Effects of stresses on forest growth in models applied to the Solling spruce site

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Abstract

Forests are rarely limited by only a single pollutant or environmental factor, yet experimental investigations are usually limited to one or two stress factors and to short durations. Simulation models provide a means of exploring the long-term effects of multiple natural and anthropogenic stresses on forest health. Sixteen simulation models were applied to a Norway spruce site at Solling (Germany) for a workshop comparing forest–soil–atmosphere models. Five of these models were applied under various environmental conditions to quantify forest damage at Solling and to analyze interactions of multiple stresses. The models agreed that the forest damage caused by drought stress and nutrient deficiency was more important than that caused by short-term, direct air pollution stress. The models did not agree on the magnitude of some effects because the models differed in complexity, in the choice of stresses and processes modelled, and in the assumed mechanisms of stress effects. Stress interactions in the models were explored by comparing the effects of single stresses with those of multiple stresses. Multiple stresses tend to be less damaging than the sum of individual stresses, but more damaging than the single most damaging stress. However, the exact form of the effects of multiple stresses is not predicted by the mechanism of the stress as implemented in the model, even in the most simple models, due to feedback mechanisms and integration over time.

There is a lack of knowledge about long-term effects of direct stress and a lack of data of manipulation experiments to validate the simulations. Future research should be focused on long-term effects of SO_2 and O_3 exposure and on manipulation of field plots.

Keywords: Acidification; Drought; Forest ecosystems; Model comparison; Nutrients; Soil; Spruce; Stress

1. Introduction

Developing simulation models of forest systems makes it possible to explore the relationships between multiple stresses and to estimate the degree to which specific stresses are damaging forest health. Different models represent forest processes and forest stresses in different ways. Comparing simulations by different forest models reveals areas of consensus and areas of uncertainty in estimating the effects of natural and anthropogenic stress on forests. Simulating differ-

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ent combinations of multiple stresses can also illuminate relationships between stresses that would be difficult to measure experimentally, as far as the mechanisms of stresses are understood or measured experimentally.

Sixteen simulation models were applied to the F1 Norway spruce site in Solling (Germany) (Bredemeier et al., 1995) for a workshop comparing forest–soil–atmosphere models (Van Grinsven et al., 1995). The models were applied in a series of exercises designed to reveal the different strengths and weaknesses of the models and to answer questions about the current and future response of this forest to environmental conditions (Van Grinsven et al., 1995). Eleven of these models included a dynamic forest module of which five were applied for comparison of relationships between stresses. Four of these models are described in individual papers in this volume (Mohren and Ilvesniemi, 1995; Mohren and Van de Veen, 1995; Schall, 1995; Van Heerden et al., 1995; Van Minnen et al., 1995). The comparative study of relations between stresses involved simulating forest growth under different combinations of stresses: in the actual state of multiple stress, in the absence of air pollution (sulphur or nitrous oxides, ammonium, or ozone) and in the absence of drought or nutrient stress.

The purpose of this integrating paper is to report the model results for different combinations of stresses and to focus attention on questions pertaining to forest stress across the participating models. We summarize the stresses implemented in the models, and we propose a classification of relations between multiple stresses based on their representation in the models. We argue that in most cases the outcome of multiple stresses cannot be predicted from the mode of action of the individual stresses; simulation modelling, therefore, provides a means of integrating multiple stresses. More specifically, the models provide a means of estimating the degree to which the Solling forest has been affected by various environmental stresses. Comparing the results of model simulations also helps to reveal the consequences of the assumptions that differ across models for the estimation of stress response.

2. Classification of stress effects as implemented in the models

2.1. Definitions

We define stress as a condition that (i) reduces the effectiveness of plant processes (not necessarily causing damage to the plant, e.g., the effect of vapour pressure deficit on photosynthesis) or (ii) reduces plant structure directly (e.g., the effect of herbivores or snowstorms on the canopy). Multiple stress is defined as several stresses affecting the plant simultaneously. Forest damage is defined as reduced growth or biomass of forest organisms (in this paper restricted to trees), caused by a stressed condition.

It can be difficult to establish a reference condition by which such damage may be identified, since naturally occurring stresses always limit forest growth and biomass; an 'unstressed' condition does not exist in nature. Therefore the models use optimal conditions as a basis of comparison, which are the best conditions given ambient temperature and irradiance, without growth reduction due to drought, nutrient deficiency, acid deposition, or air pollution.

2.2. Modes of action of single stresses

In representing the effect of environmental stress on forest growth, modellers have necessarily defined modes of action for each single stress affecting processes or plant structure, and they have defined relationships among the stresses. The modes of action of single stresses can differ from one model to another, because of differences in the hypothesized mechanisms of plant response to stress and because of differences in model structure and the processes represented. However, the relationship between a single stress and the process most directly affected by it in the model, generally falls in one of three categories. Most of the stresses in the models are implemented either as (i) multipliers, (ii) addends, or (iii) limiting factors.

To illustrate this classification of stress responses, consider a simple model of plant growth that represents the processes of photosynthesis,
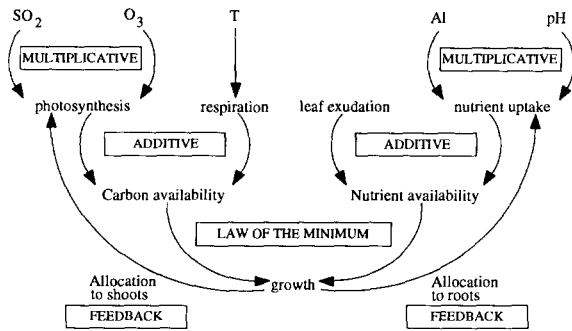
Fig. 1. Example of a relation diagram of a simple forest model.

respiration, and nutrient uptake (Fig. 1). Some environmental stresses to be included are the effect of the air pollutants sulphur dioxide and ozone on photosynthesis, the effect of temperature on respiration, and the effect of soil Al and pH on nutrient uptake.

(i) *Multipliers*: Most of the plant–soil–atmosphere models implement air pollution stresses and soil stresses as multiplying factors that modify the rates of modelled processes. For example, the effect of Al in soil solution on uptake of Mg could be described by a multiplier, itself some function of Al concentration, on root uptake of nutrients.

In the model depicted in Fig. 1, the five environmental stresses at the top of the figure are implemented as multipliers on the process directly affected by the stress.

(ii) *Addends*: Alternatively, stresses can be implemented as a toll exacted by subtraction. For example, herbivores consume leaves. The amount of leaf mass consumed is subtracted from the plant leaf mass.

When calculating the amount of carbon or nutrient available for growth, most models use addition and subtraction to calculate the effects of environmental change. For example, if increased temperature were to increase respiration, we would subtract the carbon respired from the pool of carbon available for growth. Similarly, changes in nutrient uptake rates subtract from the pool of nutrients available for growth (Fig. 1).

(iii) *Limiting factors*: Finally, the law of the minimum is commonly used to determine plant

growth from the amount of carbon and nutrient available. Where multiple nutrients are concerned, the one in least supply determines the possible growth rate.

2.3. Relationships among stresses

In certain well-defined cases, the classification of stress effects as implemented in the models can be extended to describe the nature of action of multiple stresses. For example, in Fig. 1, both sulphur dioxide and ozone are multipliers (F_{SO_2} and F_{O_3}) on photosynthesis (P):

$$P = F_{SO_2} * F_{O_3} * P_{pot} \qquad (1)$$

where P_{pot} is the potential photosynthesis.

The effects of photosynthesis (P) (and of alterations to photosynthesis caused by air pollutants) and respiration (R) on carbon availability (C_{av}) are both additive:

$$C_{av_t} = C_{av_{t-1}} + P - R \qquad (2)$$

The effect of carbon availability and nutrient availability (X_{av}) on growth rate (GR) follows the law of the minimum:

$$GR = \text{Minimum}(GR_{pot,C_{av}}, GR_{pot,X_{av}}) \qquad (3)$$

where GR_{pot} is the potential growth rate with respect to carbon or nutrients available.

These three examples show combinations of stresses in which the nature of the relationship between stresses, at least at the point of action of the stresses, can be clearly defined as multiplicative, additive, or limiting. For stresses that do not act upon the same process, however, the relationship is difficult to identify. For example, how should the relationship between ozone (F_{O_3}) and temperature (T) on carbon availability be described?

$$C_{av_t} = C_{av_{t-1}} + F_{O_3} * P_{pot} - 2^{((T-20)/10)} * R_m \qquad (4)$$

where R_m is maintenance respiration with a Q_{10} of 2.

Simulation models, of course, provide a means of calculating this effect. Even in cases where the mechanism of action is well defined, it may be impossible to predict the effect of multiple stresses from the mechanism of action of the

individual stresses, especially when this effect is accumulated over time. It is because of these limitations to prediction of stress relationship from hypothesized mechanisms of stress effects (i.e. from model principles) that the behaviour of the models provides a very good means of evaluating the interactions of multiple stresses. Since multiple stresses, both natural and anthropogenic, limit forest growth, a modelling approach can also help to assess the contributions of individual stresses to forest damage.

3. Methods of modelling multiple stresses

3.1. Overview of the implemented stresses

The environmental factors included in the models are summarized by Tiktak and Van Grinsven (1995). These include air pollutants (sulphur and nitrous oxides, ammonium, and ozone) and other limitations to forest growth (light, moisture, temperature, and nutrient availability).

In Table 1 an overview is given of the implemented stresses. The availability of carbon and nutrients to the trees can limit their growth rate and thus all factors affecting carbon and nutrient availability can be considered stress factors. Both 'natural' factors influencing growth (e.g. radiation, temperature, water, and nutrients) and anthropogenic factors (e.g. acid deposition and air polluted with O_3 and SO_2) are included in this table. Herbivory and disease are types of stresses not included in any of the models.

Natural stresses

Carbon balance is included in all of the forest models except NAP and FORSOL. Various approaches are used by the models to calculate the gross photosynthetic rate. SOILN, NICCCE, FIWALD, PNET, FORGRO, and TREGRO use a photosynthetic light-response curve to simulate the assimilation of carbon dioxide. SOILVEG uses an empirical

Table 1
Overview of stress implementations in the applied models

Subject	1	2	3	4	5	6	7	8	9	10	11
Direct effects on nutrient uptake											
nutrient availability in soil	+	+	+	+	+	+	+	+	+	.	+
drought	.	+	.	.	.	+	+	+	.	.	.
temperature	.	+	.	.	.	.	+	.	.	.	.
root density (mass)	.	.	.	.	.	+	+	.	.	.	.
pH in soil solution	.	.	.	.	.	.	+	+	.	.	.
Al concentration in soil solution	.	.	.	.	.	.	+	+	.	.	.
Direct effects on carbon uptake											
irradiance	+	+	.	+	+	+	.	.	.	+	+
nutrient concentration in leaves	+	+	.	+	+	+	.	.	+	.	+
transpiration	+	+	.	.	+	+	+	.	.	+	+
temperature	+	+	.	+	+	+	.	.	.	+	+
SO_2 ambient air	.	.	.	+	.	+	+	+	.	.	.
O_3 ambient air	.	.	.	+	.	+	+	+	.	.	+
CO_2 ambient air	.	+	.	.	.	+	.	.	.	.	+
Effects on C balance and growth											
maintenance respiration:											
temperature	+	+	.	+	+	+	+	.	+	.	+
nutrient content trees	.	+	.	.	.	+	+	+	.	.	.
O_3	.	.	.	.	.	+	.	.	.	.	+
effect of [Al] on fine roots	.	.	.	.	.	+	+	.	.	.	.

1 SOILN; 2 NICCCE; 3 NAP (Van Oene and Ågren, 1995); 4 FIWALD (Schall, 1995); 5 PNET/CHESS (Postek et al., 1995); 6 FORGRO; 7 SOILVEG (Van Heerden et al., 1995); 8 EXPECT-FORSOL (Van Minnen et al., 1995); 9 ForM-S (Oja et al., 1995); 10 FORSUM; 11 TREGRO (Weinstein et al., 1991).

linear relationship between actual transpiration and photosynthetic rate. PNET/CHESS combines the relationships between transpiration and carbon gain, and between leaf N-content and carbon gain.

Soil drought (Bouten and Jansson, 1995) can affect tree growth in several ways. It can affect closure of stomata, which results in increased resistance to CO_2-uptake (SOILN, NICCCE, FORGRO, and TREGRO). Several methods are used to calculate the actual transpiration (Tiktak and Van Grinsven, 1995).

All models except FORSUM included a nutrient balance, and in one way or another the availability of nutrients in the soil. Most models included a soil module to calculate the nutrient concentrations in the soil solution. However, FORGRO reads nutrient concentrations in the soil solution which are calculated by the NUCSAM model, and TREGRO uses a fixed availability of nutrients in the soil. In FIWALD, availability of nutrients is defined as the sum of deposition, silicate weathering, and litter decomposition, minus seepage. The approaches used to calculate the uptake of available nutrients are also very different (Mohren and Ilvesniemi, 1995). Drought conditions in the soil affect nutrient uptake through mass flow in the models NICCCE, FORGRO, and SOILVEG.

Temperature can affect plant growth in various ways. It can affect plant growth directly through effects on the rates of metabolic processes or indirectly by affecting evapotranspiration, and thus the water status of the plants. The processes affected by temperature are photosynthesis, maintenance respiration, and, in the models NICCCE and SOILVEG, the active part of nutrient uptake.

The effect of temperature on tree growth is complex and difficult to predict because, in addition to direct effects of temperature on photosynthesis and respiration, temperature affects transpiration which in turn affects both carbon uptake, and, through mass flow, nutrient uptake.

Anthropogenic stresses

Anthropogenic stresses include the direct effects of air pollution (O_3, SO_2) on photosynthesis and respiration and indirect effects of acid depo-

sition on the nutrient status of the soil solution. FIWALD, FORSOL, and SOILVEG use empirical relations between air pollutant concentrations and photosynthetic rate. The relation is expressed as a reduction factor, which is multiplied with the potential photosynthetic rate to get the gross rate. In FORGRO and TREGRO, the effect of an air pollutant on photosynthetic rate and maintenance respiration is also expressed as a reduction factor, but this factor is related to the flux of the pollutant through the stomata, instead of the ambient pollutant concentration. During drought stress stomatal closure reduces not only uptake of CO_2, but also uptake of air pollutants.

The anthropogenic stresses can alter the influence of the 'natural' stress factors. In FORSOL and SOILVEG, nutrient uptake is affected by Al concentration and pH in the soil solution, both indirect effects of acid deposition. In both models, the Al concentration in the soil solution affects fine root growth, which can cause a change in water and/or nutrient uptake.

3.2. Methods for application of the models

The instructions for applying the models to the Solling site for the purposes of the workshop defined two no-stress scenarios aimed at quantifying forest damage due to natural and anthropogenic stress. These scenarios were to (1) eliminate all pollution stress (set concentrations of SO_x, NO_x, NH_4 and O_3 equal to zero), and (2) eliminate water and nutrient stress. To better understand the interactions of multiple stresses, we suggested additional scenarios, (3) applying each stress singly and (4) applying each combination of stresses.

Of the models participating in the workshop, four were applied to the suggested scenarios of stress interactions. In addition, the TREGRO model (Weinstein et al., 1991) was used to evaluate interactions of multiple stresses, although it was not applied to the Solling site with the same criteria for calibration as the others. These TREGRO simulations are described in Appendix A.

To evaluate the results of the simulations it is important to understand the methods of stress elimination, which differed across the models.

Elimination of pollution stress

In FIWALD pollution stress was eliminated by reducing anion deposition and increasing cation deposition. In FORSOL, FORGRO, SOILVEG, and TREGRO, O_3 and SO_2 effects were eliminated. Additionally, FORSOL eliminated pH effects on root uptake of nutrients.

Elimination of drought stress

In FORSOL, which uses a yearly timestep, drought stress is eliminated by setting the number of dry days to zero. This means that the soil solution concentrations are not influenced. In FIWALD the soil water potential was kept constant at -0.005 MPa. In FORGRO drought stress was eliminated by ignoring the drought in the soil. FORGRO uses tabulated input of nutrient concentrations in soil solution. Therefore the nutrient concentrations were not influenced by elimination of the drought stress. In SOILVEG, simulated irrigation was used to eliminate drought stress by adding to the water flux into the upper soil layer. The amount of water added daily made up the difference between daily potential transpiration and the daily rain fall.

Elimination of nutrient stress (deficiency)

In FIWALD nutrient deficiency is eliminated by a tenfold deposition of base cations. In FORSOL nutrient deficiency is eliminated by forcing the nutrient uptake to fulfil the optimal content in the tree tissues, which is a content that does not limit the growth rate. In FORGRO optimal nutrient uptake is accomplished by taking up a fraction of nutrient demand, because maximum nutrient concentrations are not optimal for plant growth in this model. In SOILVEG, simulation of fertilization is used to eliminate nutrient deficiency. This is accomplished by a daily addition of nutrients to the nutrient flux into the upper soil layer. In TREGRO elimination of Mg deficiency was obtained by increasing the Mg availability in the soil solution.

Note that simulations with optimal conditions are a combination of elimination of pollution stress, drought stress, and nutrient deficiency, except FIWALD, which excluded elimination of pollution stress.

4. Results

4.1. Quantification of forest damage

The magnitude of stress effects and the nature of stress interactions depend on the indicator analyzed. We selected three output variables, namely gross photosynthesis, maintenance respiration, and stem growth rate, for assessing the degree of forest damage attributable to natural and anthropogenic stress at Solling. The basis for comparison is the calibrated (Solling) simulation (Fig. 2). The simulated elimination of various stresses should indicate the quantitative importance of these stresses at the Solling site.

The four models that simulated the Solling forest agreed that the short-term, direct effects of air pollution are small (less than 5%) on all three outputs: stem growth rate, gross photosynthesis, and maintenance respiration. FIWALD predicts a small negative effect on photosynthesis of eliminating pollution. In FIWALD, photosynthesis is related to the Mg concentration in the leaves. In the no pollution scenario, deposition of Mg is lower than the actual Mg deposition. This explains the predicted negative effect of pollution reduction on photosynthesis. FORGRO predicts a negative effect of pollution reduction on mainte-
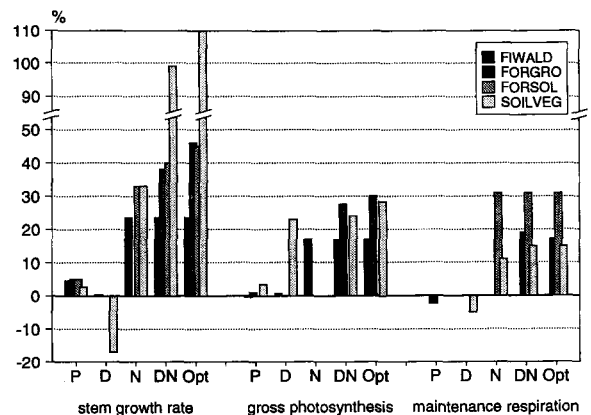

Fig. 2. Simulated stem growth rate, gross photosynthesis, and maintenance respiration, expressed as percentage increase over the Solling simulation, with applied elimination of pollution stress (P), drought stress (D), nutrient stress (N), drought and nutrient stress (DN), and elimination of pollution stress, drought stress, and nutrient stress (Opt).

nance respiration, which is proportional to the nutrient content of plant tissue. This negative effect can be explained by the inhibiting effect of pollution on nutrient uptake through changes in root morphology. In contrast, the effect of nutrient stress was quite large; stem growth was predicted to be 24 to 99% higher in the absence of nutrient stress. Some models included effects of nutrient stress on photosynthesis and respiration; others did not (Table 1). The models were in greatest disagreement over the effects of drought stress. FIWALD and FORSOL predicted little effect of drought, while SOILVEG predicted decreased growth with drought removed. Stem growth rate calculated with SOILVEG is decreased by simulated irrigation (at a irrigation rate that just eliminates transpiration reduction), because dilution of nutrients in the soil solution causes nutrient stress.

The magnitude of forest limitation from all sources of stress, natural and anthropogenic, is indicated by comparing the actual Solling simulations with the optimal simulations. The models varied in their assessment of this effect on stem growth (from 19% to 53%; Table 2). Differences between the models result from (i) different conditions used to simulate the optimal growth rate and (ii) different model structures; optimal growth rate is established in different ways. In FORSOL a site index growth curve determines the maximum possible growth rate. In FORGRO and TREGRO the growth rate is limited by nutrient uptake and by CO_2 uptake, which is limited by stomatal resistance and by radiation. Maximum nutrient uptake in FORGRO is determined by the demand of the trees. In SOILVEG growth rate is also limited by CO_2 uptake, but this uptake is proportional to the actual transpiration. Also nutrient uptake

Table 2
Simulated gross photosynthesis, maintenance respiration, and stem growth rate, expressed as percentage reduction of optimal simulation

Scenario \ model	FIWALD [a]	FORGRO [b]	FORSOL [b]	SOILVEG [b]	TREGRO [c]
Gross photosynthesis					
only pollution stress	1.0	2.0	–	3.3	6.4
only drought stress	0.0	–	–	19.1	–
only nutrient stress	13.7	–	–	1.2	0.0
only drought/nutrient	14.7	22.3	–	19.3	–
only drought/pollution	–	23.2	–	21.8	–
only nutrient/pollution	–	–	–	4.4	6.4
actual Solling	14.5	23.1	–	22.1	–
Maintenance respiration					
only pollution stress	–	– 1.6	0.0	0.1	– 15.1
only drought stress	–	–	0.0	3.3	–
only nutrient stress	–	–	23.7	17.2	11.1
only drought/nutrient	–	16.5	23.7	13.0	–
only drought/pollution	–	15.4	0.0	3.5	–
only nutrient/pollution	–	–	23.7	17.2	– 7.9
actual Solling	–	14.5	23.7	13.1	–
Stem growth rate					
only pollution stress	3.6	5.7	3.4	5.3	8.3
only drought stress	0.1	–	4.8	34.2	–
only nutrient stress	18.8	–	27.6	60.6	15.3
only drought/nutrient	15.2	27.8	27.6	52.0	–
only drought/pollution	–	30.7	8.3	37.9	–
only nutrient/pollution	–	–	31.0	60.8	17.1
actual Solling	19.1	31.5	31.0	53.4	–

[a] Average 1973–1991.
[b] Average 1976–1989.
[c] Average 1968–1970; nutrient stress is only Mg stress, pollution stress is only O_3 stress.

limits growth rate, but uptake is proportional to the actual transpiration and the nutrient concentration in soil solution.

4.2. Stress interactions

Comparing the magnitude of forest damage due to individual and combined stresses shows how multiple stresses interact in the models. Table 2 shows the percentage change in the three output variables (gross photosynthesis, maintenance respiration, and stem growth rate) in each stress combination compared to the optimal simulation where pollution, drought, and nutrient stress are eliminated.

All stress interactions affecting gross photosynthesis show less than additive effects. In FORGRO the combination of direct stress (air pollution) and drought stress gives less decrease of gross photosynthesis than the sum of the stresses taken alone. This can be explained by the fact that drought stress leads to increased stomatal closure, and increased resistance to uptake of air pollutants (feedback). In SOILVEG the sum of the effects of direct stress, drought stress, and nutrient stress (23.6%) is more than the combined effect (22.1%). One explanation is that in SOILVEG the effect of air pollution is relative to the potential gross photosynthesis. Because photosynthesis in SOILVEG is proportional to the actual transpiration, drought decreases gross photosynthesis, and thus decreases the effect of air pollution. FORGRO, SOILVEG, and TREGRO show a less than additive effect of stress on maintenance respiration. In FORSOL the effect is predictable, because only nutrient availability affects respiration.

Most of the models simulate a less than additive effect of stresses on stem growth rate. Additive effects of stress on stem growth rate are seen only in the FORSOL simulation of air pollution with nutrient deficiency and air pollution with drought. In FORSOL, the combination of drought and nutrient deficiency follows 'the law of the minimum', which in this case is the effect of nutrient deficiency. In SOILVEG the effect of drought/nutrients is less than the sum of the single stresses, and is even less than only nutrient

stress. The explanation is that drought stress is eliminated by irrigation. Irrigation causes dilution of the nutrients in soil solution and thereby increases the nutrient deficiency, despite the increased mass flow (increased actual transpiration). Thus the nutrient stress as a single stress is not of the same order of magnitude as nutrient deficiency combined with drought stress. In TREGRO the effect of O_3 and Mg stress is less than the sum of single stresses. In TREGRO, O_3 affects stem growth through carbon availability by affecting photosynthesis and maintenance respiration; Mg stress also affects stem growth rate as a limiting factor.

5. Discussion: stress interactions

General patterns of stress interactions may be described by observing or simulating plants and forests. The effect of multiple stresses is generally not less than the effect of the single strongest stress (law of the minimum). It is usually less than the sum of all the worst effects. However, these rules describing the effect of multiple stresses on whole plants or forests cannot be deduced from the action of the individual stresses at the process level, even in deterministic models where the modes of action are known.

There has been much discussion of whether multiple stresses 'interact', meaning that their combined effect on the plant is not what would be predicted from the effects of the stresses taken separately. This approach implies that there is a straightforward method for predicting how multiple stresses should combine without 'interaction'. It is not clear, however, how to predict a combined effect from two stresses taken separately. At least three types of stress combination are readily defined: additive, multiplicative, and minimum. Each of these stress combinations gives a different rule for predicting stress effects. Because the three predictions are different, it is necessary to specify the nature of the expected stress combination when looking for 'unpredicted' effects. There are three reasons why such 'unpredicted' effects should be expected.

First, there are multiple feedbacks in even a simple plant system (Fig. 1). These feedbacks,

both positive and negative, alter the effect of stress on the plant. A plant may alter its allometry, increasing carbon allocation to roots during nutrient stress, for example, in order to alter its ability to capture resources or avoid stress. The effect of the stress on plant growth in this case will be less than in the absence of this feedback. On the other hand, one stress can increase plant susceptibility to another stress. Nutrient stress, in the case of N or Mg deficiency, can have a negative effect on photosynthesis, which reduces the ability of the plant to allocate carbon to roots. In this case, the effect of the stress will be greater than in the absence of the feedback. Even the most simple feedback can alter the effect of the stress over time and distance in the plant. For this reason, the effect of stresses that act on specific plant processes cannot be easily translated into an effect on the overall growth and function of whole forests. The proximate effect of a stress as implemented in a model does not determine its effect away from the point of action.

Second, the nature of the stress effects depends on the output variables we consider. For example, ozone may reduce photosynthesis per unit leaf, but increase carbon allocation to leaves, resulting in little loss to whole-canopy photosynthesis. This compensatory mechanism has the indirect effect of reducing carbon allocation to stems and roots. The magnitude of the effect of ozone on each of these plant processes can be quite different, even when only one stressor is considered. Likewise, when pH in the soil solution affects root uptake of nutrients, it may or may not affect photosynthesis and growth, depending on whether nutrients are limiting. Therefore, a cation stress combination might be more than additive on one process and less than additive on another.

Third, although the three types of stress relationships (multiplicative, additive, and law of the minimum), seem to apply to certain simple cases of multiple stress, variation in time of the stressors can increase the complexity of the relationship. For example, although SO_2 and O_3 are both defined in a model as independent multipliers on photosynthesis (Fig. 1), and the relationship is

also defined as multiplicative, the depression of photosynthesis with both pollutants present is not the multiplied effect on photosynthesis of each of the pollutants taken alone, if the pollutant exposures vary over time.

$$\sum_{t=1}^{n}(a \cdot b) \neq \sum_{t=1}^{n} a \cdot \sum_{t=1}^{n} b \qquad (5)$$

Likewise, although growth is the minimum of carbon and nutrient availability, growth in the presence of both stresses is not necessarily equal to the lesser of growth in the presence of carbon limitation only.

$$\sum_{t=1}^{n} \min(a,b,c)$$
$$\neq \min\left\{ \sum_{t=1}^{n} \min(a,b), \sum_{t=1}^{n} \min(a,c) \right\} \qquad (6)$$

Only in the case of additive stresses can the combined stress be predicted from the independent stresses. That is, if two stresses act by decreasing the same pool (non-structural carbon or available nutrients, for example), and are independent of that pool, the effect of the two stresses will be the sum of the individual stresses on that pool (barring other feedbacks, as discussed above).

$$\sum_{t=1}^{n}(a+b) = \sum_{t=1}^{n} a + \sum_{t=1}^{n} b \qquad (7)$$

Thus, even in the case of very simple stresses acting without explicit interactions, simple rules cannot predict the cumulative effects of stresses that act over time in complex patterns. The amount of growth reduction due to one stress, taken over time, cannot be combined with the growth reduction due to another stress to predict the effect of the multiple stresses.

Because of these limitations on predicting the combined effects of multiple stresses, modelling is an important tool for assessing forest damage due to anthropogenic and natural causes. Although there is little chance of using experimental methods to study all possible combinations of stresses, more long-term experimental manipulations are needed to calibrate and validate the

models. Models differed in the estimation of stress effects at Solling because they considered different processes and used different representations of the mechanisms of stress effects. Most important to the results were the differences in the methods of stress elimination used by the different models groups.

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Appendix A

The TREGRO model

The TREGRO model was used to explore stress effects and interactions, but because it was not calibrated to the site, the results cannot be used to estimate forest damage at Solling, and so it is excluded from Fig. 2. TREGRO is a detailed physiological model of individual tree response to multiple environmental stresses (Weinstein et al., 1991). To illustrate the relationship between the effects of environmental stresses as simulated by TREGRO for the purposes of the workshop, the parameter set developed for a red spruce tree was altered to represent a mature Norway spruce tree characteristic of the Solling site. The biomass values of stem, branches, current and total needles, and coarse roots were taken from Ellenberg et al. (1986), converted from a stand basis to an individual tree using the reported tree density of 595 stems ha^{-1}. A constant fine root mass of 3 Mg ha^{-1} was assumed for the simulations. Hourly ozone concentrations were taken from Ithaca in

1988 and multiplied by a factor of ten in the years of simulation (1967–1970). This degree of ozone stress was selected in order that the combined effects of ozone and nutrient stress could be described; it does not represent forest response at Solling.

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