

Developing adaptive forest management strategies to cope with climate change

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Summary Numerous investigations have indicated that projected climate change will impact strongly on forest growth and composition. To adapt managed forests to changing environmental conditions it may be necessary to modify traditional forest management strategies. An extended version of a forest gap model was applied to a managed forest district in northeastern Germany. The model was initialized with forest inventory data and run using routines devised to simulate three management scenarios: (1) maximized timber production, (2) climatically well-adapted forest composition, and (3) maximized tree species diversity. The strategies were compared with a baseline scenario of traditional management without any response to climate change. The comparisons were based on simulated wood production and species composition after 110 years of development. The results underline the important influence that management strategies have on forest growth. Forest management may adopt a variety of strategies to respond to the expected changes in climate. Process-oriented forest gap models can aid in the assessment of these strategies.

Keywords: *adaptation strategies, Carpinus betulus, forest gap model, FORSKA, Pinus sylvestris, productivity, Quercus petraea, simulation, Tilia cordata.*

Introduction

Climate change may have different impacts on different forest ecosystems. Expected changes in tree growth will influence the competitive relationships between species, the potential species composition and the choice of species available in managed forests. Although the impacts of climate change on physiological processes and natural species composition have been studied (e.g., Kirschbaum et al. 1996, Melillo et al. 1996, Shugart and Smith 1996, Mohren et al. 1997), there has been little research on the possible consequences of climate change in managed forests.

Because traditional, empirically based models and growth and yield tables are not suitable for use under changing environmental conditions, there is an urgent need to develop simulation methods that can be applied under changing climatic conditions. Forest gap models have been used to simulate possible impacts of climate change on natural forests (e.g., Solomon 1986, Pastor and Post 1988, Bugmann 1994, Lindner et

al. 1997a). However, these models need further development to include management activities, because many forests, particularly in Europe, have been managed intensively over several hundred years. Lindner (1998) extended a forest gap model to include regional analyses of the impacts of climate change in managed forests of Central Europe. First applications of this model have shown that management strategies strongly influence forest growth and development under conditions of climatic change (Lindner 1999).

Common forest management strategies for stand regeneration, silvicultural treatments and harvesting differ considerably with respect to the flexibility of response of the managed trees to changing environmental conditions. For example, natural regeneration limits the choice of tree species. Thinning strategies influence the adaptability of forest stands. Conservative thinning from below does not increase the adaptation potential, whereas selective thinning, which also extracts dominant trees, enables the development of a diverse forest structure and the early introduction of species to the stand. Furthermore, forest management may not only respond to climate change at the stand level, but also at higher hierarchical scales (e.g., at the district level), where the diversity of species and forest types can be increased as a means of risk reduction (Thomasius 1991).

In this study, an extended forest gap model that incorporates management routines was used to simulate three forest management strategies: (1) maximized timber production, which is the most important goal in many private forest enterprises; (2) climatically well-adapted forest composition, which is a silvicultural goal in nature-oriented forest management; and (3) maximized tree species diversity, a possible strategy to reduce the risk of dieback under changing environmental conditions. The strategies were evaluated in two forest types occurring in northeastern Germany—an even-aged pure stand of Scots pine (*Pinus sylvestris* L.), and a mixed-aged oak–lime–hornbeam stand (*Quercus petraea* (Matt.) Liebl.–*Tilia cordata* Mill.–*Carpinus betulus* L.).

Methods

The simulation model

The forest gap model, FORSKA, was originally developed to simulate natural dynamics in the boreal forests of Scandinavia

(Prentice and Leemans 1990, Prentice et al. 1993). It considers growth, regeneration, and mortality of individual trees on small forest patches. State variables of a tree are age, diameter, tree height, height of the crown base, and leaf area. The model employs long-term mean monthly climate data that are interpolated to yield quasi-daily values for the calculation of environmental response functions (Prentice et al. 1993). Tree growth, regeneration, and mortality are simulated with an annual time step. Model outputs are stand characteristics (e.g., total biomass, basal area, stem number, mean diameter and height). The model can also generate additional information on size distributions and individual tree characteristics (e.g., height/diameter ratio).

Before FORSKA was applied in managed forests, the model's simulation of stand density effects on tree growth was improved (Lindner et al. 1997b). The simulation of size distributions was further improved by means of an efficiency factor E_{eff} , which increases the growth efficiency of suppressed and intermediate trees. Net primary production P , as the balance of assimilation A and respiration R , was modified by:

$$P = E_{\text{eff}}(A - R), \quad (1)$$

where

$$E_{\text{eff}} = 1 + a_{\text{eff}} \left(1 - \frac{H}{H_{\text{top}}} \right), \quad (2)$$

and H is tree height, H_{top} is the maximum tree height of the stand, and a_{eff} is a parameter. The parameter values for the modified model, FORSKA-M, are given in the Appendix (Table A1).

With the current model version, a variety of forest management activities can be simulated based on three modes of regeneration (unrestricted seed availability, natural regeneration of species with mature trees, planting of selected species), different harvesting techniques (clear cut, shelterwood harvesting, and selective harvesting), and a Weibull distribution-based stochastic thinning routine (Gerold 1990, Wenk and Gerold 1996):

$$x = b_{\text{TH}}^{c_{\text{TH}}} \sqrt[c_{\text{TH}}]{-\ln(1-u)} + a, \quad (3)$$

where x is the diameter of a thinned tree, a is the minimum diameter of the stand, b_{TH} and c_{TH} are parameters of the Weibull distribution of the ensemble of all thinned trees, and u is a random number between 0 and 1.

In most applications of the stochastic thinning routine, the parameters b_{TH} and c_{TH} are fitted with research plot data; however, in this simulation experiment, it was necessary to find mean values representing typical thinning strategies. Because the parameters change with stand development, they were estimated from the diameter distribution of the simulated forest stand before thinning (Gerold 1990).

Thus, parameter b_{PT} of the Weibull function describing the diameter distribution of the simulated forest stand before thinning can be estimated using a quantile of the diameter distribu-

tion, because approximately 63% of the trees have a diameter smaller than $(a + b_{\text{PT}})$:

$$b_{\text{PT}} = d_{63\%} - a. \quad (4)$$

By analogy, c_{PT} can be estimated from another quantile ($d_{95\%}$):

$$c_{\text{PT}} = \frac{1.09719}{\ln((d_{95\%} - a) / b_{\text{PT}})}. \quad (5)$$

The relationship between the diameter distributions of the stand before and after thinning was characterized by the constant K_b :

$$K_b = b_{\text{PT}} / b_{\text{TH}}. \quad (6)$$

Parameter a was identical for both distributions, and it was assumed that c_{TH} equals c_{PT} . Thinning strategies could be characterized by the specific value of K_b (Table 1), and thus the choice of K_b determined the thinning strategy in FORSKA-M. Thinning intervals depended on height growth of the dominant trees in the stand, and thinning intensity was determined by basal area values given in beech and pine yield tables for East Germany (Lembcke et al. 1975, Dittmar et al. 1986). The rotation period is determined by a prescribed harvest age or harvest diameter of the dominant trees, or both.

Another new management option introduced to FORSKA-M was the active planting of selected species that bypassed the environmental filter functions in the regeneration module. The selection of suitable species depended on the applied management strategy as described below. The planting routine introduced all suitable species at the rate of N saplings ha^{-1} on each patch, where:

$$N = (1 / N_{\text{spe}}) p_{\text{area}} 4000, \quad (7)$$

N_{spe} denotes the number of climatically well-adapted species, and p_{area} is the size of a patch (0.1 ha in FORSKA-M).

To run the model with forest inventory data, a series of stand initialization routines was implemented to generate individual tree data from stand-level characteristics. The method of Nagel and Biging (1995) was used to generate a diameter distribution. The diameter at breast height of individual trees, D_i , was calculated with a derivation of the Weibull function:

$$D_i = b_w [(T / b_w)^{c_w} - \ln(1-u)]^{1/c_w}, \quad (8)$$

where b_w and c_w are parameters of the Weibull function, T is a

Table 1. Values of the constant K_b (Equation 6) of the thinning routine for different thinning strategies

| Thinning strategy | K_b |
|------------------------------|-------|
| Light thinning from below | 2.5 |
| Moderate thinning from below | 1.8 |
| Thinning from above | 1.2 |

threshold for the minimum diameter, and u is a random number between 0 and 1. Parameters b_w and c_w were estimated from regression analysis of 2242 measurements on 450 research plots in northern Germany (Nagel and Biging 1995):

$$b_w = wp_0 + wp_1 D_g \quad (9)$$

$$c_w = wp_2 + wp_3 D_g + wp_4 D_{\max}, \quad (10)$$

where wp_0 – wp_4 are species-specific parameters (Appendix; Table A2), D_g is the quadratic mean diameter, and D_{\max} is the maximum diameter. If D_{\max} was not available, it was estimated from D_g (Gerold 1990):

$$D_{\max} = a_m + b_m D_g - c_m D_g^2, \quad (11)$$

where $a_m = 8.2$, $b_m = 1.8$ and $c_m = 0.01$.

If the mean diameter of the generated diameter distribution, $D_{g\text{gen}}$, deviated by more than 20% from the observed D_g , the parameters wp_1 and wp_4 of Equations 8 and 9 were adjusted iteratively:

$$wp_{1\text{mod}} = wp_1 D_g / D_{g\text{gen}} \quad (12)$$

and

$$wp_{4\text{mod}} = wp_4 D_{\max} / D_{\max\text{gen}}, \quad (13)$$

with wp_1 and wp_4 modified separately, because each of the parameters influences both D_g and D_{\max} of the generated diameter distribution.

Height of a tree was calculated from standard height curves given by Weimann (1980) or Kuleschis (1981, cited in Gerold 1990) (see Appendix; Table A3). Bole height, H_{bc} , was estimated from diameter and height (Nagel 1997):

$$H_{bc} = H \left(1 - e^{-\left(c_1 + c_2 \frac{H}{D} \right)^2} \right), \quad (14)$$

where c_1 and c_2 are species-specific parameters.

Finally, leaf area, L , was estimated from the relationship between sapwood and leaf area in young unshaded trees (Pren-

tice and Leemans 1990), with the assumption that older trees maintain 20 years of sapwood:

$$L = \sqrt{N_{\text{swr}} / N_{\text{yr}}} c_1 D^2, \quad (15)$$

where N_{swr} is the number of sapwood rings, N_{yr} is the age of the tree and c_1 is a species-specific parameter. The leaf area estimate of the individual tree contains considerable uncertainty because this variable is rarely included in research plot measurements.

The simulation experiment

Simulations were run for two forest types in northeastern Germany (Table 1). Type 1 was an even-aged stand of Scots pine, a commonly occurring forest type in northeastern Germany. Type 2 was a mixed-aged oak–lime–hornbeam forest, which is thought to be the potential natural forest composition on intermediate to fertile soils in northeastern Germany (Krausch 1993). Because young forest stands may respond differently to the impacts of climate change than old stands, three simulations were conducted for each forest type starting with stands aged 25, 60, and 100 years. Site data and climatic characteristics for the two forest types are given in Tables 2 and 3. Each simulation with 50 replications was run for 110 years, (almost a complete forest rotation period) from 1990 to 2100. To smooth the short-term effects of thinning and harvesting, the results were averaged over the last 20 simulation years.

Climate scenarios

The simulation experiment was run for the current climate (BASC) based on long-term (1951–1980) monthly means from the climate station at Angermünde, and for two climate change scenarios that were developed at the Climate Research Department, Potsdam Institute for Climate Impact Research (Werner and Gerstengarbe 1997). These scenarios mimic temperature trends obtained from global circulation models (Kattenberg et al. 1996), but they are built on the basis of multivariate statistical analyses of long-term meteorological observation data. Scenarios SE15 and SE30 are characterized by temperature increases of 1.9 K and 3.4 K, respectively. Precipitation is fairly constant in both scenarios (Table 3).

Table 2. Stand data for the initialization of the simulations. Abbreviations: n = tree number ha^{-1} ; d = quadratic mean diameter at breast height (cm); H = height of the tree with d (m); and G = basal area of the stand ($\text{m}^2 \text{ha}^{-1}$).

| Forest type | Initial stand age: 25 years | | | | Initial stand age: 60 years | | | | Initial stand age: 100 years | | | |
|-------------------------|-----------------------------|-----|------|------|-----------------------------|------|------|------|------------------------------|------|------|------|
| | n | d | H | G | n | D | H | G | n | d | H | G |
| 1: Scots pine | | | | | | | | | | | | |
| <i>Pinus sylvestris</i> | 4070 | 7.9 | 9.1 | 23.8 | 960 | 22.3 | 19.3 | 35.2 | 400 | 36.8 | 26.0 | 37.6 |
| 2: Oak–lime–hornbeam | | | | | | | | | | | | |
| <i>Quercus petraea</i> | 7760 | 6.5 | 10.0 | 17.3 | 860 | 19.5 | 20.5 | 23.5 | 350 | 34.0 | 26.0 | 25.6 |
| <i>Tilia cordata</i> | 2710 | 6.0 | 7.6 | 3.6 | 2970 | 6.0 | 7.6 | 3.6 | 280 | 18.5 | 19.8 | 5.7 |
| <i>Carpinus betulus</i> | 2710 | 6.0 | 7.6 | 3.6 | 2970 | 6.0 | 7.6 | 3.6 | 280 | 18.5 | 19.8 | 5.7 |

Table 3. Site characteristics. Abbreviations: BASC = current climate; SE15 and SE30 = climate change scenarios; bs = bucket size, i.e., available soil water (mm); avln = available nitrogen ($\text{kg ha}^{-1} \text{ year}^{-1}$); t = annual mean temperature ($^{\circ}\text{C}$); and p = annual precipitation sum (mm).

| Forest type | Soil | | Climate | | | | | |
|-------------|------|------|---------|-----|------|-----|------|-----|
| | bs | avln | BASC | | SE15 | | SE30 | |
| | | | t | p | t | p | t | p |
| 1 | 113 | 35 | 8.3 | 535 | 10.2 | 472 | 11.7 | 506 |
| 2 | 165 | 75 | | | | | | |

Management scenarios

Three management strategies were assessed to illustrate the broad applications of the model and to highlight the effects of a broad variety of management goals, each of which began from the same traditional management condition.

Traditional management (SCEN0) The baseline scenario is a conservative strategy. Only dominant species prior to harvesting are available for regeneration by either natural or artificial regeneration, or both. No species shift is considered in response to the changing climate. The forest rotation period is 120 years for Scots pine and 180 years for oak.

Maximized timber production (SCEN1) This is an exploitive strategy involving the most productive tree species for each site \times climate scenario combination. The most productive species were identified by a series of simulations with even-aged pure stands of all species in the FORSKA-M model. The selected species was then planted at 4000 saplings ha^{-1} after partial cuts or final harvesting.

Climatically well-adapted forest (SCEN2) In this scenario, only climatically well-adapted species were regenerated, i.e., new species could invade if the climate became suitable. The combination of species-specific environmental response factors in FORSKA-M (Prentice et al. 1993) was used as a test criterion. The water balance is the most critical climatic factor determining species distribution limits in northeastern Germany (Bugmann and Cramer 1998). The FORSKA-M model uses a site-specific ratio of actual to potential evapotranspiration to calculate a drought stress index α (Prentice et al. 1993). All tree species are given the maximum value of α that they can tolerate. Two thresholds were introduced into the model to characterize the adaptation of the species to climatic conditions: a lower threshold below which a species is considered to be susceptible to drought stress, and a second threshold above which a species is considered to be well-adapted to the prevailing climate (see Figure 1). Because there is no spatial consideration of seed source availability from neighboring stands in FORSKA-M, it is assumed that the three best adapted species are nearby or planted at the site.

Maximized tree species diversity (SCEN3) This scenario is similar to SCEN2, but to achieve maximized tree species diversity, all species with a drought stress response factor above the lower threshold are planted.

Results

Forest development under different climate scenarios is shown in Figure 2 for the pure Scots pine forest and the management scenario SCEN3. There was a clear effect of the climate change scenarios on stand productivity. Under current climatic conditions, the simulated stands showed considerable biomass growth, whereas in response to climatic change there was little increase in stand biomass. Over the 110-year simulation period, there was a clear effect of initial stand age on the simulation results. The forest stand of initial age 25 years was harvested shortly before the end of the simulation period and hence it did not show any shift in species composition. The stands of initial age 60 and 100 years developed into mixed stands with birch and oak; additionally, in the current climate scenario, beech and some other species were also present.

The results with the second forest type and the effects of the alternative management scenarios are shown in Figure 3 as mean values per forest type. In this graph, the results of the three different initial ages were averaged to enable a clear comparison of scenarios. Under current climatic conditions,

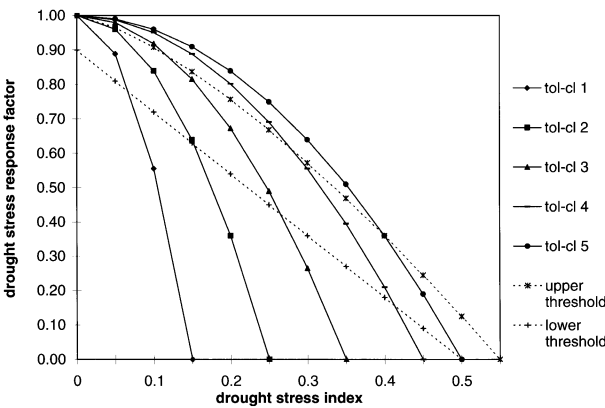


Figure 1. Drought-stress response function of the FORSKA-M model and thresholds determining the climatic adaptation of tree species. The drought stress index of a site is calculated as the ratio of actual to potential evapotranspiration. The tolerance classes of the species are defined by the maximum drought stress that a species tolerates (drought sensitive = $dri = 0.15$; drought tolerant = $dri = 0.5$). Species with a drought-stress response below the lower threshold are considered to be susceptible to drought stress. Species with a drought-stress response above the upper threshold are considered to be well adapted to the prevailing climate.

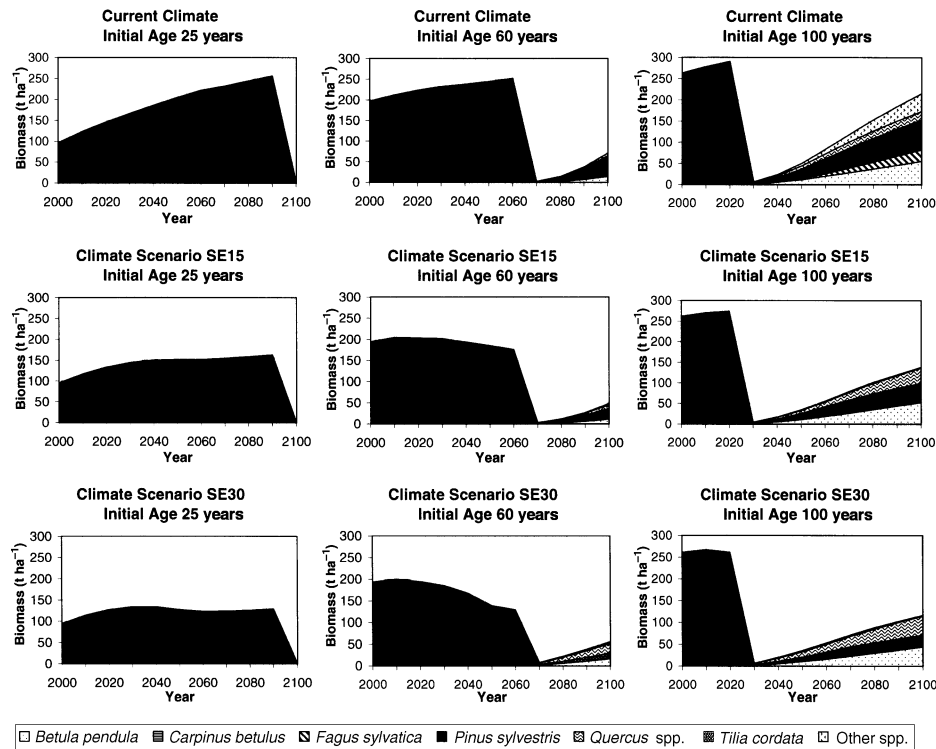


Figure 2. Simulated biomass of three stands of forest type 1 at the Angermünde site (initially Scots pine stands of different age) for the current climate and two climate change scenarios, SE15 and SE30, which are 1.9 K and 3.4 K warmer, respectively, than the current climate. The applied management scenario SCEN3 favors climatically well-adapted species and aims at a maximized diversity of tree species. Simulation results represent means of 50 plots and the biomass is averaged over the last 20 simulation years of each simulation run.

the different management scenarios produced different types of forests by the year 2100. Although the baseline simulation for the pure Scots pine stand with a conservative management strategy showed little change compared with the stand initialization, the three management alternatives each led to characteristic changes in the simulated forest composition. With climate change, which favoured drought-tolerant species, the pure stand of Scots pine developed into an oak–birch stand.

The maximum productivity scenario favored birch, which showed very high productivity, although this seems unrealistic. In the maximized species diversity scenario, the number of co-dominant species increased.

The climate change scenarios resulted in reductions in simulated biomass at the end of the simulation period. However, the large reductions in biomass in the simulation experiments with the oak–lime–hornbeam forest type were partly caused

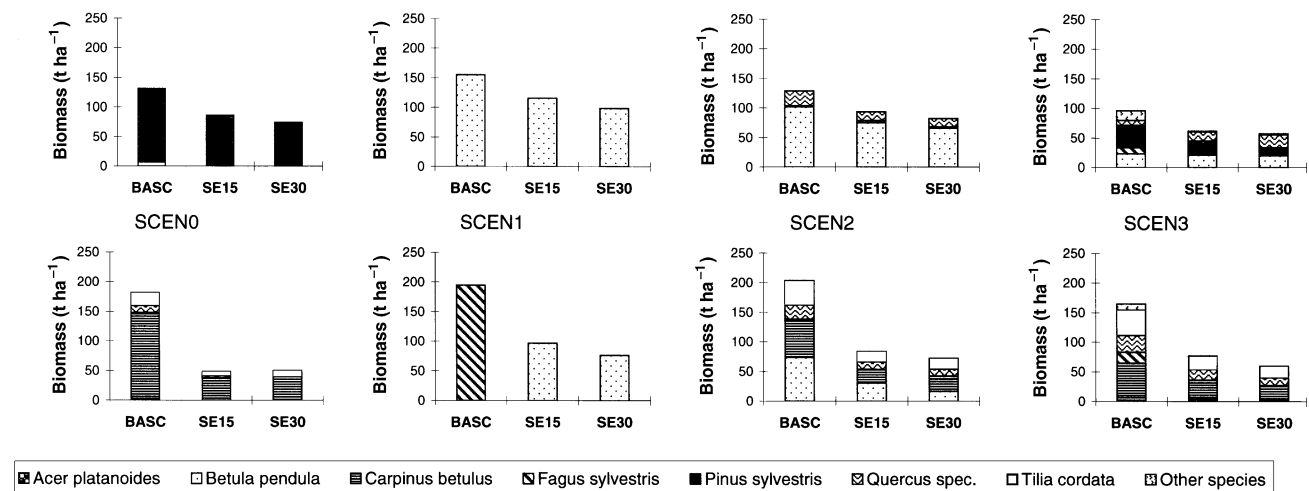


Figure 3. Simulated biomasses at the Angermünde site after 110 simulation years for the investigated forest types under different management (SCEN0 = traditional management, SCEN1 = maximum productivity, SCEN2 = climatically well-adapted forest composition, SCEN3 = maximum diversity of tree species) and climate scenarios (BASC = current climate, SE15 and SE30 are climate change scenarios that are 1.9 K and 3.4 K warmer, respectively, than the current climate). The simulation results represent means of 3×50 plots for different initial ages (25, 60, 100 years) and the biomass is averaged over the last 20 simulation years of each simulation run.

by the prescribed management. In the climate change scenarios, both the initially 25-year-old and the initially 60-year-old stand reached the harvest diameter shortly before 2100, whereas in the current climate scenario this occurred only for the youngest of the three investigated stands. Changes in species composition in response to climate change occurred only in the maximized species diversity scenario, where a minor share of beech was lost as the climate warmed.

Discussion

In agriculture, where rotations are short, it is assumed that cultivation systems may adapt fast enough to respond to possible changes in climate (Rosenberg 1992, Reilly et al. 1996). This is unlikely to occur in forestry, especially in temperate and boreal regions, where average rotation periods may be as long as 120 to 240 years. A modeling study was undertaken to determine the influence of forest management on the impacts of climate change in forest regions with long rotation periods. The model was also used to assess climate change impacts on all possible management measures, to determine if there is enough time to mitigate or adapt to the impacts of climate change.

The results of this simulation experiment suggest that management strategies are important. Within the 110-year time frame, the choice of management strategy largely determines the future forest characteristics. The relatively small impact that climate change has on species composition is site-specific. Other studies have shown that small changes in climate may lead to relatively strong shifts in species composition, if the former dominant trees become less competitive (e.g., Bugmann 1997, Lindner et al. 1997a). The study region lies in the lowlands of northeastern Germany, where temperature has little influence on species distributions (Sykes et al. 1996). At the study site, Angermünde, none of the initial species were close to their drought limits and the projected climate change primarily influenced their vitality and productivity. Thus, at this site, management probably has a stronger impact on simulated species composition than changing climate. The relative importance of different factors may also be influenced by the investigated time horizon. Lasch et al. (1999) have pointed out that forest succession would need more than one forest rotation until a climax forest composition is reached in a changed climate.

The speed of the adaptation process under changing environmental conditions is strongly determined by the length of the rotation period, which, therefore, had a noticeable influence on the simulation results. With an extended rotation length some investigated stands would not be harvested by the year 2100, so regeneration could not affect species composition and standing biomass. Figure 2 shows that it is necessary to analyze more than one age class to get a complete picture of the response of managed forests to climate change. Because of the long rotation period in the investigated forest stands, there was little effect of climatic change on species composition in the first 50 simulation years. Therefore, it is important to investigate time horizons of at least 100 years.

The results of this simulation experiment should be interpreted with care. Some limitations of the applied model have been identified previously (Bugmann et al. 1996, Lindner et al. 1997a), and this investigation applied the model in a way that has not yet been thoroughly tested. For example, single species simulations, which were used in the maximum production scenario, are not commonly performed with a forest gap model. Model performance with monospecific stands was only evaluated for the four main tree species in Germany (Norway spruce, Scots pine, beech, and oak), because suitable data sets were available only for these species (Lindner 1998). The model overestimated the productivity of birch; therefore, improved species parameter values would change some simulation results. However, the FORSKA-M model has already been tested and applied in many different circumstances (Leemans 1991, Leemans 1992, Desanker et al. 1994, Price and Apps 1996, Lindner et al. 1997a, Lasch et al. 1998) and it generally showed satisfactory results when simulating species composition and forest development in unmanaged forests. Therefore, it seems well suited for analyzing the viability of tree species in different environmental conditions. The choice of species is the most important aspect in the management strategies investigated in this study.

The extensions to the FORSKA-M model enabled the evaluation of risks concerning the choice of species in managed forests under changing environmental conditions. For example, the maximized species diversity scenario suggests that, in the current climate, beech is competitive on the more fertile site. But, the simulation results with the projected climatic change show that beech loses competitive strength if drought stress increases at this site, which lies just outside the current natural distribution range of beech. Thus, beech may not be a good choice for the transformation of pine monocultures into deciduous or mixed pine-deciduous forests in northeastern Germany. The model was also used to determine the risk in terms of loss of species or decreasing productivity to be expected if the traditional management is maintained. Although only a decrease in productivity was simulated at the study site, a conservative management strategy may also lead to forest dieback, if the environmental limits of the prevailing species are exceeded by changing environmental conditions.

There is a need for more detailed simulation studies to assess the sensitivity of managed forest ecosystems to changes in climate and management. Investigations under boreal conditions in Finland have shown that, in managed Scots pine stands, climate change may affect the optimum timing of thinnings and the length of the rotation period (Kellomäki and Kolström 1993). In Finland, forest management concentrates on only few species, whereas temperate forests are much more diverse. In northeastern Germany, current forest management is trying to transform coniferous monocultures into mixed uneven-aged forests. The possible impacts of climate change add a new dimension of uncertainty to the difficult choice of tree species for this endeavor. It is important to note, however, that forest management strategies need not focus only on individual stands. For example, increasing the variability of tree species mixtures between neighboring forest stands or within a

forestry district could decrease the sensitivity of a forest to environmental change (Thomasius 1991).

Decision making in forest management should incorporate risk assessments and risk reduction strategies that acknowledge the uncertainties of current scientific understanding. Forest gap models are suitable tools to be applied in such analysis. They may be used to evaluate alternative strategies and thus enable managers to assess the impacts of management strategies in the context of global climate change. Comparisons of different management strategies indicate how much climate change restricts forest management. The potential applications of the model indicate that further model testing should be undertaken so that this methodology can be applied to management problems in practical forestry.

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Appendix: Estimation of initial tree height

Tree height is calculated from diameter based on standard height curves for beech, oak and spruce (Weimann 1980) and for alder, ash, aspen, birch and pine (Kuleschis 1981, cited in

Gerold 1990). The standard height function of Weimann for trees with $D \geq D_g - H_g/2$ is:

$$H = H_g + (k_1 + k_2 H_g)(\ln(H_g - D_g + D) - \ln H_g), \quad (A1)$$

and for trees with $D < D_g - H_g/2$ is:

$$H = (H_g + (k_1 + k_2 H_g) \left(\ln \left(\frac{H_g}{2} \right) - \ln H_g \right) - 1.3) \left(\frac{D}{D_g - H_g/2} \right)^{1/2} + 1.3, \quad (A2)$$

where k_1 and k_2 are parameters (see Table A4).

The standard height function of Kuleschis uses function:

$$H = \left(a_{ku} + \frac{b_{ku}}{D + D_g/2} D_g + \frac{c_{ku}}{(D + D_g/2)^2} D_g^2 \right), \quad (A3)$$

with

$$a_{ku} = 1 - (ku_1 + ku_2 D_g + ku_3 D_g^2), \quad (A4)$$

$$b_{ku} = ku_4 + ku_5 D_g + ku_6 D_g^2, \quad (A5)$$

$$c_{ku} = ku_7 + ku_8 D_g + ku_9 D_g^2. \quad (A6)$$

ku_1 – ku_9 are parameters (Table A3).

Table A1. Parameter values of the extended version of the FORSKA model.

| Species | H_{\max}^1 | hgro | slo | c_1 | s_{\min} | e_1 | a_{eff} | mort ₀ | mort ₁ | dri _{max} | gdd _{min} | T_{wm} | ntc | estab | harv _{age} | harv _d |
|---------------------------|--------------|------|------|-------|------------|-------|------------------|-------------------|-------------------|--------------------|--------------------|-----------------|-----|-------|---------------------|-------------------|
| <i>Acer platanoides</i> | 30 | 0.85 | 0.80 | 0.16 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.50 | 1150 | 14 | 4 | 400 | 120 | 55 |
| <i>A. pseudoplatanus</i> | 35 | 0.95 | 0.80 | 0.16 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.35 | 1500 | 10 | 5 | 400 | 120 | 55 |
| <i>Alnus glutinosa</i> | 33 | 0.95 | 1.11 | 0.20 | 0.5 | 1.5 | 1.0 | 0.0 | 0.05 | 0.00 | 1000 | 10 | 3 | 400 | 80 | 55 |
| <i>Betula pendula</i> | 28 | 1.00 | 1.08 | 0.12 | 0.5 | 1.5 | 1.0 | 0.0 | 0.05 | 0.50 | 500 | 10 | 1 | 400 | 80 | 55 |
| <i>Carpinus betulus</i> | 30 | 0.70 | 0.80 | 0.34 | 0.4 | 0.3 | 2.5 | 0.0 | 0.05 | 0.50 | 1550 | 14 | 4 | 400 | 120 | 55 |
| <i>Castanea sativa</i> | 30 | 0.85 | 0.80 | 0.30 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.50 | 2150 | 18 | 3 | 400 | 120 | 55 |
| <i>Fagus sylvatica</i> | 48 | 0.85 | 0.80 | 0.34 | 0.4 | 0.3 | 2.5 | 0.0 | 0.05 | 0.25 | 1400 | 12 | 2 | 400 | 160 | 55 |
| <i>Fraxinus excelsior</i> | 35 | 0.95 | 0.80 | 0.20 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.35 | 1300 | 14 | 5 | 400 | 120 | 55 |
| <i>Picea abies</i> | 55 | 1.05 | 0.80 | 0.32 | 0.4 | 0.3 | 3.0 | 0.0 | 0.05 | 0.25 | 600 | 10 | 2 | 400 | 100 | 55 |
| <i>Pinus sylvestris</i> | 40 | 0.85 | 0.80 | 0.13 | 0.5 | 1.5 | 1.0 | 0.0 | 0.05 | 0.50 | 500 | 10 | 1 | 400 | 120 | 55 |
| <i>Populus tremula</i> | 27 | 1.00 | 1.26 | 0.10 | 0.5 | 1.5 | 1.0 | 0.0 | 0.05 | 0.35 | 400 | 10 | 2 | 400 | 80 | 55 |
| <i>Quercus petraea</i> | 40 | 0.95 | 0.80 | 0.23 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.50 | 1500 | 10 | 2 | 400 | 200 | 55 |
| <i>Q. pubescens</i> | 20 | 0.50 | 0.80 | 0.30 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.50 | 2150 | 18 | 3 | 400 | 180 | 55 |
| <i>Q. robur</i> | 45 | 0.95 | 0.80 | 0.23 | 0.5 | 1.0 | 2.0 | 0.0 | 0.05 | 0.50 | 1200 | 10 | 2 | 400 | 200 | 55 |
| <i>Tilia cordata</i> | 30 | 0.60 | 0.80 | 0.37 | 0.4 | 0.3 | 2.5 | 0.0 | 0.05 | 0.50 | 1050 | 14 | 4 | 400 | 120 | 55 |
| <i>Ulmus glabra</i> | 35 | 0.70 | 0.80 | 0.30 | 0.4 | 0.3 | 2.5 | 0.0 | 0.05 | 0.25 | 1150 | 10 | 5 | 400 | 120 | 55 |

Abbreviations: H_{\max} = maximum tree height (m); hgro = maximum height growth (m); slo = initial slope of diameter versus height (m cm^{-1}); c_1 = initial leaf area to D^2 ratio ($\text{m}^2 \text{cm}^{-2}$); s_{\min} = minimum slope of diameter versus height growth (m cm^{-1}); a_{eff} = growth efficiency factor; mort₀ = intrinsic mortality rate (year^{-1}); mort₁ = stress induced mortality rate (year^{-1}); dri_{max} = drought stress tolerance limit; gdd_{min} = minimum temperature sum in growing season; t_{wm} = temperature of warmest month ($^{\circ}\text{C}$); ntc = nitrogen tolerance class; estab = sapling establishment rate (ha^{-1}); harv_{age} = harvest age (year); and harv_d = harvest diameter (cm).

Table A2. Parameters of the initialization routines to generate a diameter distribution (wp_0 – wp_4 ; Nagel and Biging 1995) and to estimate the height of the crown base (c_1 and c_2 ; Nagel 1997).

| Species | wp_0 | wp_1 | wp_2 | wp_3 | wp_4 | c_1 | c_2 |
|---------------------------|--------|--------|--------|--------|--------|--------|--------|
| <i>Acer platanoides</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.8035 | 0.2165 |
| <i>A. pseudoplatanus</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.8035 | 0.2165 |
| <i>Alnus glutinosa</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.5037 | 0.3556 |
| <i>Betula pendula</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.7455 | 0.1929 |
| <i>Carpinus betulus</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.721 | 0.2485 |
| <i>Castanea sativa</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.802 | 0.1761 |
| <i>Fagus sylvatica</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.802 | 0.1761 |
| <i>Fraxinus excelsior</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.7043 | 0.3162 |
| <i>Picea abies</i> | –2.492 | 1.104 | 3.418 | 0.353 | –0.192 | 0.6412 | 0.3677 |
| <i>Pinus sylvestris</i> | –0.047 | 1.047 | 3.64 | 0.332 | –0.18 | 1.0157 | 0.1707 |
| <i>Populus tremula</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.802 | 0.1761 |
| <i>Quercus petraea</i> | –1.937 | 1.082 | 4.669 | 0.366 | –0.234 | 0.925 | 0.1158 |
| <i>Q. pubescens</i> | –1.937 | 1.082 | 4.669 | 0.366 | –0.234 | 0.925 | 0.1158 |
| <i>Q. robur</i> | –1.937 | 1.082 | 4.669 | 0.366 | –0.234 | 0.925 | 0.1158 |
| <i>Tilia cordata</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.802 | 0.1761 |
| <i>Ulmus glabra</i> | –3 | 1.132 | 4.518 | 0.317 | –0.2 | 0.802 | 0.1761 |

Table A3. Parameters of the standard height functions.

| Species | ku_1 | ku_2 | ku_3 | ku_4 | ku_5 | ku_6 | ku_7 | ku_8 | ku_9 | k_1 | k_2 |
|---------------------------|----------|-----------|------------|----------|-----------|------------|----------|-----------|------------|--------|---------|
| <i>Acer platanoides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>A. pseudo-platanus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>Alnus glutinosa</i> | –0.79704 | 0.007542 | 0.0003034 | –1.2812 | 0.02187 | 0.0005271 | 0.12847 | –0.015836 | –0.0001081 | 0 | 0 |
| <i>Betula pendula</i> | –1.5677 | 0.069321 | –0.0008694 | –3.02931 | 0.159893 | –0.0021644 | 1.01665 | –0.083867 | 0.0012905 | 0 | 0 |
| <i>Carpinus betulus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>Castanea sativa</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>Fagus sylvatica</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>Fraxinus excelsior</i> | –0.601 | –0.000715 | 0.0002792 | –0.83195 | –0.009868 | 0.0007665 | –0.10432 | 0.013194 | –0.0005216 | 0 | 0 |
| <i>Picea abies</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6.6247 | 0.0585 |
| <i>Pinus sylvestris</i> | –1.61506 | 0.059408 | –0.0005901 | –3.29487 | 0.142404 | –0.0015008 | 1.30841 | –0.079939 | 0.0009236 | 3.7743 | –0.0094 |
| <i>Populus tremula</i> | –0.97754 | 0.026455 | –0.0001122 | –1.71826 | 0.055625 | –0.0002023 | 0.37793 | –0.023913 | 0.0000509 | 0 | 0 |
| <i>Quercus petraea</i> | –1.05927 | 0.042563 | –0.000489 | –1.80468 | 0.084581 | –0.0009408 | 0.32366 | –0.031105 | 0.0003111 | 7.1482 | –0.135 |
| <i>Q. pubescens</i> | –1.05927 | 0.042563 | –0.000489 | –1.80468 | 0.084581 | –0.0009408 | 0.32366 | –0.031105 | 0.0003111 | 7.1482 | –0.135 |
| <i>Q. robur</i> | –1.05927 | 0.042563 | –0.000489 | –1.80468 | 0.084581 | –0.0009408 | 0.32366 | –0.031105 | 0.0003111 | 7.1482 | –0.135 |
| <i>Tilia cordata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |
| <i>Ulmus glabra</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8.2692 | –0.0701 |

