Large-scale ecosystem experiments: ecological research and European environmental policy

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Accepted 11 March 1997

Abstract

During the last three decades the experimental manipulations of whole ecosystems have been a useful and widely-used tool for investigation of the effects of air pollution, air pollution reduction strategies and management practices on the health and productivity of forests and the acidification of catchments and fresh waters. NITREX and EXMAN projects involve whole-ecosystem manipulations of forest ecosystems in Europe. The aims of these ecosystem experiments have been to investigate the impact of a continued or increased load of air pollutants on the ecosystems, and the possibilities of reversing the acidifying effects by soil amelioration, addition of buffer-acting substances or by removal of the air pollutants. Along with the field experiments, models have been used to predict future effects and dynamics in the ecosystems under different air pollution scenarios. The major findings from those projects have been used in political decisions on reduction of sulphur emission in Europe via the sulphur protocol signed in 1994. Today work is going on to formulate a NO_x protocol. NITREX and EXMAN results contribute to the scientific information base for these protocols. Large-scale ecosystem manipulation projects have increased our understanding of ecosystem function and response to external change and created scientific evidence for political environmental decisions and legislation. In the future, controlled-ecosystem experiments clearly play an important role in new research on ecological effects of changes in the global atmosphere and climate. © 1998 Elsevier Science B.V.

Keywords: Ecosystem; Manipulation; Air pollution; Nitrogen; Sulphur; Policy

1. Introduction

Research on the influences of environmental factors on ecosystems has traditionally focused on individual components of the system such as single plant species or soil chemistry. Environmental impacts of air pollution will often influence the whole ecosystem and the effects are a result of the complex interaction between the different constituents of the ecosystem. Attention to the dynamics of the whole ecosystem has increased over the past 30 yr, as exemplified by the research on catchment ecosystems at the Hubbard Brook Experimental Forest, New Hampshire, USA (Likens et al., 1977) and on lake ecosystems at the Experimental Lakes Area, northwestern Ontario, Canada (Johnson and Vallentyne, 1971). Work at these sites pioneered the 'whole-ecosystem' approach and have inspired similar studies all over the world.

Manipulation experiments with terrestrial ecosystems have become an important means by which
environmental impacts can be studied. The term 'whole-ecosystem manipulation' is generally used to describe field experiments that entail a major change in the input of substances, nutrients and/or water to the system or intervention in the system by, for example, clear-cutting. The 'whole-ecosystem manipulation'-approach traditionally treats the ecosystem as a 'black-box'. The basic principle of 'manipulation' has been used for more than hundred years to study effects of fertilisation, liming and irrigation. It has always been a part of forest management, since abrupt changes like clear-cutting and fire cause 'manipulation' of the forest ecosystem.

Whole ecosystem manipulations have provided data for development and testing of models for predictions of the effects of environmental impacts on ecosystem function and structure. The role of predictive models has expanded in scope to cover applied problems of ecosystem management and pollution control policy, most recently with the development of the critical load/level concept (Nilsson, 1986; Nilsson and Grennfelt, 1988; Grennfelt and Thörnlof, 1992).

Policy-makers recognise the need for good scientific and technical data for formulation of environmental policy. An environmental problem is generally first identified by scientists, administrators or the general public. This leads next to research on causes, mechanisms and possible remedies, and ultimately to formulation of environmental policy (Fig. 1). Whole-ecosystem research often plays a central role in the hierarchy of scale in ecological experiments (Table 1), and predictive models in many cases provide a tool for the political decisions.

European concern over the cause and consequences of forest decline, acidification of soils and surface waters, and the nutrient enrichment of terrestrial and aquatic ecosystems led to the establishment of the NITREX and EXMAN projects, two research networks of large-scale manipulation experiments under the auspices of the EU Commission of European Communities. NITREX (Nitrogen saturation experiments) comprises 10 experiments at eight sites in seven countries at which nitrogen is either added to or removed from ambient atmospheric deposition to simulate major changes in nitrogen deposition (Dise and Wright, 1992; Wright and van Breemen, 1995). EXMAN (Experimental Manipulation of Forest Ecosystems in Europe) comprises experiments at six sites in four countries at which ambient atmospheric deposition is experimentally altered in chemical composition and/or quantity (Beier and Rasmussen, 1993). The ultimate goal of this research was to contribute to the scientific basis required for the refinement of EU policy on atmospheric quality.

Table 1

<table>
<thead>
<tr>
<th>Research approach</th>
<th>Level of organization</th>
<th>Degree of reality</th>
<th>Variables</th>
<th>Reproducibility</th>
<th>Time period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laboratory experiments (microcosms, plants in pots)</td>
<td>Cell/organism</td>
<td>Low</td>
<td>Few</td>
<td>High</td>
<td>Short</td>
</tr>
<tr>
<td>Growth chambers, OTC (mesocosms, model ecosystems)</td>
<td>Organism/population</td>
<td>Medium</td>
<td>Some</td>
<td>Medium</td>
<td>Medium</td>
</tr>
<tr>
<td>Whole ecosystem manipulations (intact plant/soil/atmosphere environment Models)</td>
<td>Ecosystem</td>
<td>High</td>
<td>Many</td>
<td>Low</td>
<td>Long</td>
</tr>
<tr>
<td>Models</td>
<td>Cell to ecosystem</td>
<td>Low to high</td>
<td>Few to many</td>
<td>Low to high</td>
<td>Short to long</td>
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</table>
and the legislation which will emanate from that policy.

Here, we place the results from whole-ecosystem manipulations obtained in the NITREX and EXMAN projects in context with the parallel development of critical loads of sulphur and nitrogen deposition, and the political and legislative developments for the reduction of atmospheric sulphur and nitrogen emissions.

2. Principles of ecosystem experiments

The goal of ecosystem science is to integrate information from studies of the interactions between individuals, populations, communities and their abiotic environments, including the changes in these relationships with time (Likens, 1992). Ecosystem studies include empirical and natural-history studies, analyses of balances and budgets, experimental manipulations, comparative assessments, and modelling simulations. The combined application of these approaches should provide a solid basis for critical analysis, for comprehension of the complexity of natural ecosystems, and for providing useful information to environmental managers and policymakers.

The hierarchy of scale in ecological experimentation goes from short-term experiments at the organism level (microcosms, plants in pots), to simple interactions in controlled environments (model ecosystems, mesocosms), to long-term manipulations with intact whole ecosystems (Table 1). Ecological process models and predictions models may be applied at all levels. The application of a model at one level may often lead to new hypotheses, which can be scaled to another level below or above.

Whole-ecosystem experiments with forests are of key importance because they (1) comprise mature trees in situ, (2) comprise air-plant, plant-soil, soil-water interfaces, (3) perturb the system in a controlled manner, (4) reveal key links, processes, interactions, responses and rate of response, (5) place empirical time/space data into dynamic context, (6) demonstrate directly whole-ecosystem response to change of specific dose of pollutant or stress factor, (7) generate data for development and test of dose/response models, and (8) place small-scale, short-term experiments in the growth chamber and laboratory into proper and relevant context.

Large-scale ecosystem experiments often entail major commitment of labour and capital investment. The expense often precludes the use of replications in experimental design, as is the case for most of the NITREX and EXMAN manipulations. The ‘paired ecosystem’ approach is usually taken in which one ecosystem is manipulated while one or more similar ecosystems serve as untreated references. Comparisons of results from similar, parallel experiments at other sites provides the basis for generalising the findings. In cases with multiple controls, effects can be interpreted relative to the variance within the controls (Schindler, 1988). A reference system may be particularly valuable for assessing natural, temporal variability during long-term experiments. A true reference is difficult, if not impossible, to establish because of the inherent complexity and variability of natural ecosystems (Likens, 1985). Nevertheless, carefully designed whole-ecosystem experiments play a unique role for studying process-level questions relative to forest ecosystems.

In addition, experimental ecosystem research often holds an element of surprise (Schindler, 1991; Carpenter et al., 1995). The element of unpredictability often confounds environmental forecasting at several scales. There are many examples that ecosystem experiments can expose unforeseen factors (Gundersen et al., 1995; Gundersen et al., 1998).

3. Interaction between environmental research and policy

The NITREX and EXMAN projects have the dual objectives of investigating fundamental scientific aspects of ecosystem function while at the same time providing information relevant for formulations of European and national policy on air quality and the legislation which emanates from that policy. NITREX and EXMAN are prominent among the experimental field studies where changes in the input of air pollutants to the ecosystem are imposed and the effects on the system or single processes are studied (Beier and Rasmussen, 1994, Rasmussen et al., 1993). Experiments comprised investigation of the impact of both continued or increased load of air
pollutants on forest ecosystems, as well as possibilities of reversing negative effects of air pollution by soil amelioration, addition of buffer acting substances or by removal of the air pollutants.

Numerical simulation models have been used to extrapolate these results in space and time. The models are used to project the potential effects of increased or decreased air pollutants over larger areas and greater time periods (Beier et al., 1995; Cosby et al., in press; Rasmussen et al., 1995; Van Dam and Van Breemen, 1995; Warfvinge et al., 1998; Wright et al., 1990). The model projections are frequently used as the basis and justification for public policy decisions and legislation. It is therefore important that the models be evaluated; experimental manipulations provide robust data sets for these model evaluations.

4. Relevance of NITREX and EXMAN data for setting limits to \( \text{SO}_2 \) emissions in Europe

Scientific information was fundamentally important in the international negotiations leading to the
‘Protocol to the 1979 convention on long-range atmospheric transboundary air pollution on the reduction of sulphur emissions’ which was signed by most countries in Europe in 1985 (UN-ECE, 1985). But it was already clear at that time that the 30% across-the-board reduction in emissions would be insufficient to remedy the problems of acidification and damage to forests, soils and surface waters. And the scientific research continued with increasing focus on the reversibility of acidification and the critical loads for acidifying substances.

The NITREX and EXMAN experiments with addition or removal of sulphur input to forest ecosystems contributed to this scientific information base. The removal of sulphur from the input caused reduced sulphate concentrations in the soil solution at all sites almost immediately (a few months to 1 year) (de Visser et al., 1994; Farrell et al., 1994; Beier et al., 1998) (Fig. 2). The expected decrease in aluminium and proton concentrations in the soil, however, did not occur until some years later, and for some sites not even after 6 yr of reduced acid input.

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Fig. 2. Results from NITREX and EXMAN experiments at Klosterhede (DK), Solling (D), Höglwald (D), Ysselsteyn (NL), Risdalsheia (N) and Aber (UK). Soil solution concentrations from the A- and B-horizon of soils or catchment stream-outlet in the treatment plots (‘clean rain’, liming, acidification, N-addition) as percentage relative to the control plots (100%).
The negative effects of acidification such as decreased base saturation and decreased Ca/Al ratio may be avoided or buffered by addition of lime or fertilisers (Kreutzer, 1991). Liming will primarily increase the pH of the soil matrix only in the uppermost layers (surface humus) (Kreutzer, 1995). During the first years after application, liming may also lead to increased concentrations of other ions in the soil solution due to increased turnover of organic matter and ion-exchange processes (Fig. 2). The direct effect of liming on the pH of the mineral soil, however, seems small due to buffering processes, and may be exceeded by proton production from liming induced nitrification (Fig. 2). Short-term addition of acidity also seems to have only a minor effect on pH in the soil solution in the uppermost layers due to soil-buffering processes (Fig. 2). In areas with high nitrogen-deposition a reduced nitrogen deposition relatively quickly leads to reduced concentrations of both NH$_4^+$ and NO$_3^-$. At sites where N already is in excess of ecosystem demands, increased nitrogen-deposition will be reflected in increased NH$_4^+$ and NO$_3^-$ in the soil solution in the upper horizons, and increased NO$_3^-$ also in the deeper horizons (Fig. 2). This situation may lead to nitrate leaching (Fig. 3).

The findings from the NITREX and EXMAN projects have indicated that reversibility is fast for some acidification processes and slow or even irreversible for others. Model predictions based on NITREX and EXMAN results have shown to which level atmospheric deposition of sulphur should be reduced to avoid negative ecosystem effects (Beier et al., 1995; Emmett et al., 1998a; Warfvinge et al., 1998).

This knowledge has been adopted as an important part of the work on setting critical load values for sulphur (Nilsson, 1986; Nilsson and Grennfelt, 1988; Downing et al., 1993; Hornung et al., 1994). Critical load for deposition of sulphur and nitrogen is defined as 'the highest deposition of a compound that will not cause chemical changes leading to long-term harmful effects on ecosystem structure and function' (Nilsson, 1986). NITREX and EXMAN scientists have been active in the critical load work (e.g., Dise and Wright, 1995; Tietema and Beier, 1995; Reynolds et al., 1998).

The findings contributed significantly to the scientific evidence used to implement a new protocol in 1994 to the 1979 convention on long-range transboundary air pollution on further reduction of sulphur emissions (UN-ECE, 1994). This protocol relied very much on the scientific work behind the 'critical load' and 'critical level' concept (Hornung et al., 1994; Bull, 1995). For some countries the protocol requires 80% reduction of sulphur in year 2000 from the base year 1980. In other countries this goal will not be met until year 2010.

5. Relevance of NITREX and EXMAN data for setting limits to NO$_x$ emissions in Europe

With the new sulphur protocol in place, attention has now moved towards determining critical loads for nitrogen as the foundation for a NO$_x$ protocol (Bull, 1995). Nitrogen deposition and turnover processes in ecosystems are much more complicated than for sulphur, however, and interactions with other air pollutants, including sulphur compounds, have to be taken into account.

The experimental manipulations with nitrogen input to forest ecosystems in the NITREX and EX-
MAN project showed that in high-N deposition areas reduced input rather quickly and unexpectedly led to reduced nitrate leaching from the root zone (Dise and Wright, 1992; Wright et al., 1995) (Fig. 3). At the intermediate range of N deposition the NITREX and EXMAN data indicated that for the first 2 yr most of the added N was lost to runoff at sites where N losses were already large prior to treatment, whereas most of the added N was retained at sites where N losses were negligible prior to treatment. The rapid response in the former depended on the form of nitrogen. Ammonium was effectively retained within the forest ecosystem whereas the added nitrate resulted in an equivalent increase in nitrate output (Emmett et al., 1998b). At the low-N deposition site outputs were very low, and a doubling of the input had only little effect on the output.

The hypothesis of nitrate leaching from forest soils by rewetting after dry summer periods (the nitrification pulse theory, Ulrich and Matzner, 1983) was tested by NITREX and EXMAN drought experiments, and appeared not to be a general feature, and therefore not a factor of importance for the critical load assessment (Lamersdorf et al., 1998). However, the influence of drought stress might very well be of importance in relation to growth and turnover processes in a future CO₂ protocol (Schlaepfer, 1993).

The nitrogen input–output data from the NITREX and EXMAN projects are consistent with the general pattern of nitrogen fluxes from forest ecosystems in Europe (Fig. 4) (Gundersen, 1995). Sites with high N deposition (> 25 kg N ha⁻¹ yr⁻¹) were characterised by high input of ammonia. The deposition of oxidised N was usually only 10–15 kg N ha⁻¹ yr⁻¹. Of all the sites included, 60% leached more than 5 kg N ha⁻¹ yr⁻¹. Elevated nitrate leaching appeared at inputs above 10 kg N ha⁻¹ yr⁻¹. At several sites with inputs of 15–25 kg N ha⁻¹ yr⁻¹, however, nitrate leaching approached the N input indicating a nitrogen saturation of the ecosystem, whereas ammonium-dominated sites with high input still retained about 50% of the input. The NITREX and EXMAN projects have shown that it is very difficult to establish general critical load values for atmospheric nitrogen deposition on forest ecosystems, since site and stand-specific characteristics will influence the calculations.

The results of the NITREX and EXMAN project support the general picture that a NO₂ protocol for emission reductions will be more complex than for sulphur, and more compounds and effects have to be taken into account. The results of the NITREX and EXMAN projects, however, indicate that N emissions must be reduced by perhaps 90% in the highest emission areas in Europe, in order to restore the ion balance and reduce nitrate leaching to the natural pre-industrial level.

In the work with the coming NO₂ protocol it is the intention to maintain the principle of an effect-based and cost-effective protocol, as for sulphur, i.e., control should in some sense achieve the cheapest control strategy given a scientifically-determined reduction in environmental effects. Early on it was realised that the NO₂ emissions had a number of potential effects: acidification of soils and waters, eutrophication of terrestrial ecosystems, and as a precursor for tropospheric ozone with adverse effects to vegetation. This implies many links between emission sources, emission control and costs, critical loads and levels, and resulting effects on the environment (Fig. 5). Possible consequences for human health effects from ozone and nitrogen dioxide should also be considered. The complexity is further increased since the effects are not caused solely by nitrogen oxides. For most of the effects, other compounds are of similar (or larger) importance than nitrogen oxides; sulphur dioxide and ammonia for acidification, ammonia for eutrophication, and VOC and carbon monoxide for photochemical oxidants.

The NITREX and EXMAN projects have contributed much to the knowledge on the effects of air pollutants on the environment, and during recent
years model calculations have predicted the potential effects of emission reductions. For many effects, there are quantitative data of sufficient quality to develop effect-based strategies, while they are still lacking for others. The process of mapping emission and deposition loads/levels in relation to critical loads/levels is under way for acidification and eutrophication of terrestrial ecosystems. Within the near future, it may also be possible to assess the effects of NO\textsubscript{x} emissions on ozone levels and forest and health effects.

6. Future directions

Whole-ecosystem manipulation studies have shown that even large crop and long-lived ecosystems such as forests will be affected by changes in the atmospheric input. Anthropogenic acidification processes in the soil can be stopped by removing the acidic input or reversed by liming, and growth can be increased and nutritional balance in the trees improved by fertilisation. The complexity of the ecosystem and the factors controlling vitality and sustainability of the ecosystem, however, are still not fully understood. Whole-ecosystem manipulation will continue to provide a research tool for assessment and evaluation of future impacts of air pollution and management practices on ecosystems. These studies should not stand alone but should be combined with specific process-oriented studies in the field or in the laboratory.

The duration of ecosystem studies is important. Changing the input to the soil will inevitably lead to
a transition state, and the effects observed during this transition may not necessarily be representative of the long-term changes in the system. Generally, moderate manipulations show moderate and slowly-developing effects. The response time may be shortened if the manipulation is more drastic, but then the manipulation may be unrealistic in comparison to the changes simulated, and therefore the effects may also be unrealistic. The need for long-term studies is generally recognised, but often difficult to achieve, since most research programmes deal with at most 3–5 yr funding periods.

Whole-ecosystem manipulation projects have increased our understanding of the complexity of the ecosystem and highlighted the need for studies integrating field and laboratory work as well as integrating different disciplines. The use of tracers in field manipulation projects is a significant advancement. Results reported from whole-ecosystem manipulation projects have so far mainly focused on the ecosystem response rather than the response on a process specific level. Many unexpected ecosystem responses could not have been predicted from small-scale experiments. Field manipulation will also be useful for process-oriented studies and for evaluating methods.

Whole-ecosystem manipulation has mainly been used in lakes and coniferous forest ecosystems. In the future, the concept of ‘whole-ecosystem manipulation’ might likely be used to study other types of ecosystems. In Europe, there is growing concern for increasing the number of broad-leaved forests by afforestation of former agricultural areas and by conversion of coniferous forest areas. This raises several questions with respect to the sustainability of broad-leaved forests in the present, and future, pollution climates, and the influence of broad-leaved forests on ground and fresh water quality. Scientific understanding is critical for making wise choices about mitigation or management of a complex environmental problem.

In the future, controlled ecosystem experiments could clearly play an important role in research regarding ecological effects of changes in the global atmosphere and climate. Indeed, controlled experiments may offer the only realistic approach to quantifying the potential effects of future changes that have as yet no modern analogues. Findings from such experiments will be invaluable in evaluating and further developing predictive models of ecological change. The first political steps to break the increasing CO₂ curve, however, need not wait until scientific evidence is available, but the required refinement of the policy and the legislation which will emanate from that policy clearly need to be well-founded on scientific evidence as was the case for the sulphur and NO₂ protocols.

Acknowledgements

This research was funded in part by the Commission of European Communities (NITREX EV5V-CT930264 and EV5V-CT940436; EXMAN STEP-CT90-0038, EV5V-CT920091 and EV5V-CT940429), the Norwegian Research Council, the Norwegian Institute for Water Research, the Danish Environmental Research Programme and several other national funding agencies. C. Beier, P. Gundersen and P. Grennfelt contributed to the presented figures.

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