and R^2 between ions concentrations and other variables in the two brooks before the start of selective thinning. The significance of the correlation is given as ^{ns} = not significant * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$. Values within parenthesis are number of observations.*

Variable sampling period	**BIRCH Average±1 s.e (n)**	**PINE Average±1 s.e (n)**	**Correlation R^2 (d.f)**
pH	5.97 ± 0.10 (27)	5.99 ± 0.06 (27)	0.31* (25)
Alkalinity (meq l^{-1})	0.07 ± 0.04 (27)	0.04 ± 0.01 (27)	0.25^{ns}
Conductivity (mS m^{-1})	6.16 ± 2.55 (9)	4.05 ± 0.91 (9)	$0.02^{n.s}$ (7)
Ca (mg l^{-1})	3.29 ± 0.49 (27)	3.80 ± 0.29 (27)	0.62*** (25)
Mg (mg l^{-1})	0.46 ± 0.03 (9)	0.68 ± 0.05 (9)	0.79* (7)
Na (mg l^{-1})	1.41 ± 0.04 (9)	1.74 ± 0.07 (9)	0.77* (7)
K (mg l^{-1})	0.28 ± 0.06 (9))	0.28 ± 0.03 (9)	0.72* (7)
Mn (mg l^{-1})	Not detectable	Not detectable	Not analysed
Fe (mg l^{-1})	0.21 ± 0.04 (9))	0.29 ± 0.04 (9)	0.97*** (7)
SO_4 – S (mg l^{-1})	2.42 ± 0.53 (27)	2.61 ± 0.35 (27)	0.46** (25)
Cl (mg l^{-1})	0.92 ± 0.10 (9)	1.03 ± 0.06 (9)	0.87** (7)
NO_3 – N (mg l^{-1})	0.02 ± 0.01 (9)	0.03 ± 0.01 (9)	0.36^{ns} (7)
NH_4 – N (mg l^{-1})	Not detectable	Not detectable	Not analysed
Kjeldal – N (mg l^{-1})	0.27 ± 0.05 (9)	0.34 ± 0.05 (9)	0.84** (7)
Tot-P (mg l^{-1})	0.01 ± 0.00 (9)	0.01 ± 0.00 (9)	0.02^{ns}(7)
Al (mg l^{-1})	0.13 ± 0.02 (27)	0.20 ± 0.02 (27)	0.65*** (25)
Colour (mg Pt l^{-1})	42.59 ± 4.45 (27)	70.96 ± 6.47 (27)	0.41** (25)

Results and Discussion

For the constituents that were measured from 1996 and onwards until thinning, i.e. pH (H^+), alkalinity, Ca, SO_4, and Al (n = 27 in all cases) there was a statistically significant correlation between the two brooks, except for alkalinity (Table 1), before the treatment. Of the constituents that were introduced in 1998, Mg, Na, K, Fe, Cl and Kjeldal-N (n = 9 in all cases) were significantly correlated, while conductivity, Mn, NO_3-N, NH_4-N and total-P, were not correlated between the two brooks (Table 1). The concentrations of Mn, NO_3-N, NH_4-N and total-P were extremely low and for most sampling events under the detection limit given for each constituent, respectively.

During the first year after treatment (1999), no obvious changes because of the species specific thinning appeared in steam-water concentrations (Fig. 1). Two of the variables, alkalinity and conductivity, that had a non-significant correlation before treatment now showed significant correlations between the two brooks (Table 1), while the opposite was true for Fe. The regressions between the two brooks before and after treatment is still 3 years after thinning best described by a common regression line, rather then separate lines (Fig. 2)

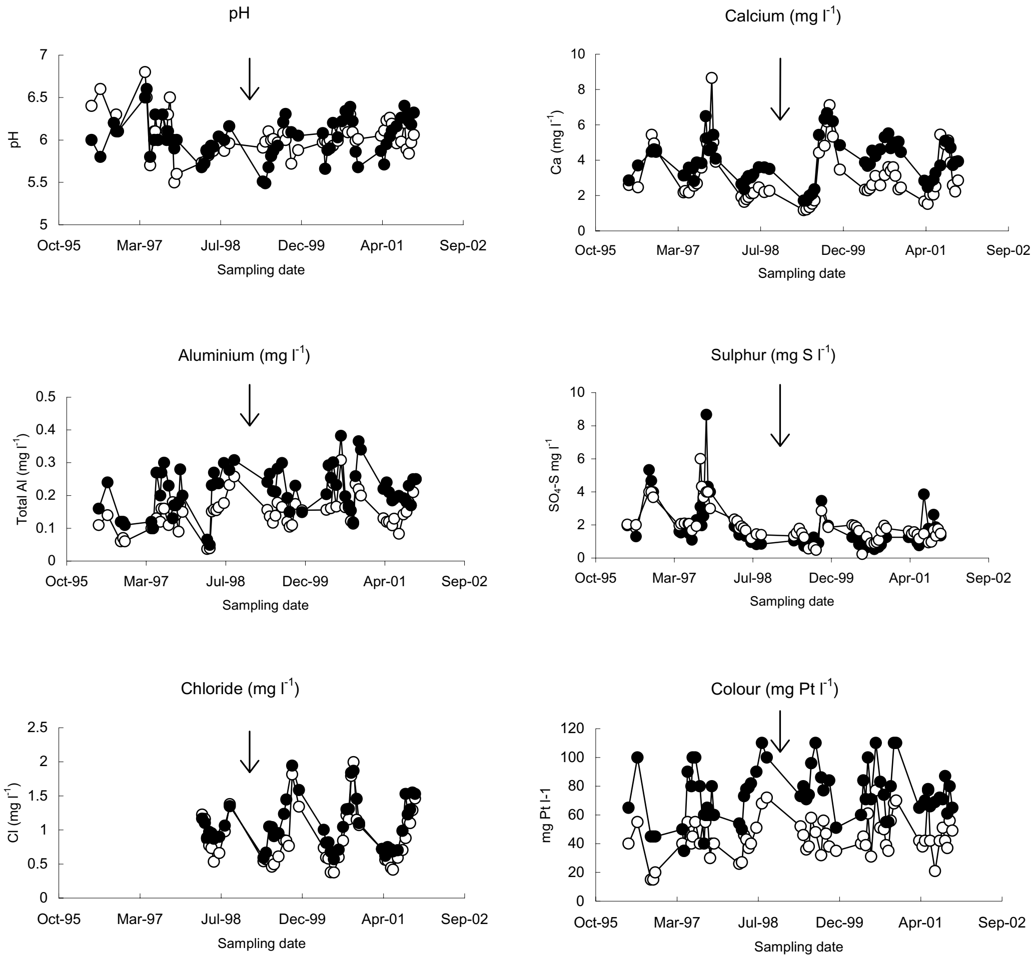

Figure 1. Time series of concentrations of a) pH, b) Ca^{2+} (mg l^{-1}), c) total-Al (mg l^{-1}), d) SO_4^{2-} (mg S l^{-1}), e) Cl mg l^{-1} and d colour (mg Pt l^{-1}). BIRCH (○) and PINE (●). Arrows indicates time for selective thinning.

There was no clear difference between the two brooks as regards the water temperature before the thinning (data not shown). A regression analysis of data from the two brooks showed that the water temperatures were significantly correlated during this period ($R^2 = 0.99$, $p<0.001$, n = 20). The first year after the thinning revealed no changes in this pattern ($R^2=0.98$, $p < 0.001$, n = 12).

Before thinning leaf litter production along the BIRCH brook was 40 g m^{-2} higher that the PINE brook. The production of needle litter was also higher at the BIRCH brook. The thinning has strongly affected the litter production along the two brooks (Table 2). This will obviously have effects on the bentic fauna in the future since many of these species are depending on the litter for their survival. But up to now these changes have not affected the species composition.

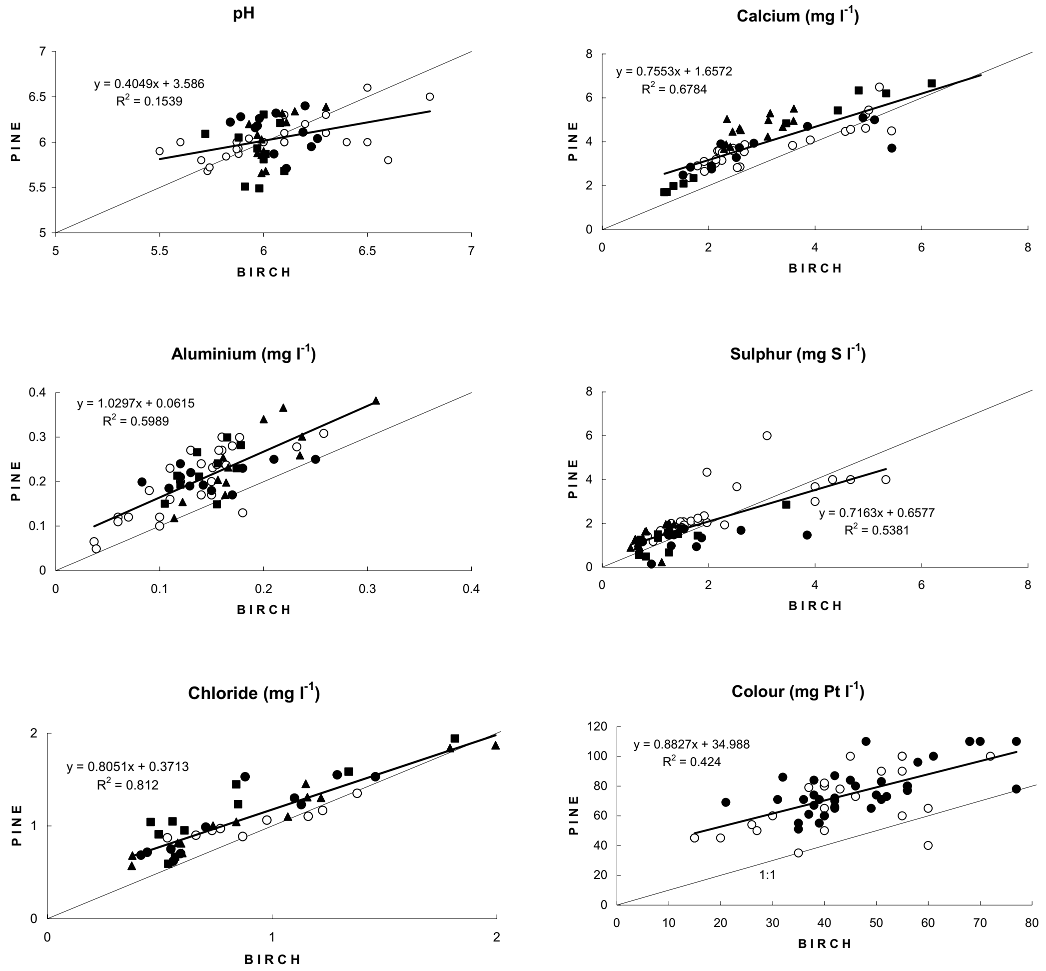

Figure 2. *Correlation between some of the studied parameters before and after the species specific thinning a) pH, b) Ca^{2+} (mg l^{-1}), c) total-Al (mg l^{-1}), d) SO_4^{2-} (mg S l^{-1}), e) Cl mg l^{-1} and d colour (mg Pt l^{-1}). The thin solid line represents the 1:1 line while the bold line represents the regression line for the whole material. ○ = before thinning, ■ = 1999, ▲ = 2000 and ● = 2001.*

Table 2. *Amounts of leaf and needle litter collected in the riparian zones along the two studied brooks (g* m^{-2}*), in 1997 and 1998 (before thinning) and 1999 (the year following thinning). The material was sampled between April and October each year. The values are mean values ± 1 s.e, n=10.*

	BIRCH				**PINE**			
	leaf litter		needle litter		leaf litter		needle litter	
Year	average ± 1 s.e.	% of total litter	average ± 1 s.e.	% of total litter	average ± 1 s.e.	% of total litter	average ± 1 s.e.	% of total litter
1997	105.36±5.97	73	38.75±6.77	27	67.42±5.58	84	12.44±2.06	16
1998	147.40±5.97	76	47.18±6.31	24	107.36±5.7	83	21.60±2.33	17
1999	102.76±5.94	98	2.06±0.35	2	2.24±0.20	8	25.58±3.28	92
2000	211.97±21.5	99	1.94±0.67	1	3.16±0.75	7	44.84±14.9	93
2001	167.72±6.51	99	6.61±0.69	1	2.50±0.23	1	48.88±5.71	99

A brief summary of the faunal composition of the two brooks is given in Table 3 (more describing data could be produced on request). The composition of the fauna at two brooks showed a high degree of similarity although declining, (Sørensens similarity index was 77.3 %, 71.4 %, 67 % and 62 %, for 1997, 1998, 2000 and 2001, respectively). Further estimated will be done in order to see if this declining trend in similarity that possibly could be discerned is true or not. The two brooks were more similar to each other than to any other brook in the Swedish brook-faunal database (REF). The between year variation for the BIRCH brook had a similarity index (Sørensens index) of 78.3 % and the PINE brook had a similarity index of 75%. The pre-treatment study of fauna will provide baseline data for the further analysis on effects on brook fauna of tree species composition close the brook channel.

Table 3*. Faunal composition in the two brooks, list of found taxas. A more detailed list could be produced upon request*

	BIRCH				**PINE**			
Taxa	**1997**	**1998**	**2000**	**2001**	**1997**	**1998**	**2000**	**2001**
Tricladia	-	-	1	11	1	1	-	13
Oligochaeta	97	32	31	151	43	25	19	2
Nematoda	50	73	63	659	16	171	18	30
Copepoda	2	2	2	62	18	24	-	-
Isopoda	21	5	89	69	17	-	41	-
Ostracoda	4	24	26	46	-	223	11	73
Ephemenoptera	-	1	-	91	-	1	-	-
Plecoptera	312	796	325	-	603	1802	364	-
Hemiptera	-	-	1		-	-		-
Coleoptera	1	6	11		2	3	-	-
Tricoptera	6	29	5	-	6	37	-	13
Diptera	189	743	102	-	229	1945	145	277
Acari	8	2	-	-	12	52		26
Gastopoda	-	-	2	-	-	50	-	
Bivalvia	194	55	147	-	16	7	11	

Conclusions

The two brooks could be regarded to be rather similar, regarding most of studied parameters. Pre-thinning brook-water chemistry revealed no major difference as regards the studied constituents between the two brooks. Further, no apparent differences were found in the bentic species composition. As for the first year following treatment no treatment-induced changes in brook water chemistry could be detected. However, a rapid change of the studied parameters was not expected, since these induced changes would probably take time (3-10 years) to be recorded. As judged from the pre-thinning base-line data the two brooks are well suited for further analysis. And further studies during the coming years will probably reveal is the species composition will have any effect on the bentic fauna and brook water chemistry.

Acknowledgement

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Litterfall in beech stands as a source for elements - an example of a 5 years study on monitoring plots in Ojców National Park and Forest Experimental Station in Krynica - Southern Poland

Stanisław Małek Ph.D. Eng., Dep. of Forest Ecology, Forest Faculty
Agricultural University of Cracow,
Al. 29-go Listopada 46, PL-31-425 Cracow, Poland
e-mail: rlmalek@cyf-kr.edu.pl

Abstract

This article presents the results of five 5 years studies (1996-2000) on changes in the amount of elements deposited to the soil surface with the litterfall in beech stands of different fertility (Ojców National Park and the Forest Experimental Station in Krynica). The sites are exposed to different amounts of industrial emissions. On each site three subplots were established, with 16 traps for litterfall with the inlet surface of 0.1697 m^3 installed in each of them. The litter was collected every 15-30 days, dried and sorted into leaves, seed coats, seeds, shoots and others. The total content of C, N, S, Na, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb and Cr was determined.

The average amount of litterfall in the *Dentario glandulosae-Fagetum* association - the poor variant (Ojców) varied from a minimum of 2313 kg/ha (1997) to a maximum of 3628 kg/ha (2000). In the fertile variant of Ojców the variation in litterfall was from 2828 kg/ha (1998) to 4612 kg/ha (2000). On plots in Krynica – typical variant - the amount of litterfall increased continuously from 2485 kg/ha (1996) to 3141 kg/ha (2000). Leaves constituted the greatest part of the litterfall (over 90 %). Leaves constituted the main source for mineral elements (from 72,7 to 96,9 %). The second biggest fraction, which yielded considerable amounts of elements were shoots: above 4 % for e.g. C, Zn, Cr, Cu, Fe and Pb. The fraction "others" yielded above 4 % for Cu, Na, Fe and Pb, while seed covers yielded Cr above 9 % in Ojców and above 3 % in Krynica. The smallest amount of seeds yielded below 1 % except for K in the fertile variant and N and Ca in the typical variant in Krynica.

The amounts of elements deposited to the soil with litterfall did not correspond to the beech stand uptake for Mg, Ca, K and N neither in Krynica, nor in Ojców. The litterfall was the second main source for elements of the beech stands next after soil, and more important than wet and dry deposition.

Introduction

In a forest ecosystem the complex nutrient cycle processes are continuous with absorption of nutrients from the soil and return in the form of organic litterfall. The litterfall is one of the most important fluxes in the nutrient cycle in forest ecosystems. It is composed of every aboveground plant organ or its parts deposited on the ground. The study of litterfall allows for determination of the amount of substances returned to the soil (Waring and Schlesinger 1985).

The trees take up necessary nutrients from the soil, including old litter, and use part of the nutrients for the build-up of their woody parts, and dispatch yearly a great amount to the soil as litterfall. According to the data by Mayer-Krapolla (1958), an individual beech tree accumulate on an average 1,54 kg of N, 0.17 kg of P, 1.1 kg of K, 2.97 kg of Ca, and 0.45 kg of Mg in order to produce 1 m^3 of timber. The demand of beech for N is greater than for spruce or fir, but smaller than for pine. As far as P, K, Mg, and especially Ca are concerned, beech also has a greater demand than the above-given species. This data does not include the demand for elements in the production of the foliage that varies for different species.

A regular and efficient nutrient cycle should meet the demands of the tree stand even if the content of nutrients in the soil is minimal. A soil fertilisation process occurs when the elements taken from deeper soil layers return with the litterfall to the surface layer. Especially important is the enrichment of the soil in N, as well as the elements Ca, Mg, K, Na, and S. The litterfall has substantial importance as an organic fertiliser, and is composed of almost optimal amounts of nutrients that are needed for the development of new generations of tree stands.

This study presents a portion of the scientific program for monitoring plots in southern Poland realized under the grant project “Monitoring of processes occurring in beech stands under changing conditions of the natural environment, with the examples of Ojców National Park and Forest Experimental Station in Krynica” (KBN 5 P06M 007 11), and the SUFOR-program in South Sweden. The study has been aimed at monitoring the organic fall, changes in the number and composition of tree seeds, natural regeneration, qualitative and quantitative analysis of precipitation and the chemistry of ground water, selected parameters of climate and air quality (concentrations of SO_2 and NO_2), following ICP Forest Manual (1998).

Areas of Southern Poland are among the most polluted areas of Central Europe. However, owing to the land relief and directions of local winds part of the pollutants goes outside the immediate emission area (Grodzińska *et al.,* 1995). The area of Ojców National Park has been acknowledged to be the most polluted with industrial emission in Poland, whereas Krynica is not (Małek *et al.,* 1998a,b,c, Małek 2001).

The basic goal of the studies made on the "Mt Chełmowa Góra" plot, located in Ojców National Park, and on Mt Jaworzyna Krynicka (Forest Experimental Station in Krynica) was to determine the amounts of elements supplied by the tree stand through the litterfall to the surface layer of the soil, in different fertility conditions of the *Dentario glandulosae-Fagetum* association within 1996-2000.

Material and methods

Field studies were made in Ojców National Park in "Mt Chełmowa Góra" study plot (compartment no. 30, section "a"). Six study plots of 0.16 ha each (40m x 40m) were established in two fertility variants. Each variant was composed of three subsequent plots (poor fertility variant - plots I, II, and III at the elevation of 430 m a.s.l., and a more fertile fertility variant - plots IV, V, and VI at the elevation of 350 m a.s.l.).

Plots I, II, and III were located at the summit part of Mt Chełmowa Góra in the *Dentario glandulosae-Fagetum typicum* association. The field vegetation of the low productive variant was dominated by *Asperula odorata* L, which occupies rendzina soils on lime stone (Greszta and Małek 2000). In a highly compact tree stand (average density 90%) from 80 to 100 years old *Fagus sylvatica* L. was absolutely dominant, wood biomass was 554,9 m^3/ha with 394 trees/ha and yearly increment was 20,7 m^3/ha (Małek, *et al*. 2000a,b).

Plots IV, V, and VI were located at the bottom of the Sąspowska Valley in the *Dentario glandulosae-Fagetum typicum* association, where the field vegetation was dominated by

Dentaria glandulosa W.K. , also on rendzina soils on lime stone (Greszta and Małek 2000). In a highly compact stand (average density 90%), 80 to 100 years old *Fagus sylvatica* L. with a casual admixture of *Acer pseudoplatanus* L. were dominant. The wood biomass was 498 m^3/ha with 364trees/ha and the yearly increment 17,1 m^3/ha (Małek *et al.* 2000a,b).

Plots VII, VIII and IX were located at Mt Jaworzyna Krynicka at 900 m a.s.l., in the Jaworzyna Forest district in Forest Experimental Station in Krynica, compartment no. 56, section c; in *Dentario glandulosae-Fagetum typicum* version with *Rubus hirtus* dominating on a brown acid soil on magurskie sandstone (Greszta and Małek 2000). In the highly compact tree stand (average density 90%) from 80 to 100 years old *Fagus sylvatica* L. were dominant. The wood biomass was 558,4 m^3/ha with 557 trees/ha, and the yearly increment 23,3 m^3/ha (Małek *et al*. 2000a,b).

On each study plot (plots I to IX) on January 01, 1996 16 litterfall collectors were installed, with inlets 1 meter above ground, and with a collecting surface of 0.17 square meter each. Sampling was performed each 2 or 4 weeks. (Małek *et al*. 1998 a, b, c, 2000 a, c, 2001).

All litterfall was dried at 65°C. Next the study material was separated into fractions: leaves, seed coats, seeds, shoots, and other parts (to this last fraction were assigned smaller amounts of sycamore leaves and seeds, beech inflorescence, leaf bud scales, bark) and tiny invertebrates. The dried plant fractions were weighed and then crumbled. A "combined sample" from 16 catchers was prepared separately for each fraction of the litterfall, study plot, and sampling date for the analysis. The following element concentrations were determined: C, N and S with LECO CNS 2000 and Na, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb, and Cr after wet digestion in a mixture of HNO_3 and $HClO_4$ in the 1:4 ratio with the use of the Varian Spectr AA-20 atomic absorption spectrophotometer (Lityński *et al.* 1976).

Results of studies and discussion

Studies on the amount of litterfall in the beech stands have been made for over one hundred years. Ebermayer (1876)(cit. Nielsen 1977) reported that the beech stand of 60 to 90 years of age yields 3370 kg/ha of litterfall over one year, while a 90 years old and older beech stand yields 3270 kg/ha of litterfall. Up-to-date studies report that the amount of annual litterfall reaches 1570 – 2860 kg/ha (Bonnevie-Svendsen and Gjelms 1957), 2000 – 2700 kg/ha (Chalupa 1961), about 2600 kg/ha (Donov 1964), about 2900 kg/ha (Myczkowski 1967) and 3106 – 5366 kg/ha (Nielsen 1977) and 5700 kg/ha (Nihlgard 1972, including also big branches). In 60 to 120 years old beech stands in Germany the annual organic litterfall was from 3000 to 3400 kg/ha (Heller 1971). The average amount of litterfall of the poor variant (Ojców) varied from 2816 kg/ha (in 1996) through 2313 kg/ha (minimum in 1997) to 2571 kg/ha (1998), 3112 kg/ha (1999) and 3628 kg/ha (2000). In a fertile variant (Ojców) the variation in the litterfall was from 3244 kg/ha (1996) to 3237 kg/ha (1997), 2828 kg/ha (1998), 3646 kg/ha (1999), and 4612 kg/ha (2000). In plots in Krynica the amount of the litterfall increased systematically from 2485 kg/ha (1996) to 2780 kg/ha (1997) and 2856 kg/ha (1998). Then it decreased to 2607 kg/ha (1999) and increased again up to 3141 kg/ha (2000) (Tab.1, 2,3).

Studies made over the years 1967 – 75 in beech stands (90 years of age) in Denmark gave a wide spectrum of results demonstrating the variability in the amounts of the total litterfall and its fractions over seven years that followed (Nielsen 1977). The results obtained for the total litterfall were from 3106 kg/ha to 5366 kg/ha. The mean values were: leaves 2789 kg/ha, seed coats 468 kg/ha, seeds 118 kg/ha, shoots and twigs 834 kg/ha, and others (inflorescence, buds) 408 kg/ha. The largest amount of the litterfall was in the mast year when the proportion of leaves in the litterfall was 2498 kg/ha, seeds 535 kg/ha, seed coats 1425 kg/ha, shoots and twigs 436 kg/ha, and remaining fractions (buds, inflorescence) 472 kg/ha. The smallest amount of litterfall was produced by the stand after the seed year, when the proportion of leaves was 2429 kg/ha while the remaining fractions (buds, inflorescence, seeds, seed coats, and shoots) were 677 kg/ha (Nielsen 1977).

Table 1. Total mass of elements (in kg/ha) reaching the surface soil layer with different litterfall fractions (L- leaves, Sc – seed coats, S - seeds, Sh - shoots, O - others) on Dentario glandulosae-Fagetum association in the poor variant of Ojców National Park averaging 1996-2000.

Year	**Fraction**	**Dry weight**	**S**	**N**	**C**	**Na**	**K**	**Ca**	**Mg**	**Fe**	**Mn**	**Zn**	**Cu**	**Pb**	**Cr**
1996	L	2520,58	3,343	23,233	971,057	0,237	5,534	66,996	4,366	0,647	0,475	0,268	0,018	0,051	0,005
1996	Sc	162,52	0,051	0,372	45,205	0,005	0,386	0,333	0,033	0,023	0,004	0,003	0,001	0,001	0,002
1996	S	25,49	0,018	0,684	8,811	0,000	0,125	0,146	0,033	0,001	0,002	0,001	0,000	0,000	0,000
1996	Sh	107,41	0,049	0,950	36,365	0,006	0,075	2,058	0,030	0,008	0,002	0,006	0,001	0,002	0,000
1996	**Sum**	**2816,00**	**3,461**	**25,239**	**1061,438**	**0,248**	**6,120**	**69,533**	**4,462**	**0,679**	**0,483**	**0,278**	**0,020**	**0,054**	**0,007**
1997	L	2130,70	3,185	21,824	779,465	0,278	4,846	43,046	1,776	0,272	0,331	0,159	0,014	0,019	0,000
1997	Sh	161,77	0,074	1,362	62,287	0,009	0,119	3,182	0,043	0,023	0,007	0,016	0,002	0,005	0,000
1997	O	20,07	0,026	0,325	6,358	0,004	0,022	1,051	0,016	0,079	0,004	0,005	0,000	0,002	0,000
1997	**Sum**	**2312,53**	**3,285**	**23,511**	**848,110**	**0,291**	**4,988**	**47,279**	**1,835**	**0,374**	**0,342**	**0,180**	**0,016**	**0,026**	**0,000**
1998	**Sum**	**2570,57**	**2,954**	**26,208**	**1047,315**	**0,146**	**5,934**	**48,016**	**2,776**	**0,580**	**0,356**	**0,164**	**0,019**	**0,034**	**0,001**
1999	L	2904,46	2,373	23,450	1437,580	0,133	7,625	58,406	2,987	0,575	0,454	0,151	0,015	0,059	0,004
1999	Sc	56,53	0,017	0,242	28,661	0,002	0,391	0,174	0,017	0,005	0,001	0,001	0,000	0,000	0,000
1999	S	18,62	0,018	0,437	10,148	0,000	0,096	0,157	0,024	0,001	0,001	0,000	0,000	0,000	0,000
1999	Sh	74,02	0,031	0,518	39,874	0,004	0,078	0,840	0,030	0,010	0,003	0,004	0,006	0,000	0,000
1999	O	58,06	0,059	0,750	28,477	0,031	0,108	1,268	0,041	0,054	0,007	0,008	0,000	0,002	0,000
1999	**Sum**	**3111,69**	**2,498**	**25,397**	**1544,740**	**0,170**	**8,298**	**60,845**	**3,099**	**0,645**	**0,466**	**0,164**	**0,021**	**0,061**	**0,004**
2000	L	3072,60	2,421	21,016	1573,625	0,107	7,613	66,205	3,683	0,721	0,485	0,151	0,013	0,035	0,008
2000	Sc	15,12	0,002	0,021	3,737	0,000	0,038	0,018	0,002	0,001	0,000	0,000	0,000	0,000	0,000
2000	S	3,35	0,002	0,052	1,830	0,000	0,014	0,024	0,004	0,000	0,000	0,000	0,000	0,000	0,000
2000	Sh	236,50	0,094	1,193	116,068	0,006	0,204	2,847	0,056	0,024	0,006	0,015	0,001	0,003	0,001
2000	O	300,27	0,153	1,918	150,254	0,009	0,385	3,134	0,172	0,150	0,019	0,016	0,003	0,010	0,001
2000	**Sum**	**3627,85**	**2,672**	**24,200**	**1845,514**	**0,122**	**8,254**	**72,228**	**3,917**	**0,896**	**0,510**	**0,182**	**0,017**	**0,048**	**0,010**

Table 2. Total mass of elements (in kg/ha) reaching the surface soil layer with different litterfall fractions (L- leaves, Sc – seed coats, S - seeds, Sh - shoots, O - others) on Dentario glandulosae-Fagetum association in the fertile variant of Ojców National Park averaging 1996-2000.

Year	**Fraction**	**Dry weight**	**S**	**N**	**C**	**Na**	**K**	**Ca**	**Mg**	**Fe**	**Mn**	**Zn**	**Cu**	**Pb**	**Cr**
1996	L	2885,86	3,464	26,944	1125,885	0,265	6,219	80,082	5,341	0,714	0,390	0,269	0,021	0,052	0,003
1996	Sc	289,84	0,085	0,79	94,112	0,013	0,645	0,649	0,064	0,034	0,007	0,007	0,001	0,001	0,003
1996	S	35,09	0,019	0,779	12,245	0,001	0,168	0,164	0,044	0,002	0,001	0,001	0,000	0,000	0,000
1996	Sh	33,68	0,014	0,198	13,560	0,001	0,002	0,480	0,003	0,003	0,001	0,003	0,000	0,001	0,000
1996	**Sum**	**3244,47**	**3,512**	**28,711**	**1245,802**	**0,280**	**7,034**	**81,375**	**5,452**	**0,753**	**0,399**	**0,280**	**0,022**	**0,054**	**0,006**
1997	L	2968,34	3,889	29,027	1074,542	0,363	5,674	60,652	2,737	0,306	0,263	0,192	0,017	0,030	0,000
1997	Sh	236,55	0,122	1,783	91,294	0,008	0,116	4,386	0,060	0,024	0,007	0,017	0,002	0,006	0,000
1997	O	31,73	0,048	0,594	9,882	0,008	0,038	1,511	0,022	0,055	0,003	0,002	0,000	0,001	0,000
1997	**Sum**	**3236,62**	**4,059**	**31,404**	**1175,718**	**0,379**	**5,828**	**66,548**	**2,819**	**0,385**	**0,273**	**0,211**	**0,019**	**0,037**	**0,000**
1998	**Sum**	**2827,82**	**3,108**	**29,041**	**1118,083**	**0,178**	**5,285**	**54,295**	**3,232**	**0,564**	**0,234**	**0,169**	**0,021**	**0,037**	**0,001**
1999	L	3374,95	2,514	27,783	1683,959	0,147	8,204	66,897	3,962	0,575	0,277	0,151	0,015	0,065	0,007
1999	Sc	49,52	0,014	0,111	25,376	0,000	0,218	0,152	0,011	0,004	0,000	0,000	0,000	0,000	0,000
1999	S	37,33	0,047	1,034	20,874	0,000	0,188	0,291	0,046	0,001	0,001	0,001	0,001	0,000	0,000
1999	Sh	49,47	0,017	0,259	26,203	0,001	0,045	0,683	0,014	0,004	0,000	0,003	0,000	0,001	0,000
1999	O	134,45	0,107	1,474	66,313	0,009	0,269	2,963	0,135	0,049	0,006	0,007	0,001	0,002	0,001
1999	**Sum**	**3645,74**	**2,699**	**30,661**	**1822,725**	**0,157**	**8,924**	**70,986**	**4,168**	**0,633**	**0,284**	**0,162**	**0,017**	**0,068**	**0,008**
2000	L	3797,22	2,878	25,906	1946,344	0,134	7,827	78,867	4,752	0,831	0,293	0,166	0,019	0,042	0,013
2000	Sc	51,73	0,009	0,109	13,607	0,001	0,083	0,083	0,008	0,004	0,000	0,001	0,000	0,000	0,000
2000	S	5,78	0,004	0,076	3,069	0,000	0,022	0,046	0,008	0,000	0,000	0,000	0,000	0,000	0,000
2000	Sh	373,81	0,163	1,855	187,889	0,008	0,223	5,039	0,105	0,057	0,008	0,025	0,002	0,006	0,002
2000	O	383,51	0,238	2,597	193,787	0,012	0,677	4,036	0,276	0,160	0,016	0,024	0,003	0,013	0,003
2000	**Sum**	**4612,05**	**3,292**	**30,543**	**2344,696**	**0,155**	**8,832**	**88,071**	**5,149**	**1,052**	**0,317**	**0,216**	**0,024**	**0,061**	**0,018**

Over the study period 1996 - 2000 leaves always constituted the greatest part of the litterfall: 91 % in Ojców in the poor variant, 90 % in Ojców in the more fertile variant, and 92 % in Krynica. The second main part of the litterfall was shoots 4 % in Ojców and 3 % in Krynica. Others (to this last fraction were assigned smaller amounts of sycamore leaves and seeds, beech inflorescence, leaf bud scales, bark) and a proportion of tiny invertebrates was around 3 %, seed coats were around 2 % in Ojców and 1 % in Krynica, and seeds 0,5 % (Tab. 1,2,3).

Table 3. Total mass of elements (in kg/ha) reaching the surface soil layer with different litterfall fractions (L-leaves, Sc – seed coats, S - seeds, Sh - shoots, O - others) on Dentario glandulosae-Fagetum association in the typical variant of Forest Experimental Station in Krynica averaging 1996-2000.

Year	**Fraction**	**Dry weight**	**S**	**N**	**C**	**Na**	**K**	**Ca**	**Mg**	**Fe**	**Mn**	**Zn**	**Cu**	**Pb**	**Cr**
1996	L	2235,71	2,688	25,857	960,061	0,122	6,007	19,686	1,777	0,330	1,225	0,081	0,018	0,029	0,007
1996	Sc	28,00	0,009	0,008	9,412	0,001	0,070	0,066	0,006	0,030	0,001	0,001	0,000	0,000	0,000
1996	Sh	221,14	0,096	1,900	72,725	0,012	0,155	4,116	0,060	0,016	0,004	0,012	0,002	0,004	0,000
1996	**Sum**	**2484,85**	**2,793**	**27,765**	**1042,198**	**0,135**	**6,232**	**23,868**	**1,843**	**0,349**	**1,230**	**0,094**	**0,020**	**0,033**	**0,007**
1997	L	2534,84	2,672	23,876	990,492	0,206	10,180	29,140	1,916	0,051	1,787	0,135	0,017	0,007	0,000
1997	Sc	146,56	0,091	1,322	59,466	0,005	0,111	1,186	0,043	0,063	0,038	0,012	0,002	0,005	0,000
1997	O	98,55	0,114	1,557	36,605	0,009	0,143	0,795	0,053	0,123	0,043	0,010	0,002	0,004	0,000
1997	**Sum**	**2779,95**	**2,877**	**26,755**	**1086,564**	**0,220**	**10,435**	**31,120**	**2,011**	**0,237**	**1,868**	**0,158**	**0,021**	**0,016**	**0,000**
1998	**Sum**	**2856,01**	**2,648**	**24,562**	**1135,524**	**0,203**	**9,568**	**29,896**	**2,804**	**0,431**	**2,155**	**0,137**	**0,020**	**0,025**	**0,001**
1999	L	2332,530	1,863	24,098	1244,115	0,134	10,429	23,081	1,955	0,315	1,806	0,082	0,012	0,026	0,023
1999	Sc	78,900	0,017	0,202	41,509	0,001	0,424	0,142	0,018	0,006	0,011	0,001	0,000	0,000	0,001
1999	Sh	49,050	0,027	0,380	27,423	0,002	0,068	0,392	0,019	0,004	0,008	0,003	0,000	0,001	0,001
1999	S	43,290	0,058	1,364	25,546	0,000	0,330	0,216	0,049	0,002	0,018	0,001	0,001	0,000	0,000
1999	O	103,500	0,110	1,275	54,273	0,010	0,513	1,282	0,110	0,030	0,050	0,004	0,001	0,002	0,001
1999	**Sum**	**2607,270**	**2,075**	**27,319**	**1392,866**	**0,147**	**11,764**	**25,113**	**2,151**	**0,357**	**1,893**	**0,091**	**0,014**	**0,029**	**0,026**
2000	L	2861,890	1,908	22,869	1539,662	0,066	10,722	24,325	2,355	0,489	2,689	0,081	0,014	0,028	0,029
2000	Sc	74,400	0,022	0,117	39,502	0,001	0,403	0,114	0,020	0,006	0,010	0,001	0,000	0,001	0,001
2000	Sh	28,900	0,013	0,240	15,964	0,000	0,052	0,211	0,012	0,003	0,008	0,002	0,000	0,001	0,000
2000	S	11,710	0,008	0,208	6,343	0,000	0,069	0,064	0,014	0,001	0,007	0,000	0,000	0,000	0,000
2000	O	164,560	0,157	2,067	87,449	0,007	0,437	1,290	0,099	0,085	0,102	0,008	0,003	0,004	0,002
2000	**Sum**	**3141,460**	**2,108**	**25,501**	**1688,920**	**0,074**	**11,683**	**26,004**	**2,500**	**0,584**	**2,816**	**0,092**	**0,017**	**0,034**	**0,032**

The comparison of the leaf mass deposited over the years 1995 – 2000 demonstrated that in the poor variant after the year 1995 (the mast year) over the next two years a decrease in the leaf mass deposition to the forest floor occurred, while in the year 1998 a tendency for the leaf mass to grow was noted, and was at its maximum in 2000. In the typical variant (Krynica) the smallest amount of deposited leaves was recorded in the seed year 1999 (Tables 1,2,3).

Analyses of the litterfall in the beech stands of different fertility variants, and especially of the production of leaves and seed coats, indicated that the more fertile soil in Ojców seemed to have a stimulating effect on the biomass production. Data established within 1996 and 2000 yielded: 2655 kg/ha of leaves, 157 kg/ha of seed coats, 31 kg/ha of seeds, 114 kg/ha of shoots and 171 kg/ha of "others", which was more than the poor fertility variant in Ojców, as well as in the comparison with beech stands from Krynica in kg/ha as follows: 3033, 210, 23, 248, and 183 (Table 1). This confirmed the data from seed year 1995 in Ojców National Park (Małek *et al.* 1998a,b, c, 2000c, 2001).

Over the years 1996 – 2000 the litterfall in the poor variant in Ojców National Park yielded (in kg/ha): 14.9 (S), 124.6 (N), 6347 (C), 0.98 (Na), 33.6 (K), 297.9 (Ca), 16.1 (Mg), 3.2 (Fe), 2.2 (Mn), 0.97 (Zn), 0.093 (Cu), 0.22 (Pb), 0.022 (Cr). The percentage proportion in the leaf mass (the biggest source of elements) was for each subsequent element: 96.0 92.9, 91.5, 92.2, 93.9, 94.9, 96.9, 88.1, 97.4, 92.3, 84.9, 88.8, 81.1. The second biggest fraction, that yielded great amounts of elements, were shoots: above 4 % of C, Zn, Cu, Pb and Cr. The fraction “others” yielded above 4 % of Na, Pb and Cr, while the coats produced above 9 % of Cr. The smallest amounts were represented by the seeds, below 1 % (Table 1).

The litterfall from the fertile variant in Ojców analyzed over the years 1996 – 2000 yielded larger amounts of all analyzed elements in comparison with the poor variant: 1.87 (S), 25.8 (N), 1359 (C), 0.17 (Na), 2.310 (K), 63.4 (Ca), 4.7 (Mg), 0.21 (Fe), 0.65 (Mn), 0.070 (Zn), 0.010 (Cu), 0.034 (Pb), 0.011 (Cr). The proportion represented by the total leaf mass gave the following percentage for each respective element: 94.7 92.2, 90.2, 94.6, 92.5, 94.3, 96.2, 88.3, 96.7, 91.2, 90.3, 87.9, 72.7. The second biggest fraction which yielded considerable amounts of elements were shoots: above 4 % (C, Zn, Pb, and Cr). The fraction “others” yielded above 4% (Fe, Pb and Cr), while coats yielded above 9% of Cr. The smallest amount was yielded by seeds, below 1 %, except for K. In spite of larger amounts of the litterfall in the fertile variant, larger amounts were provided in the poor variant by seeds: Mg, shoots: Na, K, Mg and “others”: Na, Fe, and Mg (Table 2).

A comparison of the amounts of elements deposited with the litterfall over the years 1996 – 2000 between the fertile variant in Ojców National Park, and the typical variant in Krynica demonstrated that Ojców produced larger amounts of all elements,: 4.24 (S), 18.5 (N), 1360 (C), 0.37 (Na), 225.2 (Ca), 9.5 (Mg), 1.4 (Fe), 0.47 (Zn), 0.011 (Cu), 0.12 (Pb). The percentage proportion in leaves of the total mass of elements was respectively: 94.2 91.9, 92.5, 93.8, 94.4, 92.7, 95.5, 81.4, 97.0, 90.4, 88.0, 83.9, 90.9. The second biggest fraction, which yielded a considerable amount of elements were shoots: above 4 % (Ca, Fe, Zn, Cu, and Pb). The fraction "others" yielded above 4 % (Fe, Cu, Pb and Cr), while the covers Cr above 3 %, the smallest amounts were yielded by seeds (below 1 %), with the exception of N and Cu. In spite of a greater amount of litterfall in the fertile variant (Ojców), bigger amounts of elements in the typical variant (Krynica) was yielded by leaves: K, Mn and Cr, seed coats: Mn, seeds: K, Mn, shoots: Na and Mn and “others”: N, K, Mg and Cu with a greater total mass: S, N, C, Na, Ca, Mg, Fe, Zn, Cu, and Pb (Tables 2, 3).

In spite of a greater mass of litterfall in the poor variant in Ojców National Park, a larger amount of elements was noted in the typical variant (Krynica) in leaves: N, K, Mg, Cu, and Cr, seed coats of Ca, K, Fe, and Mg, shoots of Fe, Mg , and Pb, and “others” of S, N, K, Mg, Mn, K, and Cr. In case of seeds, a greater amount fell in the typical variant in Krynica, in comparison to the poor variant in Ojców National Park, but still they yielded less Ca. In total, larger amounts of S, C, Ca, Mg, Fe, Zn, Cu, and Pb reached the soil with the litterfall in the poor variant (Tab. 1,3). This corresponded to the high content of elements, especially of Ca and Mg, in the soil of Ojców National Park (Greszta & Małek 2000)

Laskowski *et al.* (1995) noted that in the mixed beech-pine forest in the neighbourhood of Dobczyce water dam (near Krakow) the sampled elements can be put in the order of the amount of their proportion in the litterfall: N>Ca>S>K,Mg>Mn>Pb. In the experimental plots in the beech stand of the Gorce National Park the order was similar to the order given by Laskowski et al. (1994): Ca>K>S>Mg>Mn>Pb (Niemtur 1997). In the experimental plots in beech stands of Ojców National Park the order of elements over the analysed years was as follows: C>Ca>N>>K>Mg>S>>Fe>Mn>Na>Zn>Pb>Cu>Cr (variants poor and fertile), while in Krynica it was: C> Ca>N>K>SMg>Mn>Fe> Na>Zn> Pb>Cu>Cr (Tables 1, 2, 3).

The annual requirement of nutritive components of beech stands of 1st bonity is: Ca–59.0 kg/ha, Mg–8.5 kg/ha, K-47.7 kg/ha (Ehwald 1957). The litterfall fully satisfied the requirements in Ojców National Park only for Ca in both fertility variants. On the other hand, in order to produce 1 cubic meter of litterfall the organic matter yielded the required amount of N and Ca only in Ojców National Park in the fertile variant (Mayer-Krapolla 1958). This meant that the studied beech stands yielded much smaller amounts of elements over the studied years than required for their growth. Litterfall was the second main source for elements of the beech stands next after soil, and was more important than wet and dry deposition (Greszta and Małek 2000, Małek *et al*. 1998a,b, c, 2001, Małek Wężyk 1999, 2000a,b).

Summary of results and conclusions

1. The yearly variation in amount of litterfall was very large and different from one site to another within the same climatic region.)
2. Leaves constituted the greatest part of the litterfall: 91 % in Ojców on poor variant, 90 % in Ojców on fertile variant and 92 % in Krynica. The second main part of the litterfall was shoots 4 % in Ojców and 3 % in Krynica. Others (to this last fraction were assigned smaller amounts of sycamore leaves and seeds, beech inflorescence, leaf bud scales, bark and tiny invertebrates) were around 3 %. Seed coats made up around 2 % in Ojców and 1 % in Krynica and seeds 0,5 %.
3. Leaves in the presented study in Ojców National Park and Krynica (1996-2000) were also the main source of elements (from 72,7 to 96,9 % for all element). The second biggest fraction, which yielded considerable amounts of elements were shoots: above 4 % (C, Zn, Cu, Pb, and Cr and C, Fe without Cr in Krynica). The fraction “others” yielded about 4 % (Na – only the poor variant, Fe, Pb, and Cr and additionally Cu in Krynica), while covers yielded Cr above 9 % in Ojców and above 3 % in Krynica. The smallest amount of seeds yielded below 1 % except for K in the fertile variant and N and Ca in a typical variant (Krynica).
4. A larger organic amount, as well as of mineral elements, was noted for seeds deposited to the soil in the fertile variant: Mn, shoots: Na, K, and Mn and “others”: K, Fe, and Mn with the larger total mass of elements in the fertile variant were noted.
5. In spite of a larger amount of litterfall in the fertile variant in Ojców National Park, a larger amount of elements in the typical variant (Krynica) was yielded by leaves for K, Mn, and Cr as well as of S, N, C, Na, Ca, Mg, Fe, Zn, Cu and Pb, covers yielded Mn, seeds yielded K, Mn, shoots yielded Na and Mn and “others” yielded N, K, Mn and Cu.
6. In spite of recorded larger amounts of litterfall in the poor variant in Ojców National Park in relation to a typical variant in Krynica, a larger mass was yielded by the leaves: N, C, K, Mn, Cu, and Cr, covers yielded C, K, Fe, and Mn, shoots yielded Fe, Mn, and Pb and “others” yielded S, N, K, Mn, Cu, and Cr. In case of seeds, whose larger amounts were deposited in a typical variant, it was found that they yielded less Ca. In total, lower amounts were deposited to the soil in the poor variant than in the fertile variant of: S, C, Na, Ca, Mg, Fe, Zn, Cu, and Pb.
7. In the beech stands of Ojców National Park the mass ranking of elements was as follows: C>Ca>N>K>Mg>S>Fe>Mn>Na>Zn>Pb>Cu>Cr (poor and fertile variants), while in Krynica it was: C>Ca>N>K>S>Mg>Mn>Fe>NaZn>Pb>Cu>Cr. The lime stone in Ojców containing both Ca and Mg and with a higher pH, explained the ranking difference for Mg and Mn.
8. The studied beech stands yielded much smaller amounts of elements over the years of observations than they needed for their development. The internal cycle of litterfall was the second main source for elements of the beech stands next after soil, and contributed more than wet and dry deposition.

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The importance of litterfall and needle nutrients in circulation of elements and sustaining long-term productivity

- example from different age classes of Istebna Spruce stands in the Potok Dupnianski catchment, Southern Poland

Stanislaw Małek Ph.D. Eng., Dep. of Forest Ecology, Forest Faculty
Agricultural University of Cracow,
Al. 29-go Listopada 46, PL-31-425 Cracow, Poland
e-mail: rlMałek@cyf-kr.edu.pl

Abstract

Results presented here date back to 1999 and focus on the content of nutrients and needles in litterfall in stands of different age classes of the Istebna Spruce in the Potok Dupnianski stream catchment. The catchment located in Southern Poland in Beskid Slaski (N 49°35', E 18°50') close to Slovakia and Czech border, has an area of 1.68 km^2. The study was performed according to guidelines of the ICP - Forest Manual. From each spruce stand (1st, 2nd, 5th and 6th age class) one and two-years-old needles were collected in August, and nine litterfall traps with the inlet diameter of 0.170 m^2 each were installed. Material from litterfall traps was collected every 90 days, dried and sorted into: needles, cones, seeds, shoots and others. The content of C, N, S, Na, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb, Cd, Ni and Cr was determined.

The content of N in all analyzed stand age classes (apart from the 1st) was on optimum levels as well that of K and Ca. In all analyzed spruce stands the content of Mg was on clear deficiency levels. Content of S was optimum in the 4th stand age class similar to the second year needles in 1st and 2nd stand age class, but on deficiency levels in others. Low content of Mg in spruce needles was related to low content of exchangeable amount of this element in soil, and leaching of Mg with soil water was observed below the main root system level. Harmonious ranges and ratios between main elements were noticed in all spruce stands. Noticeable was high content of K, Mg, Cu, Ni, and low content of S, N, Ca, Fe and Mn in one-year-old needles in comparison with the two-years-old needles. Translocation of C, N, K and Mg was noticed from litterfall concentrations. Litterfall was the main source of nutrients in spruce stands, coming next after the soil but before wet and dry deposition, esp. concerning N, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb and Cr. On acid soils the decomposition of the plant material is low, which may affect the content of nutrients in needles and degradation of the soil.

1. Introduction

The cycle of elements in spruce tree stands affected by industrial emissions in the Beskid Śląski has been and still is the subject of a number of studies. These studies have been carried out in relatively small forest catchments such as Brenna or Salmopol (Staszewski *et al.* 1996, Godzik *et al.* 1997, Staszewski *et al.* 1999, Bytnerowicz *et al.* 1999), Potok Dupnianski stream (Małek and Wężyk 2000a, b, Małek 2001 a, b), and also in a much larger catchment Czarna and Biała Wisełka (Wróbel 1998).

In the Potok Dupnianski catchment the studies focused on the balance of incoming and outgoing elements with special attention to changes in the concentration of anions and cations in rain on open field and after it passed the canopy as throughfall, in the top soil surface water, in ground water (the lysimeter was placed at the depth of 20 cm to pick up water by horizontally and vertically flows). The studies also focused on determining the chemistry and productivity of forest soils formed from Istebna sandstone and the nutrient status of trees and amounts of litterfall at different development stages of spruce stands (1^{st}, 2^{nd}, 5^{th} and 6^{th} age class) in 1999 (Małek 2001 a,b,c).

The aim of the present work was to study the importance of litterfall and needle nutrients in the cycle of elements for sustaining long-term productivity - example from different age classes of Istebna Spruce stands in the Potok Dupnianski catchment, Southern Poland.

2. Material and methods

The Potok Dupnianski catchment of an area of 1.68 square kilometers is located in southern Poland in the Beskid Slaski (latitude 49´35, longitude 18´50). The area of the catchment is overgrown with spruce trees at different development stages, growing on the Istebna sandstone. The area of studies is not directly exposed to air pollution as it is fairly distant from the major industrial centers. The catchment was equipped with appliances for evaluating water quality and meteorological parameters in spruce stands at different development stages: 12 year -1^{st} age class, 25 years - 2^{nd} class, 92 – years - 5^{th} class, 117-years - 6^{th}class. The studies were made on the basis of the ICP – Forest Manual method (1998).

In August 1999 from each study plot needles were collected from the seventh verticil, counting from the tree top, from three individuals of the second age class: current and second year, and from 2^{nd} class according to Kraft classification). The individuals were located in the plot next to a soil strip, and equipment for evaluating water quality and quantity. At the same time, at the beginning of 1999 nine collectors for litterfall with a diameter of inlets equaling 0.170 m^2 were installed at steady intervals at the height of 130 cm above the soil level in each study plot. The sampling of litterfall was performed at three periods (Ist sampling from Jan. 01 to April 30, IInd from May 01 to Aug. 31, IIIrd from Sep. 01 to Dec. 31, 1999).

The total content of elements in the plant material of Na, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb, Cd, Ni and Cr were determined after wet mineralization in a HNO_3 and $HClO_4$ solution at ratio 1:4 with the Atomic Absorption Spectrophotometer Varian AA-20, whereas elements C, N, and S were determined with the analyzer LECO CNS 2000 (Litynski *et al.* 1976).

3. Results and Discussion

The content of elements in needles was determined for the two first age classes of the Istebna Spruces (Table 1). The results were compared with classes of content of given elements (Stefan *et al.* 1997). The results showed that the content of N in all development stages of the stand was at its optimum (class 2), with the exception of 1^{st} thickets (Fiedler and Katzschner 1990, Herman *et al.*, 1998), and at a medium deficit level in older stages (Bergmann 1983). Prominent symptoms of deficiency of N may be observed at concentrations below 1% N of dry needle mass (Fiedler *et al.* 1973, Hartmann *et al.* 1988). The contents of K and Ca at all development stages were at optimum levels. The results of Mg indicated deficiency (class 1), and according to Zöttl (1990) the values obtained demonstrated a conspicuous deficit. The content of S was at its optimum value in the mature stand, and in the second age class of needles in 1^{st} and 2^{nd} age class of spruce stands, while other values indicated deficiency (Table 1). Similar values were obtained for Brenna and Salmopol for a spruce stand of the 5th age class (Bytnerowicz *et al*. 1999, Staszewski *et al*. 1999).

Low content of Mg in spruce needles is tightly connected with relatively small content of Mg easily taken from the soil, and with its leaching out of reach of the root system (Nihlgard 1972, Małek 2001 a,b,c). Deficiency of Mg is considered as a key cause of Norway spruce yellowing damage typical for this part of Europe (Herman *et al.,* 1998). The sudden occurence of this symptom may be attributed to a series of dry years, which reduced Mg mineralization and uptake, as well as by more intensive (shorter rotation) tree harvesting and leaching of soils by acid rain (Europe's Environment, 1995). As demonstrated by studies made in spruce stands in mid German uplands (Roberts *et al*. 1989) the deficiency of Mg in needles may, to a greater degree, be caused by a reduced level of Mg in the soil, resulting from wood harvesting and leaching by acid rain, rather than by direct washing of Mg from needles in connection with air pollution. In addition, an increase in the deficit of Mg may be caused by water stress, because during dry years Mg is to a lower extent mineralized from litter, there is a decreased uptake from soil, and there is a more poor development of root systems in trees, and due to higher nitrification the leaching of nitrate can be more intensive at coming rainfall.

Table 1. Average content of elements in spruce needles (current – year 1 and second – year 2) at different age classes of Norway spruce forest stands in the Potok Dupnianski catchment.

Year	C	S	N	Na	K	Ca	Mg	Fe	Mn	Zn	Cu	Pb	Cd	Ni	Cr
	%							Ppm							
1st age class															
1	56,37	0,070	0,980	0,000	0,550	0,400	0,060	65,5	715,0	47,3	5,7	12,1	0,2	6,4	0,7
2	55,71	0,110	1,020	0,000	0,380	0,590	0,060	93,3	1061,5	59,2	2,0	12,8	0,2	1,8	0,7
2nd age class															
1	54,61	0,090	1,310	0,001	0,850	0,240	0,060	42,5	446,8	30,9	2,8	23,6	0,0	3,7	0,3
2	55,03	0,120	1,320	0,000	0,590	0,310	0,050	66,2	669,5	32,7	2,8	27,2	0,0	1,6	0,5
5th age class															
1	54,54	0,090	1,270	0,000	0,540	0,220	0,050	50,2	1067,8	24,0	2,9	26,7	0,1	3,7	0,2
2	54,1	0,100	1,220	0,000	0,460	0,380	0,040	77,8	1822,8	18,5	2,3	25,7	0,2	3,0	0,5
6th age class															
1	53,15	0,110	1,460	0,000	0,500	0,200	0,070	41,7	522,0	22,2	3,3	20,8	0,0	3,3	0,3
2	52,94	0,110	1,250	0,000	0,370	0,450	0,060	67,3	954,0	14,3	2,5	21,2	0,0	2,4	0,3

The concentration of Cu below 3 ppm in one-year old needles of the semi-mature stands, and in 2nd forest age class in the catchment of the Potok Dupnianski (Table 1) may indicate problems, as below this threshold the ends of top shoots may happen to die during autumn and winter months (Fiedler *et al*. 1973).

Increased concentrations of K, Mg, Cu, and Ni as well as of S, N, Ca, Fe, and Mn in one-year old needles in comparison with two-year-old needles (Tables 1) has been noted. This confirms that the age of the studied tissue has an important effect on internal concentrations of given elements. It is known that young, one-year old needles are characteristic of higher concentrations of N, K, Mg and lower concentrations of Ca or Mn in comparison with older, two or three-years-old needles (Fober 1998, Nihlgard 1972).

For a good nutrition of a tree the proportions between selected nutrients are important. As the studies demonstrated, in one-year-old needles of ideally growing spruce, the ratio of N:P:K was 67-8-25. With age the proportion of N may increase, while the proportion of K may decrease (Fiedler and Hohne 1987). The obtained results confirmed optimum values of the content of N and K in spruce needles in Istebna (Table 1).

The results of analyzes of litterfall (Table 2) indicate that with increasing forest age the quantity of litterfall showed increasing amounts of cones, whose participation in the litterfall mass was 75 per cent for a mature stand, and 56 per cent for a maturating stand. The importance of cones in the mass of litterfall was conspicuous in old stands, as well as the nutrient quantities in precipitation, that was more than ten times higher than in thickets. The largest quantity of needles per hectare occurred in 2nd age class (3356 kg/ha) and also in older development stages of a stand. It seemed that the culmination time for the shedding of needles came at the moment of most acute competition between trees, and strongest process of cleanup of tree trunks. The smallest amount of shed needles in thickets was probably the result of poor competition and small sizes of tree crowns. Twigs make a relatively small quantity, the maximum portion was 26 per cent (in thickets) of the total litterfall. In absolute values its largest quantities occurred in thickets and mature stands (ca 350 kg/ha), the smallest amounts occurred in 2nd age class - 125 k/ha. The largest litterfall volume was observed from late summer until autumn, and it was smallest in winter at all development stages (Table 2).

The amounts of litterfall reaching the forest floor obtained in the conditions of the Potok Dupnianski catchment (Table 2) were within the limits given by different authors (from 1 to 7 tons/ha/year). In 80 years old stands (Dietrich, cit. Schmidt-Vogt 1986) growing in bleached brown soils the value was 3 tons. Its composition included 68-86 per cent of needles and 10-26 per cent of animal debris and excrements.

Table 2. Amount of litterfall (in kg/ha) and its per cent proportion and assignment into fractions at different Norway spruce forest stands age classes in the Potok Dupnianski catchment.

Period of samp.	*01 01 – 30 04 1999*		*01 05 - 30 08 1999*		*01 09 - 31 12 1999*		*1999*	
Litterfall fraction	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%
	1st age class							
Needles	312,57	46,19	579,94	100,00	130,54	100,00	1023,05	73,75
Shoots	364,07	53,81	0,00	0,00	0,00	0,00	364,07	26,25
Cones	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Sum	**676,65**	**100,00**	**579,94**	**100,00**	**130,54**	**100,00**	**1387,13**	**100,00**
	2nd age class							
Needles	881,30	96,94	1743,41	99,50	731,22	89,13	3355,94	96,39
Shoots	27,81	3,06	8,68	0,50	89,14	10,87	125,63	3,61
Cones	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Sum	**909,12**	**100,00**	**1752,10**	**100,00**	**820,36**	**100,00**	**3481,57**	**100,00**
	5th age class							
Needles	811,51	83,68	1639,90	27,46	562,28	79,89	3013,68	39,42
Shoots	158,28	16,32	34,66	0,58	141,52	20,11	334,46	4,37
Cones	0,00	0,00	4297,37	71,96	0,00	0,00	4297,37	56,21
Sum	**969,79**	**100,00**	**5971,92**	**100,00**	**703,79**	**100,00**	**7645,50**	**100,00**
	6th age class							
Needles	740,12	86,10	1590,64	22,89	665,54	13,56	2996,30	23,56
Shoots	119,49	13,90	24,70	0,36	88,62	1,81	232,82	1,83
Cones	0,00	0,00	5333,31	76,75	4152,69	84,63	9486,00	74,60
Sum	**859,61**	**100,00**	**6948,65**	**100,00**	**4906,85**	**100,00**	**12715,12**	**100,00**

Table 3. Mass of elements (in kg/ha) reaching the soil surface with litterfall as divided into fractions of litterfall at different Norway spruce forest stage classes in the Potok Dupnianski catchment.

Fraction	***C***	***S***	***N***	***Na***	***K***	***Ca***	***Mg***	***Fe***	***Mn***	***Zn***	***Cu***	***Pb***	***Cd***	***Ni***	***Cr***
1st age class															
Needle	503,6	0,910	8,470	0,006	1,740	5,100	0,380	0,210	1,790	0,040	0,000	0,019	0,000	0,001	0,002
Shoot	185,5	0,330	2,970	0,005	0,250	0,910	0,050	0,300	0,060	0,020	0,000	0,011	0,000	0,000	0,001
Sum	**689,1**	**1,240**	**11,440**	**0,010**	**1,990**	**6,000**	**0,430**	**0,510**	**1,850**	**0,060**	**0,010**	**0,030**	**0,000**	**0,001**	**0,003**
2nd age class															
Needle	1653,2	3,440	37,130	0,010	5,360	15,760	1,610	0,710	3,020	0,170	0,010	0,061	0,000	0,001	0,005
Shoot	64,8	0,090	0,750	0,000	0,040	0,320	0,020	0,080	0,020	0,010	0,000	0,006	0,000	0,000	0,000
Sum	**1718,1**	**3,530**	**37,890**	**0,010**	**5,400**	**16,080**	**1,630**	**0,790**	**3,040**	**0,180**	**0,010**	**0,068**	**0,000**	**0,001**	**0,005**
5th age class															
Needle	1470,5	2,320	26,100	0,010	3,150	11,820	0,780	1,560	3,440	0,100	0,010	0,064	0,000	0,004	0,004
Shoot	119,1	0,190	1,570	0,000	0,080	0,620	0,030	0,190	0,070	0,010	0,000	0,011	0,000	0,000	0,001
Cone	4716,4	4,580	46,220	0,040	20,870	4,930	2,370	1,150	0,610	0,170	0,460	0,066	0,001	0,011	0,015
Sum	**6306,0**	**7,090**	**73,890**	**0,050**	**24,100**	**17,370**	**3,180**	**2,900**	**4,110**	**0,280**	**0,470**	**0,140**	**0,001**	**0,016**	**0,020**
6th age class															
Needle	1488,9	2,810	27,360	0,020	3,780	10,920	0,910	1,420	2,670	0,100	0,010	0,064	0,000	0,002	0,007
Shoot	170,8	0,250	2,220	0,000	0,210	0,740	0,060	0,270	0,050	0,020	0,010	0,013	0,000	0,000	0,001
Cone	2136,6	2,070	20,940	0,020	9,450	2,230	1,070	0,520	0,280	0,080	0,210	0,030	0,000	0,005	0,007
Sum	**3796,4**	**5,130**	**50,510**	**0,040**	**13,440**	**13,890**	**2,050**	**2,210**	**2,990**	**0,200**	**0,220**	**0,110**	**0,000**	**0,010**	**0,010**

The obtained values of element concentrations in the needles of litterfall demonstrated that before the needles were shed some translocation of C, N, and K and, above all of Mg, which was lacking both in the assimilation organ (Table 1) and soil (Małek 2001), occurred.

Compared with rainfall (Małek 2001 a,b,c), the litterfall (Table 3) supplied considerable amounts to the forest floor of the following elements: N, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb, and Cr. However, in acid, frequently drying or flooded soils where fungi, *Collembola*, and saprophytes dominate, the decomposition of spruce litter is markedly reduced, and as a result moder and raw humus are formed. As a consequence, the habitat becomes even more impoverished, and so does the content of nutrients in needles and the process of degradation moves on (Fiedler 1979).

A relatively low pH of the soils (of the surface layer in water extract pH is 3.8 – 4.3) and also of throughfall, may increase the liberation of heavy metals in the sorption complex of the soil, and at the same time, it may unfavorably affect the development and health condition of spruce stands in the future (Małek 2001 a,b,c).

4. Conclusions

1. The content of N in all analyzed stand age classes (apart from 1st) as well as of K and Ca were at optimum levels. In all analyzed spruce stands the content of Mg was on clear deficiency levels. The content of S was optimal in 5th stand age class, as in the second year needles in 1st and 2nd stand age class, but on deficiency levels in others.
2. Low content of Mg in spruce needles was related to low content of exchangeable amount of this element in soil, and high water leaching below the main root system level.
3. Noticeable were high contents of K, Mg, Cu, Ni, and low contents of S, N, Ca, Fe and Mn in one-year-old needles in comparison to second-year-old needles.

4. Harmonious ranges and ratios between the N:P:K elements were noticed in all spruce stands.
5. Translocation of C, N, K and Mg from needles were indicated before litterfall.
6. Litterfall could be the main source for nutrients in spruce stands, coming next after soil, but before wet and dry deposition, esp. concerning N, K, Ca, Mg, Fe, Mn, Zn, Cu, Pb and Cr. On acid soils decomposition of the plant material is limited, which may influence the content of nutrients in needles and a degradation of soil.

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A preliminary regional division for efficient biodiversity preservation based on disturbance regime, forest history and tree species distribution: the southern Swedish example

Mats Niklasson[1] & Sven G Nilsson[2]
[1]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences,
Box 49, S-230 53 Alnarp, Sweden
[2]Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
Corresponding author: Mats Niklasson, e-mail: mats.niklasson@ess.slu.se

Abstract

We propose a method for dividing large regions into biogeographical sub-regions based mainly on natural disturbance regime, forest history and potential tree species distribution. This subdivision could be used as a guide when designing conservational strategies and management plans for landscapes and protected areas. At present, conservational strategies and management of valuable areas on the one hand and production forests on the other, is often similar over large regions, especially from a species´ point of view. Compared to the scale at which natural disturbances, tree migration and species dispersal/interaction operate, protected areas are usually minute, isolated and found in fragmented landscapes. Therefore they will rarely, if ever, develop the multitude of successional stages found in large natural landscapes under a disturbance regime with large-scale and relatively rare disturbance events (at point scale). Consequently, in southern Sweden, structures and conditions on which many rare species are dependent are rapidly lost, both in earlier fire-prone forests and in landscapes shaped by grazing and wind disturbances. The proposed division method in managed forest landscapes could be an important guide for foresters aiming at restoring biological values through emulating natural disturbances.

Introduction

In the past, natural disturbances such as fire, wind or grazing determined successional patterns and tree species composition over most of southern Sweden (e.g. Nilsson 1997; Lindbladh, Bradshaw et al. 2000). Today, disturbances and successions are mainly driven by or strongly influenced by forestry and its operations (eg. fire suppression, clear-felling, thinnings, monoculture establishment, soil disturbances from machinery). However, in protected areas or areas where preserving or enhancing biodiversity is the primary goal, management needs other guidelines than those provided by forest management alone. Today, guidelines for nature reserve management are often vague and/or based on static perceptions of past landscapes, their origin and development.

Here we present a short review of main biotic and abiotic factors acting on natural disturbances in southern Sweden such as: lightning ignition density, soil type distribution and recent-past tree distributions. These factors are compiled and used for a subsequent preliminary division of southern Sweden into eight regions based on similarity of natural disturbance regime and potential tree species composition. This division is preliminary until further empirical knowledge is gathered on the following factors: flammability of non-coniferous forest fuels, species- and soils influence on windthrow susceptibility and various aspects of grazing. Still, we believe that decisions for biodiversity management at both local and landscape scales should be strongly helped by the proposed system. The use of fire in forest management is one example. (Details on the method and results will be published elsewhere).

Material and methods

For pragmatic reasons, we set the upper number of possible delineated regions to 10. The following factors were selected for evaluation and for further division of southern Sweden (the nemoral and boreonemoral zone *sensu* Sjörs (1965)). Information was extracted from studies in brackets:

1. Frequency of lightning ignitions (Granström 1993).
2. The main distribution of beech and spruce before large-scale agricultural activity and expansion (200- 500 years ago) (Björkman and Bradshaw 1996). These trees are rather sensitive to fires and are usually considered strong competitors on less fertile soils. Data mainly from a number of pollen analysis and other studies.
3. Distribution of soil types and soil texture.
4. Earlier studies on fire history both tree-rings and charcoal.
5. Humidity, a factor strongly affecting fire frequency (Eriksson 1986).
6. Distribution of selected vascular plants (*Ledum palustre, Geranium bohemicum*), probably reflecting influence of fire and precipitation climate (Hultén 1971).
7. The temporal and spatial distribution of slash and burn agriculture (Larsson 1980).
8. Large-scale wind climate, in particular storm frequencies.

Results and discussion

The result of the compilation and evaluation is shown in figure 1. Eight regions with similar properties were identified.

I. Nemoral zone without spruce. Natural fire probably very rare, wind disturbance very important.
II. Southwestern Götaland. High precipitation. Fire probably rare, wind disturbance important.
III. West Götaland xeric region. Fire probably rare but rather unknown history, wind probably important.
IV. Highland of southern Sweden. High precipitation. Fire probably rare, wind probably important.
V. Transitional zone with *Fagus.* Natural fire regime largely unknown but probably more common in east.
VI. Southeast Småland and Blekinge. A region with very few empirical data, fire probably common but also *Fagus* was historically more common
VII. Eastern Götaland outside the *Fagus*- region. Fires common at high frequencies.
VIII. Öland and Gotland. Fires rather uncommon. Calcareous soils, different field vegetation from the mainland.

At present there are no published similar divisions over southern Sweden. A very rough division of the whole Sweden into disturbance based regions was made by Pettersson (1991) In this division, southern Sweden has only three regions in most parts differing from our division. The strong east-west gradient we present is not evident in Petterssons division. Only our region I, the purely nemoral zone is similar to Pettersson´s division. Disturbance-based forest management models have been proposed by Angelstam, Rosenberg et al. (1993), Bergeron, Harvey et al. (1999) and Hunter (1992), all aiming mainly at boreal forests. The ASIO model (Angelstam, Rosenberg et al. 1993), being a non-spatial model is not really comparable to our division since it focuses on single stands and field layer vegetation. The ASIO model, being based on northern Swedish fire history (Kohh 1975; Zackrisson 1977) and forest type, does not take into account regional variations in natural ignitions and deciduous tree dominance. Therefore, we believe its value as a guide to forest management in many parts of southern Sweden is rather low. However, any division of an area into subareas may be criticized and discussed. In our case we wanted for simplicity and practical reasons to keep the number of regions low instead of subdividing each region *in finitum*. By this, we can expect differences between regions to be rather clear, at least when soil conditions is the main delimitation factor. At local scale within regions ($10^2 – 10^3$ ha) factors influencing wind and fire such as soil type and topography may still vary much.

This division must be regarded as preliminary until better empirical knowledge on crucial issues have been collected. There are many unanswered questions: temporal and spatial distribution of past fires and windfellings are among the most important. This has partly been done in the boreal north (Jonsson & Dynesius 1993, Niklasson & Granström 2000) but still not in the more complex southern part of Sweden. These variables are in turn dependent on a complex array of, for example, flammability variations of fuels, soil texture, topography, proportion of wet areas and lakes in a landscape and many more.

We argue that our division should be used as a basis for further planning for a cost-efficient management of biodiversity in our forests. For example, it is important to know when it is worth managing for fire-adapted fauna and flora and when not. In a region where fire has not been important, fire adapted species are not found and operations aiming at enhancing biodiversity should instead emulate the long and short-term effects of wind disturbance for example (gap dynamics). Today we see the effects of not acknowledging past disturbance regimes; Norra Kvill national park is a prime example where fire exclusion for over 200 years has led to dramatic changes and loss of structures and probably also species connected to the past and open fire-shaped landscape (Niklasson and Drakenberg 2001). In many oak-dominated areas formerly grazed, rapid succession of young deciduous trees lead to loss of sunexposed, warm oak microhabitats (Ranius & Jansson 2000). Both are examples of how the current non-intervention management regime lead to loss of substrates and probably also species in many protected areas. To leave a set-aside area to its own faith is a good thought, but in most cases it is just an illusion that the natural disturbance regime will return. This is simply because almost every set-aside area is today much too small to be affected by large-scale and rare natural disturbances. Lightning and especially lightning ignitions are rare events at the local scale, so are large tree-felling hurricanes, in addition large grazing animals are almost gone. In a 10 by 10 km-square (10 000 ha) in southeastern Sweden, lightning starts a fire once every five year (Granström 1993). Imagine then a reserve of the typical size range 10-100 ha: statistically a fire due to lightning would start every 500 to 5000 year. As a comparison Norra Kvill national park burned every 20 year before 1770. A further complicating factor is that most protected areas are almost always surrounded by managed land, be it forest or fields where fires will be suppressed and wind fellings salvaged.

To conclude, it is clear that many protected areas need some kind of restoration management, especially if we are to optimize conservation action and allocate efforts to certain areas in the future. This should not at all be confused with the management concept practised in forestry where extraction of wood is the primary goal. We believe that the disturbance-based division of southern Sweden proposed here may support planning and managing for biodiversity preservation. The division into regions should be a strong support for a more diverse view on management of protected areas. Without such management many areas will undergo unwanted development leading to loss of species diversity.

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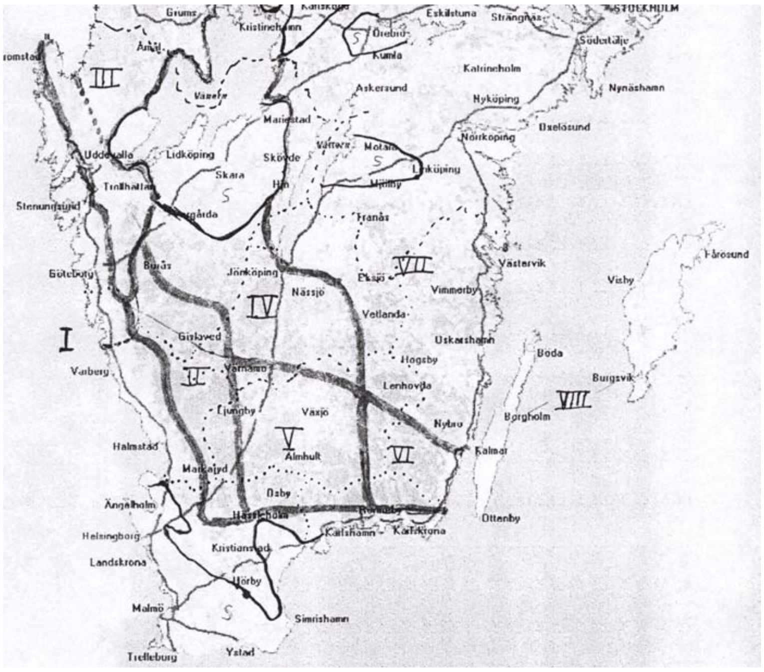

Figure 1. Proposed division of southern Sweden into regions with similar disturbance regime.

Soil and Forest Condition of Beech and Oak Stands in Southern Sweden

Kerstin Sonesson[1] & Stefan Anderson[2]
[1]Dept of Ecology, Plant Ecology, Lund University, SE-223 62 Lund, Sweden
Phone +46 46 222 9304, E-mail kerstin.sonesson@planteco.lu.se
[2]Regional Board of Forestry, Södra Götaland, Ryttarevägen 8, SE-302 60 Halmstad, Sweden

Abstract

The National Board of Forestry has, in 1988, 1993 and 1999, carried out special surveys on forest condition in beech and oak forests in southern Sweden. The condition of beech and oak has deteriorated since the first monitoring. In 1999, 27% of the beech and 59% of the oak trees showed more than 25% defoliation, compared to 3% of the beech trees and 9% of the oaks in 1988. The soil condition of the subsurface mineral layer at a depth of 20-30 cm was highly acid (i.e. pH $_{(BaCl2)}$ values lower than 4.2) in 86%, and the base saturation was less than 20% in 76% of the forest stands surveyed in 1999. The investigation revealed that poor soils, e.g. low base saturation, might have a negative impact on the forest condition as the study demonstrated a significant negative relation between defoliation and base saturation in both beech and oak plots.

Keywords: Fagus sylvatica, forest decline, monitoring, Quercus robur

Introduction

More than half of Sweden's surface area (41 million ha surface area in total) consists of forest. The bulk of the forest acreage is composed of coniferous forest, while only about 1% of the afforested area consists of deciduous hardwood forest (National Board of Forestry 1995). Both beech and oak reach their northern limit in Sweden and Norway, with only isolated finds of beech in the southern coastal lowland of Norway.

Since the middle of the 1970's it has been possible in large areas of central Europe to observe damage to forests to an extent not found before. Forest damage first appeared among stands of coniferous forest, but during the 1980's widespread damage was also observed on deciduous trees, particularly on beech and oak. The extent and wide distribution of the forest damage makes it difficult to explain in terms of already known causes. The same damage indications that were found in central Europe were soon noticed in Sweden as well.

In the summer of 1988 the first special survey of forest condition of beech and oak in southern Sweden, including 2400 trees in 233 forest stands, was carried out. The survey was based on an objective selection of permanent sample trees in a geographic network of survey plots and was repeated in 1993 and with certain additions in 1994.

Because of the current and worsened damage situation of oak in Sweden, the National Board of Forestry decided in April 1999, to carry out a new re-assessment of beech and oak. The survey included the existing survey plots in Skåne, Halland and Blekinge. In addition 25 new plots with oak in south-western Småland were included. Parallel with the survey of forest condition, soil samples were taken at a soil depth of 20-30 cm in the subsurface mineral layer for soil chemical analyses.

Stefan Anderson was the project leader and was responsible for the operational planning, training and the carrying out of the survey. *Kerstin Sonesson* was involved in the survey design and was responsible for data preparation, analysis and presentation of the results.

The objectives of the survey are:

- To describe the forest condition of beech and oak in southern Sweden in a representative way and with a resolution that can show up differences within the region.
- To demonstrate changes over time in condition of the trees by means of comparisons with the results of the surveys in 1988 and 1993.
- To illustrate the link between damage distribution and possible damage factors e.g. stand and site quality, climatic extremes, air pollutants and soil acidity.
- To investigate soil condition, at a depth of 20-30 cm, in beech and oak forest in southern Sweden in a representative way and with a resolution that can point out differences within the region.
- To illustrate connections between soil chemistry and the distribution of forest damage.

Material and methods

The method for selecting survey plots and sample trees was based mainly on international recommendations for forest condition surveys (Wijk 1989). The network of grid points is based on the land use map (scale 1:10 000). Up to 12 points (A-L) on every map page were selected according to a system based on the mid point and diagonals of the map (Sonesson and Anderson 2001). The number of grid points per map page varies according to the survey goal and the geographical distribution of beech and oak. In accordance with international norms, points in wooded areas of less than 1 ha were excluded. Remaining grid points were selected on the ground and damage assessment carried out in those cases where at least 10 sample trees, beech and oak, having a minimum age of 60 years.

A total of 268 plots, 2606 beech trees and 1642 oaks were included in the 1999 survey. The distribution of the grid points in southern Sweden is presented in Figure 1. Manuals and field protocols were compiled with the aim of minimising all sources of uncertainty, misunderstanding and error (Sonesson and Anderson 2001). The field survey was carried out between July 16 and August 27 1999. During the second or the third week of August all members of the field crew and the project leaders carried out a check survey of special ”cocmparison plots”. Accordingly 53 beeches and 33 oaks were assessed by all the field observers with the aim of synchronizing field assessments carried out by different observers.

A total number of 18 damage indicators were observed in the field. Good light conditions and binoculars were needed. Defoliation was assessed on the uppermost 2/3 of the crown and is given as a percentage of a normal ample crown (=0-10% defoliation). The estimated defoliation included leaf loss, crown transparency, branch losses and dying branches. Normal self-pruning by self-shading was not included. The crown was compared with the best tree with full foliage that could grow at the particular site. Defoliation is expressed in 1 % classes from 0 to 100.

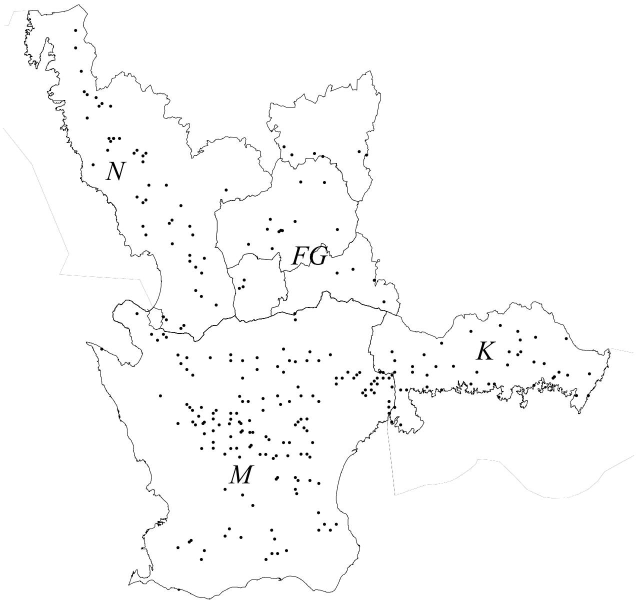

Figure 1. The geographical distribution of the 268 survey plots in the counties of Skåne (M), Blekinge (K) and Halland (N) and in the western parts of Jönköping and Kronoberg counties (FG). Map: Johan Holmquist.

Soil sampling was mainly carried out in parallel with the survey of forest condition. One general sample per survey plot was taken from the subsurface mineral layer at a depth of 20-30 cm. Soil samples were taken using a 3.2cm auger at a distance of 1-0.5 m from the trunk of the sample tree. Soil samples were collected from a total of 240 plots during 1999. An additional 18 soil samples were taken in June 2000, of which 15 were taken from holes that were dug for the purpose because it was impossible to take samples with an auger in the stony ground.

The soil chemical analyses, were carried out on soil samples dried at 40°C (up to 105°C correcting for water content) and sifted through a 2mm sieve at Dept. Ecology, Lund University (Balsberg 1990, Anon. 1998, Sonesson and Anderson 2001).

Before data preparation the defoliation parameter was divided into four classes in accordance with the ICP Forest Manual (Anon. 1998); 0-10%, 11-25%, 26-60%, >60%. Soil pH was divided into three classes; normal, slightly acid and very acid (pH_{H20} >5, 4.5-5 and <4.5 and pH_{BaCl2}>5, 4.2-5 and <4.2, while the base saturation level was broken up into three classes; normal, low and very low (>20%, 10-20% and <10%).

The check survey demonstrated the difficulties that exist in respect of subjective assessments of tree vitality. However, the differences in assessment between the nine field observers were generally within the margin of error and consideration was taken of the individual variation in damage assessment when evaluating the results.

Results

The condition of beech and oak in forests in southern Sweden has deteriorated since the first monitoring in 1988. The mean value of defoliation in beech has increased from 6% to 21% and in oak from 11% to 33% (Figure 2). In 1999, 27% of the beech and 59% of the oak trees showed more than 25% defoliation, compared to 3% of the beech trees and 9% of the oaks in 1988 (Figure 3).

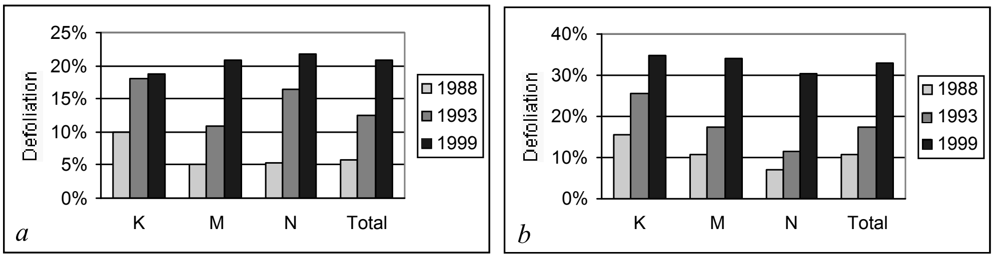

Figure 2. Mean values of defoliation in (a) beech and (b) oak in southern Sweden in 1988, 1993 and 1999.

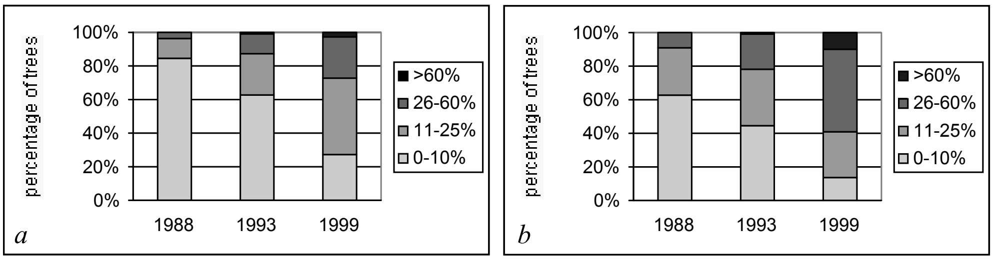

Figure 3. Defoliation according to ICP Forests in (a) beech and (b) oak in 1988, 1993 and 1999.

The study demonstrated a significant negative relation between defoliation and base saturation in both beech and oak plots (Figure 4). The soil condition of the subsurface mineral layer at a depth of 20-30 cm was highly acid (i.e. pH $_{(BaCl2)}$ values lower than 4.2) in 86% of the forest stands surveyed (Figure 5). A base saturation of less than 20% was reported from 76% of the stands, and a base saturation of less than 10% was found in 39% of the stands surveyed (Figure 6).

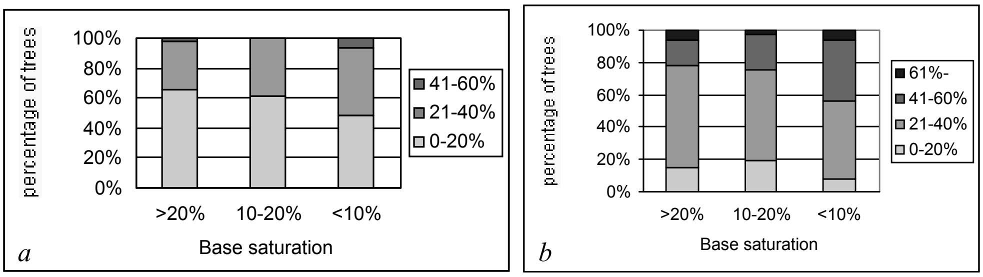

Figure 4. Defoliation in (a) beech and (b) oak in relation to base saturation.

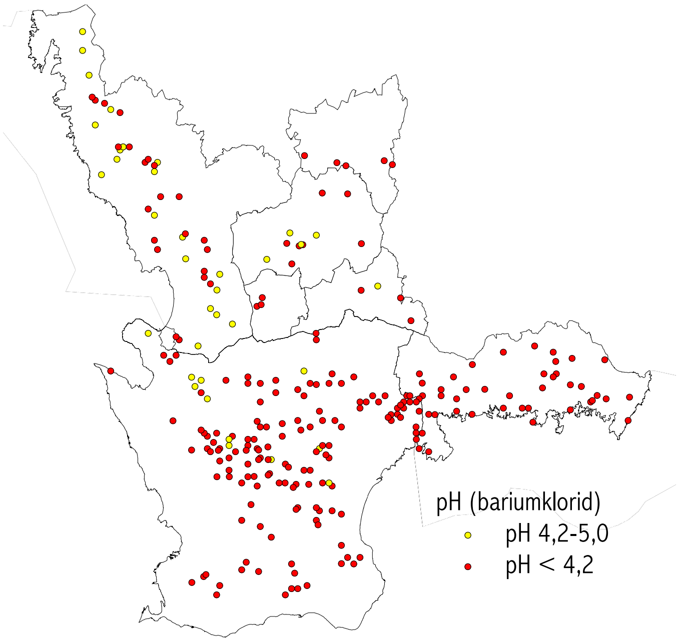

Figure 5. Geographical distribution of pH $_{(BaCl2)}$ in subsurface mineral layer, at a depth of 20-30cm at 258 survey plots. Map: Johan Holmquist.

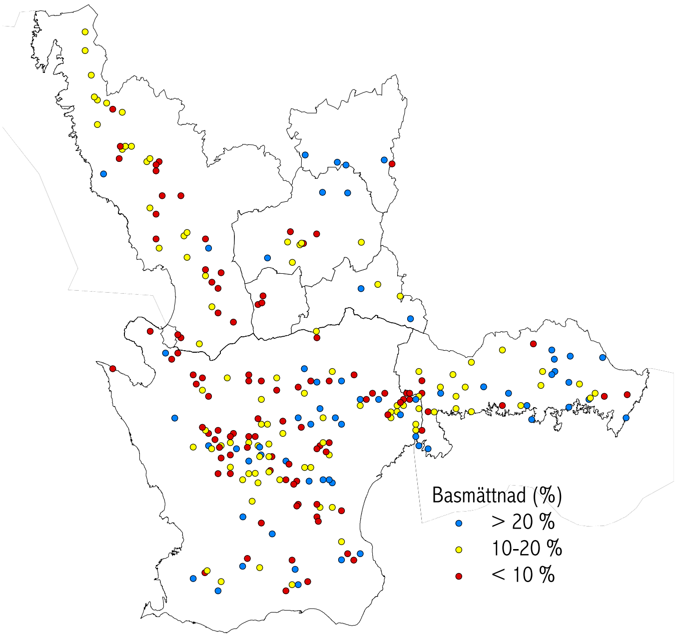

Figure 6. Geographical distribution of base saturation (%) in subsurface mineral layer, at a depth of 20-30cm at 258 survey plots. Map: Johan Holmquist.

Discussion

The results of the survey of forest condition in 1999 showed that defoliation in both beech and oak had increased since the first survey of forest condition in 1988. Mean defoliation in beech and oak was three times higher than in the first survey. However, defoliation varied to some extent between years. Weather conditions, insect attacks and seeding among other things, appreciably affect tree vitality. It can therefore be difficult to draw firm conclusions from individual surveys.

Annual or regular surveys of fixed plots are consequently important if we want to be able to interpret the development of forest damage. On the other hand the annual monitoring of forest condition in Sweden has its limitations since the network of monitoring plots is sparse and the number of sample trees few. *Level 1* and *Level 2* plots are therefore unable to give us a clear picture of the extent and development of the damage in Swedish deciduous hardwood forests

The defoliation in beech and oak in southern Sweden was comparable with the level of defoliation reported from other parts of Europe. The main area of forest damage can be found in Central and Eastern Europe (UN/ECE and EC, 2000). In EU countries broadleaves showed a higher share of damage (22.1% of trees with >25% defoliation) than coniferous trees (14.7% of trees with >25% defoliation) in 1999 (Anon 2000). Of all tree species surveyed in Europe the pedunculate oak, *Quercus robur*, showed the highest mean defoliation, 25% (n=4 987). Several other tree species, among them beech, *Fagus silvatica*, and Norway spruce, *Picea abies*, showed a 20% mean defoliation (n=11 910 and n=27 562 respectively).

The current soil acidification has been discussed many times as a contributing factor in the development of forest damage. The present report showed that the southern Swedish beech and oak forests grow on acid soil. The soil chemical analyses showed that almost all the surveyed beech and oak plots in southern Sweden were extremely acid and had a low base saturation. The base saturation level is one of the best measures of the balance between alkaline and acid elements in the soil and the investigation showed that only 24% of the survey plots had an acceptable base saturation. The results were hardly surprising. A raft of other studies has shown similar results (Falkengren & Tyler 1992, Jönsson et al. 2000, www-markinfo.slu.se). Our survey does show, however, that acidification and leaching of nutrients are far-reaching even in the richer deciduous forests. The significance to the damage problem of the current acidification of the soil cannot therefore be ruled out. The results indicate that poor soil status, i.e. low base saturation (<10%), can have a negative influence on tree vitality, as the statistical analyses showed significant negative correlation between defoliation and base saturation in both beech and oak stands of southern Sweden.

The immediate consequence of the emergent damage in beech and oak is a growing concern among forest/land owners, civil authorities, lovers of the countryside, as well as the processing industry. We know from historical documents that damaged and dead oaks have existed in Europe in previous centuries. The extent and distribution of forest damage we see today in both beech and oak is thought to be much more extensive, however.

If we are to do something about the reduced forest vitality we must increase the intensity of research into the underlying factors and possible countermeasures. We must find out clearly what is going on in the beech and oak forests of southern Sweden. Is the damage we see in beech and oak specific to these species or are the problems an indication of larger environmental problems?

Conclusion

- The damage situation for both beech and oak in southern Sweden deteriorated sharply since the first survey of forest condition in 1988. Mean defoliation at the tree level increased from 6% to 21% in beech and from 11% to 33% in oak.
- The majority of the plots surveyed were extremely acid and showed a low (<20%) or very low (<10%) base saturation.
- The study showed that poor soil status, e.g. low base saturation, may exert a negative influence on tree vitality, with a significant negative correlation between defoliation and base saturation level in both beech and oak stands.
- Surveys of forest condition such as this, with a large number of permanent plots and numbered trees followed up since 1988, are important in providing a clear picture of the forest damage situation. The large volume of survey data can, in addition, be used for further research and analysis.

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Forest continuity in relation to dispersal capacity of species – an example

Erik Öckinger[1], Mats Niklasson[2] and Sven G. Nilsson[1]

[1]Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden
[2]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences,
Box 49, 230 53 Alnarp, Sweden

Corresponding author: Erik Öckinger. Phone: 046-2229323, e-mail:
erik.ockinger@zooekol.lu.se

Abstract

Indicator species are often used to detect forest with a long temporal continuity. However, only species restricted to such forests because of their poor dispersal capacity should be used as continuity indicators. The dispersal capacity of one species suggested as a continuity indicator, the lichen *Lobaria pulmonaria* has been studied recently in southern Sweden. The results of that study suggest that *L. pulmonaria* has very poor long-range dispersal capacity, and hence would be a suitable indicator of forest continuity. It is important to pay attention to the dispersal capacity and dispersal strategy of different species when planning for nature conservation. If the focal species are short-distance dispersers, the efforts should be concentrated at protecting and enlarging biotopes where the species is found today.

Keywords: Forest continuity, indicator species, *Lobaria pulmonaria*, dispersal capacity

1. Introduction

Forests with long temporal continuity are often assumed to contain a high diversity of species (e.g. Arup *et al*. 1997, Nordén & Appelqvist 2001). Often the history of a forest is poorly known. One way to determine whether a forest has a long continuity or not can be to use some kind of indicator (e.g. Nordén & Appelqvist 2001, Rolstad *et al* 2002). Several authors have tried to find species that can be used as indicators of forest continuity, e.g. Rose (1976, 1992), Tibell (1992), Kuusinen (1996), Arup *et al*. (1997), based on the fact that some species are mainly found in forests assumed (or known) to have existed for a long time. Today, there is an ongoing debate on the use of indicator species and on the concept of forest continuity (e.g. Nilsson *et al*. 2001, Nordén & Appelqvist 2001, Rolstad *et al*. 2002). One reason for this is the knowledge that the species mainly found in these forests can be restricted to this kind of habitat either because they depend on certain microhabitats not or seldom found in younger forests, or because they have poor dispersal capacity (Sillett *et al*. 2000). Only species in the last category can be regarded as true indicators of forest continuity (Nordén & Appelqvist 2001). Some species suggested as indicators of forest continuity have later been found to have good dispersal capacity and to occur also in other types of forests (Nordén & Appelqvist

2001). Thus, there is a need for further research of the dispersal capacity of species suggested to be indicators of forest continuity (Nordén & Appelqvist 2001, Rolstad *et al*. 2002).

2. An example: *Lobaria pulmonaria*

One species suggested to be dependent on forest continuity is the epiphytic lichen *Lobaria pulmonaria* (e.g. Rose 1976, 1992, Kuusinen 1996, Arup *et al.* 1997, Nitare 2000). This species has been suggested to have poor dispersal capacity by previous studies (e.g. Fritz & Larsson 1996, Sillett *et al*. 2000, Gu *et al*. 2001), but very few studies where the dispersal capacity actually has been measured have been performed. However, a recent study in southern Sweden has investigated whether the local distribution of *L. pulmonaria* is mainly limited by its dispersal capacity or by lack of suitable substrates (Öckinger 2001). The number and position of trees with *L. pulmonaria* in 1992 and 2001 were compared. Dispersal distances were measured as the distances between newly colonised trees and trees on which *L. pulmonaria* grew in both 1992 and 2001. It was found that during nine years, several trees in stands where *L. pulmonaria* was previously found were colonised by the lichen (Öckinger 2001). However only trees close to those on which *L. pulmonaria* grew already in 1992 where colonised, and the mean distance between these trees and the new-colonised trees was only 35 m. The species had not been able to disperse to any of the adjacent forest stands where it was absent in 1992, although those stands had a similar composition of tree species and soil properties as the stands where it was present (Öckinger 2001). These results strongly suggest that the most important factor regulating the local distribution of *L. pulmonaria* is its poor long-range dispersal capacity.

L. pulmonaria, as many other lichens, has two different dispersal possibilities: small sexually produced spores and larger vegetative dispersal bodies (soredia and isidia). Fragmentation may also be an important way of reproduction and dispersal. However, large fragments created by events such as strong wind, heavy rain or by animals climbing on the trunk generally fall to the ground, to lower branches or to lower parts of the trunk of the same tree. Lichen spores are small (1-30 µm) and are probably generally wind-dispersed (Hansson *et al*. 1992), although some lichen-taxa have spores that are adapted to dispersal by insects (Tibell 1994). Since the spores are small, they can disperse farther than large vegetative dispersal bodies, and is probably the main agent when the lichen colonises new, remote patches. The dispersal by vegetative dispersal bodies is mainly short-range, can be mediated by, wind, water or animals, and is supposed to contribute more to population growth and stability than to dispersal (Hansson *et al*. 1992). In a stable, homogeneous landscape where suitable substrates for the lichen are common and evenly distributed, also a stepwise dispersal by vegetative dispersal bodies can eventually result in the colonisation of remote areas, but in the present fragmented forests, this is impossible for many species.

Some lichens, e.g. *L. pulmonaria*, are rarely fertile, and hence seldom produce spores, although they are known to have been fertile more often previously (Wirth 1995, Hallingbäck & Olsson 1987). Hence, we can assume that their dispersal capacity also was better than it is today. It has been suggested that air pollution, mainly by SO_2 could be responsible for this low fertility (Hawksworth *et al*. 1973). If this is the truth we can expect the frequency of fertile specimen of these lichens to rise slightly again, since the deposition of SO_2 has decreased. However, also genetic explanations have been suggested (e.g. Zoller *et al*. 1999).

3. Implications for conservation

L. pulmonaria has been found to indicate the presence of other rare lichens (Nilsson *et al*. 1995). This rises the question whether these species are limited by poor dispersal capacity. A good start would probably be to look at their dispersal strategies. Lichen species that mainly (or only) reproduce asexually and disperse by means of isidia or soredia can be assumed to be dispersal-limited. Species that mainly reproduce sexually and disperse by means of spores are probably not dispersal-limited. Instead they can be assumed to be limited by availability of suitable habitats. The dispersal capacity of species also has implications for conservation strategies. To gain dispersal-limited species, those sites where the focal species are found today should be protected and expanded, since they are unable to disperse to other sites, even if the conditions would be optimal to survive there. To protect species which are good dispersers but depend on rare habitats, we need to create more of, or restore, their particular habitat. This might include the reintroduction of certain disturbance-regimes.

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Abstracts of oral presentations

Session 1: Nutrient sustainability

Impact of harvest of biofuels on nitrogen fluxes in forests in Sweden
by *Cecilia Akselsson and Olle Westling*

Akselsson Cecilia, Lund University, Lund. Post adress: Chemical Engineering II, Center of Chemistry and Chemical Engineering, P.O. Box 124, SE-221 00 Lund, Sweden; Phone: +4646 2224866; E-mail: cecilia.akselsson@chemeng.lth.se
Westling Olle, IVL Swedish Environmental Research Institute, Aneboda

Sweden is planning to increase the use of biofuels in order to improve the sustainability of the energy system. Intense use of biofuels from forests will affect the nitrogen cycling. A model tool for mass balance calculations of nitrogen has been developed, in order to be able to predict future changes with different scenarios for harvest and atmospheric deposition. The model simulates accumulation in soil and trees and leaching from growing forests and clearcuts. Information about deposition, forest type, forest generation length, runoff, harvest for timber and biofuels is needed as input for the model. The model has been applied on the southern part of Sweden. The calculations show a net accumulation for the last 50 years, which leads to a risk of nitrogen saturation and leaching. However, a scenario with intense use of biofuels in the future implies a risk of net loss, according to the model calculations.

The significance of soil acidification and nitrogen deposition in storm damages: results from permanent observation plots in Switzerland
by *Sabine Braun*[1)]*, Christian Schindler*[2)] *and Walter Flückiger*[1)]

[1)] Institute for Applied Plant Biology, CH-4124 Schönenbuch, Switzerland
[2)] Institute for Social and Preventive Medicine, University of Basel, 4051 Basel, Switzerland
e-mail sabine.braun@iap.ch

In a network of permanent observation plots in Switzerland, the storm "Lothar" uprooted 18.7% of *Fagus sylvatica* and 14.8% of *Picea abies*. The percentage of uprooting was significantly inversely correlated with actual soil base saturation. At a base saturation of ≤40% (calculated as an average over 0-40cm depth) uprooting was increased by a factor of 4.8 in beech and by a factor of 3.6 in Norway spruce compared to less acidic soils. In beech, the percentage of uprooted trees was also significantly correlated with nitrogen concentration in the leaves (positively) and with coarse pore volume in the soil (negatively). There was neither a relation with seasonal ozone dose nor a relation with crown transparency, stem diameter, crown size, slenderness, social position and position within the stand. The results suggest that anthropogenic stress factors play an important role in the extent of the "Lothar" damages in Switzerland.

N induced changes in nutrition status in beech in Swiss forests and their consequence for sustainable forestry

by *W. Flückiger, E. Hiltbrunner, L. Tomova, S. Braun*

Institute for Applied Plant Biology
CH-4124 Schoenenbuch
e-mail walter.flueckiger@iap.ch

According to model calculations, average N deposition in Swiss forests increased during the second half of the past century from 11-13 kg N ha^{-1} a^{-1} to up to 30 kg N ha^{-1} a^{-1}. Stem increment and shoot growth in permanent observation plots in beech revealed a significant positive correlation with modelled N depostion. Seeds of beech germinated less with increasing N concentrations in foliage. Between 1984 and 1999, N/P ratio in foliage of beech increased by 39%. With increasing N/P ratio, a decreasing size and a growing attack of beech nuts by the moth *Cydia amplana* was observed. N fertilization experiments with 0-160 kg N ha^{-1} a^{-1} in beech afforestations showed increasing attacks by pathogens and pests with increasing N treatments and N/P, N/K, respectively, as well as a decreasing concentration of starch in roots and fungistatic phenols in roots and leaves.

The contribution of ectomycorrhizas to release and acquisition of mineral nutrients

by *Douglas L. Godbold, Patrick A. W. van Hees*[*]*, Susan. I. Vinogradoff, David L. Jones and Georg Jentschke*

School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, UK,
Dept. of Natural Sciences, Mid Sweden University, 851 70 Sundsvall, Sweden. Tel 0044 1248 382447 Fax 0044 1248 354997. E-mail d.dlgodbold@bangor.ac.uk

Ectomycorrhizas are important in the acquisition of mineral nutrients by trees. In the paper we will present a summary of our work on the uptake on N, K P and Mg by ectomycorrhizal *Picea abies* grown under controlled conditions. In addition the role of ectomycorrhizas and roots of *Picea abies* in the weathering of silicate minerals will be discussed. This information together with estimates of root turnover will be used to estimate internal nutrient cycling within the soil. This will be discussed in relation to forests under changing environmental conditions.

Defining threshold nutrient values for Swedish deciduous tree species

by *Ingrid Stjernquist & Kerstin Sonesson*

Dept of Ecology, Plant Ecology, Lund University, SE-223 62 Lund, Sweden
e-mail ingrid.stjernquist@planteco.lu.se

The concentrations of the essential nutrients in needles have been identified as useful indicators for assessing nutrient status in Scandinavian stands of Norway spruce and Scots pine. General deficiency threshold values has been defined and used to study the impact of management and deposition on tree vitality all over Europe. No such thresholds have been defined for deciduous tree species, the nutrient concentration spans given are imprecise

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[*] author for correspondence. present address: Dept. of Natural Sciences, Mid Sweden University, 851 70 Sundsvall, SWEDEN, tel. +46 60 148909, fax +46 60 148820, e-mail: patrick.vanhees@kep.mh.se

resulting in very uncertain nutrient ratios to N. This is unfortunate as deciduous tree species are identified as crucial for a sustainable forestry. Foliage data collected during the last 10-15 years shows that certain nutrient values are below the European span. This can be identified as nutrient deficiency or imbalance but the discrepancy may also depend on differences in tree species, life strategies, provenances or age. The importance of these factors will be discussed in relation to sustainable forestry and the need for improved usable tools for monitoring deciduous tree vitality in Sweden.

Production of ectomycorrhizal mycelia at different soil depths in spruce forests and mixed forests (spruce/oak) in southern Sweden

by *Håkan Wallander[1], Hans Göransson[2], Ulrika Rosengren[2]*

[1] Department of Microbial Ecology, Lund University, 223 62 Lund, Sweden
[2] Department of Plant Ecology, Lund University, 223 62 Lund, Sweden

Nutrient uptake by forest trees is greatly dependent on the nutrient absorbing ectomycorrhizal (EM) mycelia growing in symbiosis with the fine roots. We estimated the production of EM mycelia in pure spruce and mixed spruce/oak forests in southern Sweden by placing mesh bags at three different soil depths (5, 15, 30cm). The mesh bags were collected after 12 months and we found that more EM mycelia were produced in spruce (590 kg ha^{-1}) compared to mixed forests (420 kg ha^{-1}). The distribution of soil mycelia was more concentrated in the top horizon (5 cm) in the mixed stands compared to the spruce stand. The δ^{13}C and δ^{15}N value was estimated in mycelia collected from mesh bags, in saprophytic and ectomycorrhizal fruitbodies and in leaves and needles from the trees. The δ^{13}C value of mycelia collected from mesh bags was similar as values of EM frutbodies and it was not influenced by soil depth. The δ^{13}C value in mycelia from mixed forests suggested that the mycelia received more carbon from spruce threes than from oak trees. The δ^{15}N value of the mycelia and of the surrounding soil increased with soil depth indicating that the EM mycelia utilized nitrogen from the same horizon as were they were collected.

Session 2: Restoration of biodiversity

Immediate effects of patch retention felling to epixylic vegetation in boreal forest

by *Harri Hautala*, Sanna Laaka-Lindberg, Ilkka Vanha-Majamaa & Jyrki Jalonen*

Finnish Forest Research Institute, Vantaa Research Center,
P.O.Box 18, FIN-01301 Vantaa, Finland
*e-mail harri.hautala@metla.fi

We examined how patch retention felling and mechanical scarification affects the initial epixylic vegetation on coarse woody debris (CWD). Retention patches were placed on paludified spruce forest patches, as they had the highest amount of CWD and epixylic plant species diversity. Vegetation was monitored from 112 logs both inside and outside retention patches during three consecutive years after the felling. Vegetation suffered especially in the felling area as a result of high amount of CWD destroyed in fellings and especially scarification, and also close to the edges of retention patches probably as a result of altered microclimate. However, uprooted trees and understorey vegetation, which after fellings became more grass-dominated and higher, seemed to give shelter to the epixylic species and help them to survive over the regeneration stage of the forest. Also the moisture conditions in the paludified patches were even better after the fellings than before, since evaporation in the surrounding felling area was lower.

Dispersal of forest insects in relation to habitat predictability

by *Jonas Hedin*

Dept. of Ecology, Animal Ecology, Lund University, SE-223 62 Lund, Sweden
e-mail: jonas.hedin@zooekol.lu.se

In this review I show that empirical studies of the dispersal of forest insects, either direct or indirect, support the theory that the predictability of the habitats have had a great impact on species dispersal. Fire-dependent insects, species dependent on newly dead wood and species living in carrion have a very well-developed dispersal on a scale of several km up to tenth of kilometres. However, species living in and exploiting more long-lasting habitats like coarse wood debris and old hollow trees seem to have a limited dispersal, sometimes on a scale of only a few hundred meters. The conservation measures needed to preserve species depend on both their dispersal propensity and dispersal ability. In order to get an effective conservation of all species we have to adopt a landscape ecological approach that integrates the knowledge of species dispersal.

Decomposition and decay class dynamics of dead trees in Sweden

by *Nic Kruys*

Department of Forest Resource management and Geomatics, SLU Umeå, SE-90183 Umeå, Sweden.
Nic.Kruys@resgeom.slu.se
+46 90 786 9837

Dead trees are important as a carbon store and as habitat for many threatened species of plants, fungi and animals. Increasing demand for the incorporation of woody debris in managed forests calls for greater knowledge of decomposition rates and decay class dynamics, so that tools for forest management planning can be developed.
Here, a recently started research project is presented, aiming at defining decomposition rates for woody debris in Swedish forests. The project will concentrate both on the continuous decay process (i.e. mass and volume loss), as well as transition rates between decay classes (habitat-related variables). Currently existing chronosequence methods will be used and developed further. Thus decay rates will primarily be provided without time-consuming long-term studies, so as to be incorporated in the ongoing Heureka programme at SLU, Umeå.

Mortality of retention trees: a study in Scots pine stands in Småland

by *Lundberg, Åsa & Niklasson, Mats*

Southern Swedish Forest Reasearch Centre, Swedish University of Agriculture Sciences, P.O. Box 49, SE-230 53 ALNARP

e-mail: lundbergasa@hotmail.com
mats.niklasson@ess.slu.se

A study was made to give information about the mortality of pines (*Pinus Sylvestris*) that were left as retention trees. A pine-dominated landscape in Småland was chosen where retention trees have deliberately been saved since the 1970s. 21 areas were visited where tree-ring samples were taken from 100 living and 40 dead trees. Year of death was determined for around 35 trees with dendrochronological cross-dating. (Field information was taken for all trees, such as diameter, height and site type). We calculated the amounts of dead wood added into the forest. Preliminary results show that mortality varied greatly at stand level but had a mean in the same level as the results from the Swedish National Forest Inventory. Main cause of death was pine canker and wind breakage but nesting-holes from birds was also an important cause.

Session 3: Forest resource management

Forest dynamics and the effect of Moose browsing - a modelling attempt

by *Christer Kalén*[1] *and Jonas Bergquist*[2]

[1]Department of Ecology, Ecology Building, Lund university, S 22362, Sweden
[2]Asa Forest research Station, Swedish University of Agricultural Sciences, S-36030 Lammhult Sweden

The interaction between forestry and browsing by different deer species (cervids) has scalated during the past century. High populations of moose and roe deer are today a relevant issue for any forester. Although large herbivore inflicts a substantial cost to forestry, they also constitute a considerable recreation value implying that an optimal level of forest damage versus herbivore density exists. In this context, developing a model is a useful tool when analysing the interaction between herbivore population, available forage and browsing damage. Modeling is an important tool for explaining or describing complex systems. Today, the meaning of the word model is somewhat indistinct and used in many occasions. Common to all models, however, is that they are a crude simplification of the complex reality.

We elaborate on how a model with aim to predict browse utilisation could be structured and what variables that need to be included. Several modeling methodologies are utilised (conceptual, theoretical, empirical and dynamic) to sort and analyse the dynamics of herbivore feeding and biomass availability. The moose is used as a model animal and the authors discuss how the models can be extended to include also other herbivores.

The authors conclude that model accuracy is dependent on the operating spatial and temporal scale. Detailed mechanistic models are useful to analyse individual feeding pattern but have the disadvantage to be time consuming on a larger scale. Less detailed models may catch the regional browsing intensity but often falls short to describe browsing pattern in a specific stand. The authors therefore argue for multi-package-modeling to cope with uncertainty with regards to browse utilisation dynamics.

Mixed forest stands as a means of sustainable forest management: project presentation and first results

by *Julia Koricheva*

Section of Ecology, Department of Biology
University of Turku, FIN-20014 Turku, Finland
email julkoric@utu.fi

The aim of our project (which is a part of the Research Programme on Sustainable Use of Natural Reseources (SUNARE, 2001-2004) financed by the Academy of Finland) is to examine the effects of forest diversity on various aspects of ecosystem functioning (insect and mammalian herbivory, pathogens, soil fauna, microbial community, decomposition, tree growth etc) by using several long term experiments in which forest diversity has been manipulated. Our main experiment in SW Finland consists of monocultures and different two-, three- and five-species mixtures of Scots pine, Norway spruce, Siberian larch, silver birch and black alder. In addition we are using several forest diversity experiments established by the Finnish Forest Research Institute and the Swedish University of Agricultural Sciences.

First results indicate that forest diversity has a significant effect on seedling survival and tree herbivory by mammals and insects.

Defining sustainability and applying it to management - Some implications for principal thinking in forestry

by *Harald Sverdrup, Mats Svensson and Ola Sallnäs*

Lund University, Box 124, SE-221 00 Lund, Sweden
e-mail: harald.sverdrup@chemeng.lth.se

Sustainability of an activity or assembly of activities can be defined in terms of natural, societal and economic sustainability. We have suggested such definitions and subsequently operationalized these into action flow charts and management decision sequences for forest management operations, planning and economic analysis.
For forest management we can define robust criteria for nutrient sustainability assessments and goals and show how these must be integrated with economic criteria involving traditional variables but also by inclusion of hidden terms. These design plans are limited by suggested social criteria defined by public acceptance and environmental responsibilities.

Forest management and vegetation changes in Finland

by *Ilkka Vanha-Majamaa*[1] *& Jyrki Jalonen*[2]

[1]Finnish Forest Research Institute, Vantaa Research Centre, P.O. Box 18, FIN-01301 Vantaa, Finland; ilkka.vanha-majamaa@metla.fi, phone: + 358 9 85705557, fax: +358 9 85705531
[2]Mescalero Apache Tribe, Division of Resource Management & Protection, P.O. Box 227, Mescalero, NM 88340, U.S.A.

During the last 30 years, over 20% of forests in Finland have been clear-cut, which has increased the proportion of forests in early successional stages. In an experimental study comparing five different felling methods, clear felling and green tree retention felling with low (10%) level of retention resulted in major vegetation changes with little recovery during a three-year post-treatment monitoring period. In gap felling (with and without scarification) and selection felling (50-70% retention), vegetation changes were minor and recovery fast. Finnish national forest inventory (NFI) data shows a landscape level decline in the total cover of understorey vegetation during the last 50 years. In forests younger than 60 years, total understorey vegetation cover is 20-30 %-units lower than in forests older than 100 yrs. At the same period, pioneer species have become more abundant and frequent. Our results show that intensive forestry practices have serious long-term effects, but they may be partly avoided by using for example single-tree or group-selection systems.

Developing the complex forest ecosystem model FORSAFE – motives, means and the learning loop

by *Patrik Wallman and Harald Sverdrup*,

Biogeochemistry group, Chemical Engineering II
Lund University, P O Box 124, SE-221 00 Lund, Sweden
e-mail: patrik.wallman@chemeng.lth.se

The forest ecosystem is very complex; it consists of different parts that are influenced by each other and external factors, both natural and anthropogenic. The feedbacks are numerous and often non-linear. Building forest ecosystem models implies to simplify this system, also omitting parts considered insignificant. In forest growth models, soil is most often an omitted part. In this paper, we will show that the soil is so important that it cannot be omitted if we want to predict forest sustainability in a long time-perspective. We also show that a mechanistic description of the involved processes is necessary, in both the soil and the aboveground parts. The mind-maps and model diagrams will be explained to communicate parts of the modeling process and some of the important decisions made in the sorting and prioritizing process.
Developing such a model is an iterative work that is much facilitated if the work itself is modeled and this model is clear to the developers. Therefore, a group modeling approach was adopted in order to develop the present FORSAFE model that integrates the carbon-, nitrogen- and plant nutrient cycles. We also describe the learning loop model used during the development of the complex forest-soil ecosystem model FORSAFE, to illustrate how model purpose determines the model structure and complexity.

Buffer zones along small streams in managed forests

by *Westling Olle[1] and Per Petersson[2]*

[1]IVL Swedish Environmental Research Institute, Aneboda. Post address: IVL Aneboda SE 360 30 Lammhult, Sweden. E-mail olle.westling@ivl.se
[2]SLU (Swedish University of Agricultural Sciences), Asa, Sweden

A study of narrow buffer zones with deciduous forests along small streams is conducted in Asa research forest as a part of the SUFOR program. The aim of the special management near streams is to increase the occurrence of deciduous species in managed forests, and also improve water quality and the biological diversity in both the terrestrial and the limnic environment. The buffer zone was established in 1995 after cutting of all conifers up to 5 meters from the streams. The cutted areas were naturally regenerated by deciduous species. The study comprises effects on surface water chemistry and limnic organisms (benthic algae) and the growth and species composition of the buffer zone in a catchment dominated by coniferous forest. The final evaluation in 2004 will include a description of cost/benefit and recommendations for management of buffer zones, dominated by deciduous species, along small streams.

Abstracts of poster presentations

A Systems Approach to Understanding Carbon Allocation in Trees

by Salim Belyazid[1], Anna Maria Jönsson[2] & Ingrid Stjernquist[2]

[1]Chemical Engineering II, Box: 124, 22100 Lund, Day tel: +46-462224866,
Email: salim.belyazid@chemeng.lth.se
[2]Department of Ecology, Forest Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden

The present work studies the dynamics of carbon allocation in trees. It relies on a system dynamics approach to bring both tree endogenous (carbon/nitrogen ratio differences between shoots, roots, and other sink/sources of hydrocarbons, xylem & phloem flows…) and exogenous (temperature, air moisture, radiation, soil moisture, soil nutrient content...) controls affecting the allocation into one comprehensive dynamic system. The tree is divided into three connected compartments, namely foliage, fine roots, and woody tissues. Nutrient and water uptake by the roots and carbon uptake and transpiration by the foliage are controlled by both internal and external factors, and in turn control the concentrations of carbohydrates and nutrients in the shoots and roots. The differences in concentrations and in the xylem and phloem transport flows are also decisive of the target of allocation. The work is intended to start an iterative process which goes from a mental understanding of the dynamics of the system, to a causal loop diagram illustration of it, then to computer model testing its practical applicability, and back again to modifying the original mental model when needed, and so on.

Modelling the Impacts of Climate Extremes: Extreme Weather Impacts on North European Forests

by *Lars Bärring[1], Anna-Maria Jönsson[2], Peter Schlyter[3], Ingrid Stjernquist[2],Harald Sverdrup[4] & Patrik Wallman[4]*

[1] Dept of Physical Geography and Ecosystem Analysis, Lund Univ. Box 118,
SE-221 00 Lund, Sweden, [2]Dept of Ecology, Plant Ecology, Lund Univ. SE-223 62 Lund, Sweden,
[3]Dept of Physical Geography, Stockholm Univ. SE-106 91 Stockholm, [4]Dept of Chemical Engineering, Lund Univ. Box 124, SE-221 00 Lund, Sweden
e-mail lars.barring@natgeo.lu.se

Climate change due to global warming will have substantial impacts on the natural environment. It is increasingly recognized that changes in the severity and frequency of extreme events are likely to be more important than changes in the average climate. The EU-funded project "Modelling the Impacts of Climate Extremes" (MICE) will identify changes in the occurrence of extremes of rainfall, temperature and windstorm, using information from global and regional models. The Swedish group will focus on impacts on forest ecosystems. We will assess extreme-value statistics of climatic variables relevant to forest damage, catastrophic impacts of extreme weather events on North European forests and analyse interactions between weather extremes and forest production in present-day climate and for selected climate-change scenarios.
In order to achive this MICE will cooperate closely with the Sufor programme. Central to the MICE approach is a continuing dialogue with various stakeholders.

Manipulating the nutrient status of Danish Norway spruce forest ecosystems

by *Ingeborg Callesen, Morten Ingerslev, Vivian Kvist Johannsen and Karsten Raulund-Rasmussen*

Skov & Landskab, Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, 2970 Hørsholm, Tlf. (+45) 45 76 32 00, Fax. (+45) 45 76 32 33, e-mail(Ingeborg Callesen): ica@fsl.DK

Data from 55 Danish fertilization experiments were compiled and reinvestigated aiming at revealing treatment effects on needle and soil nutrient status, tree growth, and correlations between these parameters. The experiments were carried out in 17 – 100-year-old Norway spruce stands on nutrient poor soils between the 1950's and the 1990's. Data from the control plots showed that only a minor part of the experiments had trees that suffered from nutrient deficiencies and that only weak correlations between the soil nutrient pools, needle chemistry and height growth could be established. The treatments had little or no effects on the soil. The treatments increased the needle concentrations, whereas growth response varied. However, results indicate that the most pronounced treatment induced growth increase could be observed for trees that both had relatively high needle nutrient concentrations and at the same time were able to increase these concentrations further in response to treatments.

Linking regional fire activity, weather, and tree rings: an example of Komi republic

by *Igor Drobyshev*[1], *Mats Niklasson*[2] *and Per Angelstam*[3]

[1]Department of Plant Ecology, Ecology Building, Sölvegatan 37,
Lund University, S-223 62 Lund, Sweden, Igor.Drobyshev@planteco.lu.se

[2]Southern Swedish Forest Research Centre, SLU, Box 49, 230 53 Alnarp, Sweden
Mats.Niklasson@ess.slu.se

[3]Grimsö Wildlife Research Station, Department of Conservation Biology,
Forest Faculty, SLU, SE-730 91 Riddarhyttan Sweden, Per.Angelstam@nvb.slu.se

Understanding the interplay of factors affecting the pattern of natural fire regime is an important prerequisite for providing sound conclusions within a range of sustainability and biodiversity-related research topics. We considered half-a-century long, annually resolved, and spatially implicit record of fire activity in the forests of Komi republic, East European Russia, to check for a link between weather variation and fire activity and to develop a proxy of regional scale fire activity from a local set of tree-ring chronologies of Scots pine (*Pinus sylvestris* L.). Specifically we address the following questions: (1) How does regional fire behavior relate to the annual weather variation considered with monthly resolution?, (2) Is there any climatically-controlled change in the fire behavior in Komi republic during the second half of 20th century?, and, finally (3) Can tree-ring data be related to the annual pattern of fire activity at the scale of a large boreal region?

The value of historical information for biodiversity preservation

by *Eliasson, Per & Nilsson, Sven G.*

Fil. Dr. Per Eliasson
Dept. of History, Lund University, Lund and Malmö högskola, Malmö,
e-mail: eliasson.per@telia.com
Prof. Sven G. Nilsson,
Dept. of Ecology, Animal Ecology, Lund University, SE-223 62 Lund, Sweden
e-mail: sven.nilsson@zooekol.lu.se

The biodiversity of a landscape is presumed to be determined by the extent and quality of current habitats. However, what is often forgotten is that populations seldom respond instantly to changes in habitats. To some extent, the amount differing between organism groups and species, present biodiversity is also dependent on previous states in the landscape. This is especially so when changes in habitats are rapid, which have been the case in southern Sweden. Therefore, we argue that historical information is crucial for efficient biodiversity preservation. Some examples are given from our current research.

Comparative studies of growth, nutrient concentrations and amounts of 6 different tree species planted in adjacent stands

by *Hagen-Thorn[1*], A., Armolaitis[2], C., Callesen[3], I. & Stjernquist[1], I.*

[1]Lund University, Sölvegatan 37, Ekologihuset, SE-223 62 Lund, Sweden
[2]Lithuanian Forest Research Institute, Liepø 1, Girionys, Lt-4312
[3]Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11, DK-2970 Hørsholm
[*] Corresponding author

Nutrient concentrations in different compartments in tree biomass are widely used for assessment of tree nutrient uptake and as indicators of forest health, for estimation of nutrient removal with harvest and studies on sustainability of forest management. The concentrations are both influenced by site characteristics and species genetic trait. We have compared 30-40 years old adjacent stands of 6 different (mostly deciduous) species, planted on originally the same soils, in terms of growth and foliar nutrient concentrations. The results have shown that along the range of soil fertility gradient studied, species factor was more important than site factor in explaining the differences in nutrient concentrations observed, significant differences between some species in nitrogen, sulphur and base cations are reported.

Stand-level effects of patch retention felling on CWD dynamics in boreal spruce forest

by *Harri Hautala* & Ilkka Vanha-Majamaa*

Finnish Forest Research Institute,
Vantaa Research Center, P.O.Box 18, FIN-01301 Vantaa, Finland
*e-mail harri.hautala@metla.fi

We studied the immediate effects of patch retention felling and scarification on the initial volume of coarse woody debris (CWD) and tree uprooting in paludified and upland spruce forest. Felling machinery destroyed immediately 8% of the CWD, and finally scarification destroyed 65% of CWD in the felling area, mainly deciduous and highly decayed CWD. In

the paludified patches, 46% of the trees, and 12% of the trees in upland patches were uprooted two years after the felling. The size and the shape of retention patch did not have effect on uprooting susceptibility. Destruction of highly decayed CWD and new uprootings lead to altered decay stage distribution of CWD, but the new substrate for epixylic species created by uprooting is extremely important, as 2/3 of the initial CWD is destroyed by felling operations and scarification. We suggest that the continuum and more stable decay stage distribution in CWD could be best maintained with less intensive forest management methods and reduced use of scarification.

Frost hardiness in bark and needles of Norway spruce in southern Sweden

by *Jönsson, A.M.*[1]*, *Kivimäenpää, M.*[2, 3], *Stjernquist, I.*[1] *and Sutinen, S.*[2]

1) Department of Ecology, Forest Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden,
Anna-Maria.Jonsson@planteco.lu.se
2) The Finnish Forest Research Institute, Suonenjoki Research Station, FIN-77600 Suonenjoki, Finland
3) The University of Kuopio, Department of Ecology and Environmental Science, PO Box 1627, FIN-70211 Kuopio, Finland

*presenting author

Bark necrosis and resin flows in Norway spruce have increased in southern Sweden over the last few decades. Frost damage late in spring has been suggested as a possible cause, but other factors besides the climate may have contributed to the damage. The nutrient status influences the hardening processes and plants with poor nutritional conditions have an increased sensitivity to frost. In this study the sensitivity to frost of bark and the hardiness status of needles of Norway spruce were compared with the nutrient status at two sites with different soil fertility. The trees were 30-40 years old. The hardiness status of the bark and needles was negatively affected by low concentrations of P and Mg.

Acidification induced chemical changes in coniferous forest soils in southern Sweden 1988 – 1999

by *Ulrika Jönsson, Ulrika Rosengren, Gunnar Thelin and Bengt Nihlgård*

Forest Ecology, Department of Plant Ecology, Ecology Building, Lund University,
223 62 Lund
Contact: Ulrika Jönsson
Phone: +46 46 222 93 07
Fax:+46 46 222 44 03
E-mail: ulrika.jonsson@planteco.lu.se

Thirty-two Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) stands in Scania, southern Sweden, were studied for a period of twelve years to evaluate acidification induced chemical changes in the soil. Soil, at 20-30 cm depth in the mineral layer, was sampled in 1988, 1993 and 1999. Results show that pH($BaCl_2$) has decreased by on average 0.17 units between 1988 and 1999, accompanied by an increase in aluminium concentration and a decrease in base saturation in the soil. In 1999, base saturation was below 5% in 58% of the sites compared to 16% in 1988 and 7% in 1993. Soil supply of calcium, potassium and magnesium are low and declining. Based on C/N-ratios in humus, 45% of the sites may be subjected to leaching of considerable amounts of nitrate. The results show that acidification of coniferous forest soils in Southern Sweden continues, and that the plant available nutrient capital is declining.

Establishing the baseline of forest biodiversity

by *Håkan Ljungberg*

Department of Quaternary Geology, Lund University, Tornavägen 13, 223 63 Lund, Sweden

An analysis of insect macrofossils and pollen was used to study the effect of human impact on the structure and composition of an old-growth forest reserve in southern Sweden. The impact of forestry in the stand has been quite low, the forest continuity is long and the fauna of wood-living beetles is diverse. Peat cores from a small wetland cover approximately 1,000 years, a time during which an oak-dominated deciduous forest has given way to a spruce/beech mixture. In the beetle record, there is a close correspondence between the pollen percentages of tree species such as *Picea* and *Quercus* and the number of beetles monophagous on these trees. In addition, also features of the forest development such as the presence of coarse dead wood can be distinguished. The study demonstrates clearly that insect macrofossils provide a great deal of information that are not accessible by other palaeoecological methods.

Population size in relation to habitat quality in *Osmoderma eremita*, a vulnerable scarabaeid beetle living in hollow trees

by *Kajsa Mellbrand & Jonas Hedin*

Dept. of Ecology, Animal Ecology, Lund University, SE-223 62 Lund, Sweden
e-mail: krydolph@hotmail.com or jonas.hedin@zooekol.lu.se

Osmoderma eremita is a beetle living in old, hollow trees. Population sizes differs between trees and this could be explained by habitat quality. Correlations between tree characteristics and population size were examined in 71 trees by building multivariate models with multiple regression. Population sizes of adult *O. eremita* beetles were determined by mark-release-recapture using pitfall traps set in the hollows of the trees. We find that population size is larger in trees containing large amounts of wood mould, in trees where the entrance hole is higher above the ground and in trees without a living tree crown. A good knowledge of the habitat quality needs make it easier to identify suitable trees in the field but also when creating new suitable habitats for the species. Since wood mould volume is an important determinant of population size, it will take very long time before a tree becomes a good habitat.

Biomass and nutrient removals in early thinnings of Norway spruce (*Picea abies* (L.) Karst.) in western Denmark – differences between harvesting of green whole trees, dried whole trees and stems only

by *I.S. Møller*

Danish Forest and Landscape Research Institute, Hoersholm Kongevej 11, DK-2970 Hoersholm, Denmark, Tel: +45 45 17 83 12, Fax: +45 76 32 33, E-mail: ism@fsl.dk

In whole-tree harvesting of early thinnings for wood-chip production in Denmark, trees are often cut during winter and left to dry in the stands during the summer. Thereby nutrient-rich tree parts such as needles and twigs are returned to the forest ground. A study was carried out in two Norway spruce stands in western Jutland to estimate how much summer-drying reduces whole-tree nutrient removals compared to harvesting of whole green trees, and how this compares to nutrient contents of stems only. Single tree biomass and nutrient contents were determined by chipping the trees separately. Chip samples were removed for determination of dry mass and nutrient concentrations. For stems, sample disks were removed. Equations were developed for single tree biomass and nutrient contents for the three utilization intensities, and full rotation scenarios were modeled. Summer-drying reduces the nutrient removal, but still whole-tree nutrient removals are significantly larger than for stems removals.

Key words: Whole-tree harvesting, harvesting intensity, thinnings, nutrient removals, Norway spruce.

Age-related dynamics of biodiversity and carbon cycling of Icelandic woodlands (ICEWOODS)

by *Bjarni D. Sigurdsson*[1]*, Ásrún Elmarsdóttir*[2]*, Borgthór Magnússon*[2]*, Ólafur K. Nielsen*[2] *& Guðmundur Halldórsson*[1]

[1]Icelandic Forest Research, Mógilsá, 116 Reykjavík, Iceland.
[2]Icelandic Institute of Natural History, P.O. Box 5320, 125 Reykjavík, Iceland.
e-mail: Bjarni.Sigurdsson@skogur.is

ICEWOODS is a new research project in Iceland on environmental effects of afforestation with introduced Siberian larch (*Larix sibirca*). It will focus on changes in plant composition, soil invertebrates and birds as well as changes in NPP and soil efflux of carbon. Siberian larch is Iceland's second most planted tree species after the native birch (*Betula pubescens*), and as such the key species to study in terms of land-use change and forestry.

Afforestation sites of 5, 10, 15, 35, 55 years, have been selected for the study, as well as adjacent open rangeland and a site with native birch. This is the first project in Iceland looking into changes in carbon sequestration and biodiversity following afforestation.

Understanding the age-related dynamics of the plantation ecosystems is the key for sound environmental assessment of afforestation programs. They are foreseen to increase when Iceland ratifies the Kyoto-protocol. Such information is also essential for integrating forest carbon budgets across space and time.

Mass balances for mineral nutrients in forestry comparing natural sustainability against current harvest volumes

by *Harald Sverdrup, Johan Holmquist, Gunnar Thelin, Ulrika Rosengren*

Biogeochemistry group, Chemical Engineering II
Lund University, P O Box 124, SE-221 00 Lund, Sweden
e-mail: harald.sverdrup@chemeng.lth.se

Mass balances for mineral nutrients like Mg, K and Ca have been made at Asa Research Park, by using weathering rates estimated with the regional versoin of the PROFILE model, plant content measurements and deposition estimates. These mass balances have been used to analyze a number of forest management scenarios with respect to nutrient sustainability in the long term in the absence of fertilization and liming for conifer monocultures and mixed conifer-deciduous stands. The results show that the sustainability potential for production can vary significantly in a forested area, At Asa Research Park the standard forest yield is generally set significantly higher than the present estimates of the sustainability potential. Present management implies and partly unsustainable harvest. This apparent problem may easily be turned to a possibility by forest management. The implication is that with properly designed fertilization, the forest may be made sustainable at any production level.

Modeling environmental effects on ground vegetation biodiversity

by *Harald U. Sverdrup[1], Mats G. E. Svensson[1], Ingrid Stjernquist[2] and Jonas Hansson[3]*

[1]Chemical Engineering Lund University, S-221 00, Lund, Sweden
[2]Plant Ecology, Lund University, S-221 00, Lund, Sweden
[3]Netch AB, S-221 00, Lund, Sweden
e-mail;harald.sverdrup@chemeng.lth.se/www2.chemeng.lth.se

In this study, the environmental effect on the ground vegetation part of biodiversity is modeled. Ground vegetation dynamics and change in ground vegetation composition over time was modeled as a function of site status in terms of (1) present vegetation, (2) soil water, (3) temperature (4) soil nitrogen and (5) soil acidity and (6) geochemical properties of the soil. The model will cover the main process layers; historical distribution, physiochemical responses and ecological processes. The model is intended for the forested area of Southern Sweden, and make scenarios for the biodiversity future in this region. We intend to do this by combining several scientifically field tested mathematical models over spatial and temporal scale with new response modules. Response parameterization use data from Lund University Plant Ecology department archives and from the literature.

Key words; Biodiversity, systems analysis, dynamic modeling, ground vegetation, air pollution, climate change, CLRTAP-convention

Impact of ozone on growth and leaf senescence of European silver birch, Betula pendula

by *Johan Uddling[1], Per Erik Karlsson[2], Lena Skärby[1,2], Göran Wallin[1,3] and Gun Selldén[1]*

[1] Göteborg University, Botanical Institute, Box 461, SE-405 30 Göteborg, Sweden
[2] Swedish Environmental Research Institute, Box 47086, SE-402 58 Göteborg, Sweden
[3] Institute of Environmental Science and Conservation, Göteborg University, Box 464, SE-405 30 Göteborg, Sweden
Contact information:
Johan Uddling
Phone: 031-773 2631
Fax: 031-773 2626
E-mail: johan.uddling@fysbot .gu.se

Saplings of European silver birch, *Betula pendula*, were exposed to three levels of ozone in 12 open-top chambers during two growing seasons. Shed leaves were collected regularly and N concentrations were analysed in the 1998 leaves. Elevated ozone rapidly affected the birch leaves causing visible injury and premature leaf fall. The level of N in the shed leaves and the total amount of N lost through litter was increased in elevated ozone. Ozone reduced total wood biomass in general and root biomass in particular. The proportion of leaf biomass was increased by ozone, while the stem density as well as the ratio between base diameter and stem height was reduced. Ozone, causing reduced growth, smaller root systems and disturbed resorption of nutrients from the leaves, may be an important stress factor for birch in southern Sweden. The results are discussed in relation to critical levels and ambient levels in southern Sweden.

Concluding remarks

By Bengt Nihlgård

The workshop covered three main items discussed at different occasions, and a number of questions were raised around them. The first subject on "*Nutrient sustainability*" was considered as linked to soil acidification and acid rain, nitrogen fertilization and tree growth, and different problems linked to soil deterioration. The conclusions were that long-term productivity can not be retained at the today level for many reasons if it should be combined with simultaneous maintaining of water quality and a high biodiversity. The possibilities of accepting lower tree growth, changing tree species composition into mixed stands, and using more deciduous in order to make better use of the soil weathering capacity for the root systems were identified. Deciduous trees seem to act on a larger root volume and increases sustainability, and climate change will increase the demand for using different tree species. Whole tree harvesting for bioenergy purposes was considered to demand nutrient return. The scientific contribution should be laid on basic understanding of the natural processes linked to production.

The second subject was "*Restoration of biodiversity*", and the conclusion that the European landscape today misses a lot of old trees and of dead wood was obvious. A consistent management may support the existence of these. Fire and prescribed burning in the managed forest landscape was a hot subject, and was suggested to be additionally used for the same purpose, to increase the amount of dead wood, positive for biodiversity. However, many forests are continuously increasing in biomass, thereby increasing the potential risk for natural fires, and there was a general agreement that areas exposed to natural fires should be saved, without cutting down trees. Also, saving deciduous old trees for natural dieback, was stressed. For science the understanding of natural processes and the importance of constructing different models for forestry solutions was pointed out.

The third subject was "*Forest Resource Management*" in which different options trying to solve the problems of maintaining a high production simultaneously with sustaining soil, water, nutrients and biodiversity conditions, were discussed. The solution was looked upon as an evaluation of risks for the forest owner; judgement of the risk for economic failures in using high production, the effect of much wildlife, the problem of sustaining the soil and water nutritional capacity, and simultaneously considering the social demands from society. It was emphasized that increased legislation was not the optimal solution, and instead more extended information on forest policy issues and possibilities should be encouraged. The scientific contribution is to show the thresholds, present prognoses and different options for forest owners, authorities and general public.

List of participants

Akselsson, Cecilia - Chemical Engineering II, Lund University, Sweden
Alveteg, Mattias - Chemical Engineering II, Lund University, Sweden
Angelstam, Per - SLU/Örebro University, Sweden
Ask, Peter - S Swed Forest Research Centre, SLU, Sweden
Aulén, Gustaf - S Swed Farmers and Forest Owners Federation, Sweden
Belyazid, Salim - Chemical Engineering II, Lund University, Sweden
Berglund, Hans - WWF, Sweden
Björk, Lena - Plant Ecology, Lund University, Sweden
Blennow, Kristina - S Swed Forest Research Centre, SLU, Sweden
Brandtberg, Per-Olov - Dep of Ecol and Environm Research, SLU, Sweden
Braun, Sabine - Inst for Applied Plant Biology, Switzerland
Bucht, Stefan - Forestry dep, Sydved AB, Sweden
Callesen , Ingeborg - Danish Forest and Landscape Research Inst, Denmark
Christensen, Morten - The Royal Veterinary and Agricultural Univ, Denmark
Dahlin, Bo - S Swed Forest Research Centre, SLU, Sweden
van Dobben, Han - Alterra, Netherlands
Domeij, Erika - S Swed Forest Research Centre, SLU, Sweden
Drobyshev, Igor - Plant Ecology, Lund University, Sweden
Ekstrand, Anders - Region Skåne, Sweden
Eliasson, Per - Dep of History, Lund University, Sweden
Flückiger, Walter - Inst for Applied Plant Biology, Switzerland
von Gadow, Klaus - Forest Assessm/Forest Growth, Göttingen Univ, Germany
Godbold, Douglas L - Agricultural and Forest Sciences, Univ of Wales, United Kingdom
Göransson, Hans - Plant Ecology, Lund University, Sweden
Hagen-Thorn, Anna - Plant Ecology, Lund University, Sweden
Hautala, Harri - Finnish Forest Research Inst, Finland
Hedin, Jonas - Animal Ecology, Lund University, Sweden
Heilmann-Clausen, Jacob - Danish Forest and Landscape Research Inst, Denmark
Högbom, Lars - Skogforsk, Forestry Research Institute, Sweden
Johannisson, Christian - National Board of Forestry, Sweden
Johansson, Olof - Sveaskog, Sweden
de Jong, Johnny - Swedish University of Agricultural Sciences, Sweden
Jönsson, Ulrika - Plant Ecology, Lund University, Sweden
Jönsson, Anna-Maria - Plant Ecology, Lund University, Sweden
Kaila, Simo - Metsäteho Oy, Finland
Kalén, Christer - Plant Ecology, Lund University, Sweden
Karlsson, Matts - S Swed Forest Research Centre, SLU, Sweden
Koricheva, Julia - Section of Ecology, University of Turku, Finland
Kruys, Nicholas - Dep of Forest Resource Management, SLU, Sweden

Lindén, Magnus - Asa Experimental Forest, SLU, Sweden
Ljungberg, Håkan - Quaternary Geology, Lund University, Sweden
Lundberg, Åsa - S Swed Forest Research Centre, SLU, Sweden
Lundell, Sven - Swed Farmers and Forest Owners Federation, Sweden
Lundkvist, Heléne - Dep of Ecol and Environm Research, SLU, Sweden
Lämås, Tomas - Dep of Forest Resource Management, SLU, Sweden
Malek, Stanislaw - Dep of Forest Ecology, Agricult Univ of Cracow, Poland
Malmgren, Kurt - SkogsEko, Sweden
Mattsson, Leif - S Swed Forest Research Centre, SLU, Sweden
Mellbrand, Kajsa - Animal Ecology, Lund University, Sweden
Moeller, Inge Stupak - Danish Forest and Landscape Research Inst, Denmark
Niemelä, Jari - Dep of Ecology and Systematics, Helsinki Univ, Finland
Nihlgård, Bengt - Plant Ecology, Lund University, Sweden
Niklasson, Mats - S Swed Forest Research Centre, SLU, Sweden
Nilsson, Sven G - Animal Ecology, Lund University, Sweden
Nilsson, Jan - Natural Resource Management, MISTRA, Sweden
Olsson, Kurt - Plant Ecology, Lund University, Sweden
Petersson, Per - Asa Experimental Forest, SLU, Sweden
Rosén, Kaj - SkogForsk, Forestry Research Institute, Sweden
Rosengren, Ulrika - Plant Ecology, Lund University, Sweden
Sallnäs, Ola - S Swed Forest Research Centre, SLU, Sweden
Sigurdsson, Bjarni D - Icelandic Forest Research, Iceland
Sigvardsson Lööv, Carna - Plant Ecology, Lund University, Sweden
Sjunnesson, Sven - Chairman of the SUFOR board, Sweden
Sonesson, Kerstin - Plant Ecology, Lund University, Sweden
Stjernquist, Ingrid - Plant Ecology, Lund University, Sweden
Svensson, Mats - Chemical Engineering II, Lund University, Sweden
Sverdrup, Harald - Chemical Engineering II, Lund University, Sweden
Thelin, Gunnar - Plant Ecology, Lund University, Sweden
Uddling, Johan - Plant Physiology, Gothenburg University, Sweden
Wallander, Håkan - Microbial Ecology, Lund University, Sweden
Wallman, Patrik - Chemical Engineering II, Lund University, Sweden
Vanha-Majamaa, Ilkka - Finnish Forest Research Inst, Finland
Waring, Richard - College of Forestry, Oregon State University, USA
Westling, Olle - IVL Swedish Environmental Research Institute, Sweden
Öckinger, Erik - Lund University, Sweden
Örlander, Göran - National Board of Forestry, Sweden

SLU = Swedish University of Agricultural Sciences

Workshop programme

2002-04-07	**SUNDAY**
09:00-17:00	Excursion to Fulltofta, Skåne, related to sustainable forestry topics of the workshop
18:00-20:00	Registration, welcome party at the Ecology Building

2002-04-08	**MONDAY**
08:00-09:00	Registration, coffee
09:00-09:15	Opening speech, by Jan Nilsson, Programmes director, Natural Resource Management, MISTRA, Sweden
09:15-09:45	SUFOR **-** Challenging results, by Bengt Nihlgård, University of Lund
09:45-10:15	SUFOR **-** System thinking and applied modelling in sustainable forestry, by Harald Sverdrup, University of Lund
10:15-10:30	Coffee break
10:30-11:00	SUFOR **-** An approach to quantitatively estimate biodiversity preservation potential at forest stand level, by Sven G Nilsson, Univ of Lund
11:00-11:30	SUFOR **-** Decision support for risk management, by Kristina Blennow, Swedish University of Agricultural Sciences
11:30-12:00	Poster session
12:00-13:15	Lunch at Ideon Restaurant
13:15-13:45	Nutrient sustainability, by Richard Waring, Oregon State University
13:45-14:15	Restoration of biodiversity, by Jari Niemelä, University of Helsinki
14:15-14:45	Sustainable management of forest resources, by Klaus von Gadow, University of Göttingen
15:00-17:50	**Session 1: Nutrient sustainability** (further information on the next page) Chairman: Kerstin Sonesson, University of Lund
15:00-17:50	**Session 2: Restoration of biodiversity** (further information on the next page) Chairman: Sven G Nilsson, University of Lund & Mats Niklasson, Swedish University of Agricultural Sciences
15:00-17:50	**Session 3: Forest resource management** (further information on the next page) Chairman: Kristina Blennow, Swedish Univ of Agricultural Sciences
17:50-18:30	Poster session
20:00-	Dinner at Pelarsalen, the University Building

2002-04-09	**TUESDAY**
08:30-10:30	**Workshop 1: Nutrient sustainability** Chairman: Ulrika Rosengren, University of Lund
08:30-10:30	**Workshop 2: Restoration of biodiversity** Chairman: Jonas Hedin, University of Lund
08:30-10:30	**Workshop 3: Forest resource management** Chairman: Ola Sallnäs, Swedish University of Agricultural Sciences
10.30-11.15	Coffee break and poster session
11:15-12:15	Reports from the workshops and discussion Chairman: Bengt Nihlgård, University of Lund
12:15-13:30	Lunch at Ideon Restaurant
13:30-14:30	Discussion & concluding remarks Chairman: Bengt Nihlgård, University of Lund

Session 1: Nutrient sustainability

15.00-15.20 The significance of soil acidification and nitrogen deposition in storm damages: results from permanent observation plots in Switzerland, by Sabine Braun, Christian Schindler & Walter Flückiger
15.20-15.40 Effects of riparian forest tree species on brook-water quality, by Lars Högbom, Sten Nordlund, Per-Erik Lingdell & Hans-Örjan Nohrstedt
15.40-16.00 Production of ectomycorrhizal mycelia at different soil depths in spruce forests and mixed forests (spruce/oak) in southern Sweden, by Håkan Wallander, Hans Göransson, Ulrika Rosengren
16.00-16.30 Coffee break and poster session
16.30-16.50 The contribution of ectomycorrhizas to release and acquisition of mineral nutrients, by Douglas L. Godbold, Patrick A. W. van Hees, Susan. I. Vinogradoff, David L. Jones & Georg Jentschke
16.50-17.10 Defining threshold nutrient values for Swedish deciduous tree species, by Ingrid Stjernquist & Kerstin Sonesson
17.10-17.30 Impact of harvest of biofuels on nitrogen fluxes in forests in Sweden, by Cecilia Akselsson & Olle Westling
17.30-17.50 N induced changes in nutrition status in beech in Swiss forests and their consequence for sustainable forestry, by W. Flückiger, E. Hiltbrunner, L. Tomova & S. Braun

Session 2: Restoration of biodiversity

15.00-15.20 Regional division for efficient biodiversity preservation based on disturbance regime, forest history and tree species distribution: the southern Swedish example, by Mats Niklasson & Sven G Nilsson
15.20-15.40 Immediate effects of patch retention felling to epixylic vegetation in boreal forest, by Harri Hautala, Sanna Laaka-Lindberg, Ilkka Vanha-Majamaa & Jyrki Jalonen
15.40-16.00 Dispersal of forest insects in relation to habitat predictability, by Jonas Hedin
16.00-16.30 Coffee break and poster session
16.30-16.50 Decomposition and decay class dynamics of dead trees in Sweden, by Nic Kruys
16.50-17.10 Mortality of retention trees: a study in Scots pine stands in Småland, by Åsa Lundberg & Mats Niklasson
17.10-17.30 Fungal diversity on beech logs in Danish forests, by Jacob Heilmann-Clausen & Morten Christensen
17.30-17.50 Use of coupled models to predict biodiversity in managed oligotrophic ecosystems, by Han van Dobben, Wieger Wamelink, Eric Schouwenberg & Janet Mol

Session 3: Forest resource management

15.00-15.20 Mixed forest stands as a means of sustainable forest management: project presentation and first results, by Julia Koricheva
15.20-15.40 Buffer zones along small streams in managed forests, by Olle Westling & Per Petersson
15.40-16.00 Forest dynamics and the effect of moose browsing - a modelling attempt, by Christer Kalén & Jonas Bergquist
16.00-16.30 Coffee break and poster session
16.30-16.50 Forest management and vegetation changes in Finland, by Ilkka Vanha-Majamaa & Jyrki Jalonen
16.50-17.10 Developing the complex forest ecosystem model FORSAFE - motives, means and the learning loop, by Patrik Wallman & Harald Sverdrup
17.10-17.30 Managing of game resources in a context of sustainable forestry and biodiversity protection, by Olgirda Belova (Cancelled)
17.30-17.50 Defining sustainability and applying it to management - some implications for principal thinking in forestry, by Harald Sverdrup, Mats Svensson & Ola Sallnäs