

TREE SPECIES COMPOSITION IN EUROPEAN PRISTINE FORESTS: COMPARISON OF STAND DATA TO MODEL PREDICTIONS

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Abstract. The degree of general applicability across Europe currently achieved with several forest succession models is assessed, data needs and steps for further model development are identified and the role physiology based models can play in this process is evaluated. To this end, six forest succession models (DISCFORM, FORCLIM, FORSKA-M, GUESS, PICUS v1.2, SIERRA) are applied to simulate stand structure and species composition at 5 European pristine forest sites in different climatic regions. The models are initialized with site-specific soil information and driven with climate data from nearby weather stations. Predicted species composition and stand structure are compared to inventory data. Similarity and dissimilarity in the model results under current climatic conditions as well as the predicted responses to six climate change scenarios are discussed. All models produce good results in the prediction of the right tree functional types. In about half the cases, the dominating species are predicted correctly under the current climate. Where deviations occur, they often represent a shift of the species spectrum towards more drought tolerant species. Results for climate change scenarios indicate temperature driven changes in the alpine elevational vegetation belts at humid sites and a high sensitivity of forest composition and biomass of boreal and temperate deciduous forests to changes in precipitation as mediated by summer drought. Restricted generality of the models is found insofar as models originally developed for alpine conditions clearly perform better at alpine sites than at boreal sites, and vice versa. We conclude that both the models and the input data need to be improved before the models can be used for a robust evaluation of forest dynamics under climate change scenarios across Europe. Recommendations for model improvements, further model testing and the use of physiology based succession models are made.

1. Introduction

A diverse array of models has been developed to study the potential effects of climatic changes on forests. Canopy flux models and forest growth models are applied to study climate impacts on the exchange of energy and matter as well as carbon storage in forest ecosystems (e.g. Kellomäki and Wang, 2000; Cannell et



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al., 1998). These studies address questions such as CO₂ fertilization or changes in water balance in considerable detail. Gap dynamics or forest succession models (Bugmann, 2001) complement these approaches by assessing alterations in the competitive balance between species and changes in forest composition.

Application as well as testing of gap models of European forests are strongly constrained by the fact that the majority of these forests are either managed or at least have been exploited and modified by humans (timber harvesting, forest pasture, hunting, litter removal). Often pure mono-specific stands have been established, many of which are stocked with species that would have no chance to persist in competition with species currently excluded by management practices. Therefore, the comparison of model results to studies of vegetation dynamics in pristine forests under current climatic conditions (Leemans and Prentice, 1987) has played a less prominent role in Europe than in the United States. Instead, the concept of the regional potential natural vegetation (PNV *sensu* Tüxen, 1956) is often used to characterize the ecological site potential. The PNV represents a description of vegetation in equilibrium with the climatic and site conditions that is expected to develop without direct human intervention.

Gap models have been used to predict PNV and succession in European forests (Kienast and Kuhn, 1989; Kienast and Kräuchi, 1991; Bugmann, 1996; Lindner et al., 1997a). To date, the assessments of the impacts of anthropogenic climatic change on European forests that were based on gap models have emphasized the potential effects on PNV (Kienast, 1991; Prentice et al., 1993; Bugmann, 1994). Only few studies deal with the long-term effects of management schemes and the interaction of management strategies and climate change (e.g., Kienast and Kräuchi, 1991; Lindner, 2000).

However, before gap models can be applied in climate change impact studies, they must be thoroughly tested. Besides the comparison of model predictions against PNV reconstructions (Kienast and Kuhn, 1989; Bugmann, 1994; Lasch et al., 1999; Lexer and Hönninger, 2001; see Bugmann, 2001 for a more detailed discussion) several other approaches have been used in Europe. Löffler and Lischke (2001) compared model results to national forest inventory data in several ecoclimatic regions in Switzerland. In other validation approaches, pollen records were used to evaluate predictions of long-term vegetation dynamics in the Holocene (Lotter and Kienast, 1992; Lischke et al., 1998a). Bugmann et al. (1996) compared on a qualitative level different process formulations currently in use in forest gap models, and they reviewed the quantitative findings from earlier gap model comparisons. They concluded that gap models are quite sensitive to climatic factors, and they suggested that a systematic comparison of model behavior at a range of test sites would be desirable in order to assess the degree of realism in model outputs along climatic gradients.

In this paper, we present a comparative simulation study of six gap models based on a common set of input data at forest sites representing different climatic regions of Europe. The sites include alpine and boreal coniferous forests as well as

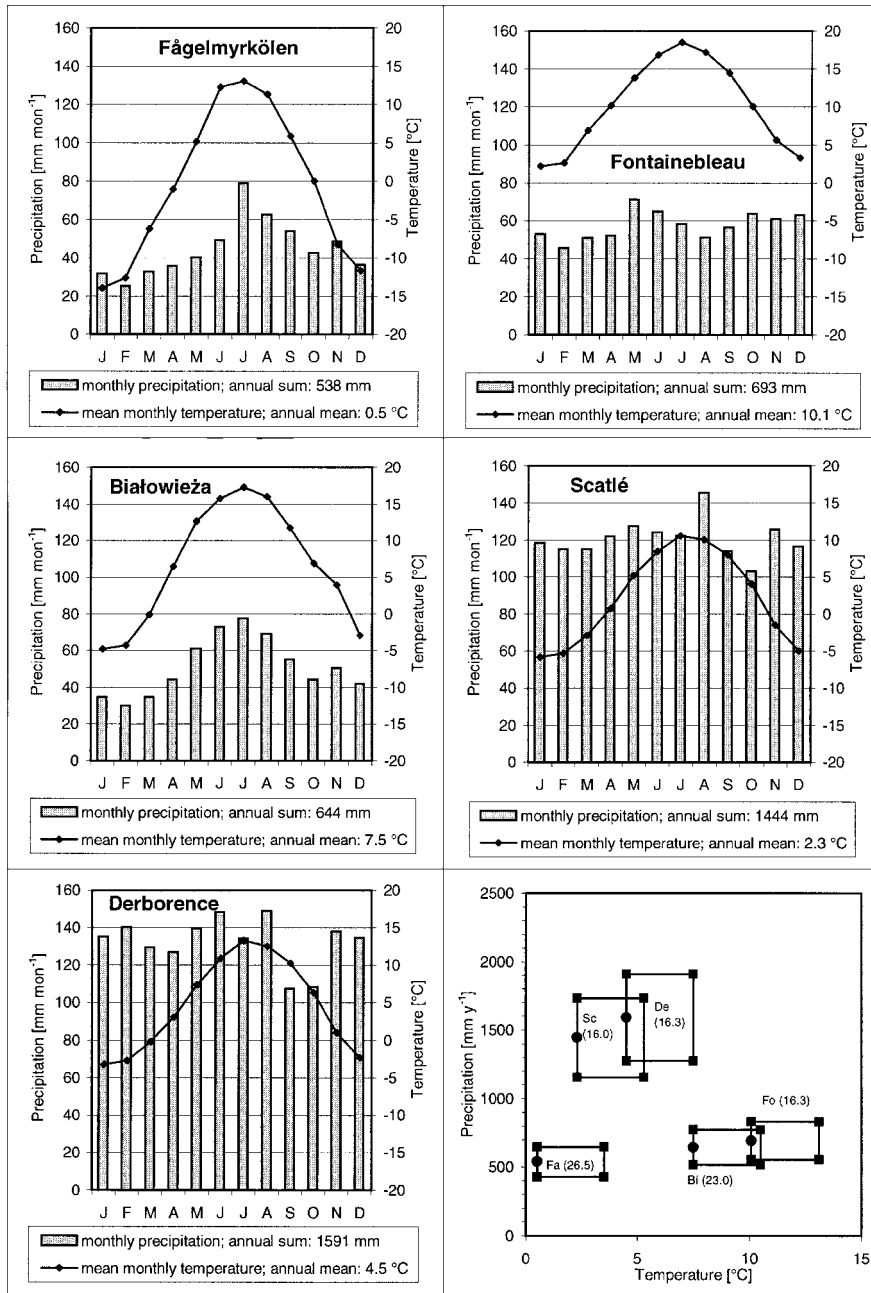


Figure 1. Mean monthly temperature and precipitation for the five sites. The lower right panel compares the climate scenarios at the sites. A dot indicates annual precipitation and mean annual temperature at the five sites, the rectangular marks at the corners of the rectangles show temperature and precipitation in the climate change scenarios 2, 3, 5 and 6. The temperature amplitude at the site calculated from monthly mean temperatures is given in parentheses.

deciduous forests in oceanic and continental climates (Figure 1). We chose forest stands that have not been subject to harvesting and silvicultural treatments for several hundred years (we will refer to these forests as pristine forests) and for which forest inventory data as well as a minimum set of information on edaphic and climatic conditions were available.

The aims of the present study are:

- to assess the degree of general applicability of these six gap models across Europe;
- to identify research priorities that will improve the ability of gap models to predict the structure and function of forests under current and future climatic conditions;
- to assess the role physiology based models can play in identifying specific processes that need to be modeled in greater detail in order to improve the current generation of gap models.

To do this, we utilize an approach which for the first time combines a comparison of gap model results to measured species composition, forest structure and biomass with an inter-model comparison. This scheme aims to track the reasons for the disagreement between simulation results and observations back to specific model formulations and parameterizations, and to assess the level of agreement among models when they are subjected to scenarios of climate change. We discuss some first results and derive recommendations for further steps in model testing.

2. Methods

2.1. MODELS

Key properties of the six gap models involved in the current study are presented in Table I. Brief descriptions of the models are provided below, including key citations where the models are described in more detail.

2.1.1. *ForClim*

In the development of FORCLIM (Bugmann, 1994, 1997a,b) special emphasis was placed on (1) developing a model with a minimum number of ecological assumptions (i.e., maximum simplicity), and (2) improving the representation of climatic influences on tree population dynamics. The applicability of FORCLIM was extended from the European Alps to central Europe through modifications of the soil moisture balance submodel and the drought response (Bugmann and Cramer, 1998; Lindner et al., 1997a). Further model modifications were introduced in a study of forests of the Pacific Northwest of the United States (Bugmann and Solomon, 2000), which are characterized by a strongly different precipitation seasonality as compared to eastern North American and central European forests.

Table I

Some characteristics of the models. A_{max} = maximal age; D_{bh} = diameter at breast height; DI = drought index; F = foliage; GDD = growing degree days; I = irradiance; N = nutrients; NPP = net primary production; rI = relative irradiance; T_{min} = minimum winter temperature, T_{max} = maximum winter temperature

	DISCFORM	FORCLIM	FORSKA	GUESS	PICUS	SIERRA
Number of species	30 (7 conifers)	30 (7 conifers)	17 (3 conifers)	Functional types	29 (7 conifers)	2 (2 conifer), herbs, shrubs
Modeled entities	Height classes	Cohorts	Individuals	Individuals (trees)	Individuals	Cohorts
Vertical crown geometry	Disc	Disc	Cylinder	Cylinder	Cylinder	Disc
Time step (bioclimatic)	Monthly	Monthly	Daily	Daily	Monthly	Daily
Patch size (m ²)	∞	833	1000	1000	100	900
Repetitions (# of patches)	1	200, identical weather	10	10	100	1
Plant state variables	Height	D_{bh}	stem Volume (V)	Foliage, fine roots, sapwood, heartwood crown area/height	D_{bh}	Foliage, wood
Seed availability	Unlimited	Unlimited	Unlimited	f(production of adult individuals on patch and surroundings)	f(seed production on patch and surroundings)	Unlimited
Regeneration	f(GDD, rI, T_{min} , DI, browsing)	f(GDD, rI, DI, T_{min} , T_{max} , browsing, I_{max})	f(GDD, rI, DI, T_{min} , $T_{min,summer}$, T_{max} , N)	f(GDD, I, DI, T_{min} , chilling)	f(GDD, rI, T_{min} , DI, N)	f(GDD, I, DI)
Growth	ΔH (GDD, rI, DI, N)	ΔD_{bh} (GDD, rI, DI, N)	ΔV (GDD, I, DI, N)	Allocation of NPP based on allometries and functional balance	ΔD_{bh} (SHI, GDD, I, T_{min} , chilling, N)	Allocation of NPP with constant factors

Table I
(continued)

	DISCFORM	FORCLIM	FORSKA	GUESS	PICUS	SIERRA
Time step (tree growth)	Yearly	Yearly	Yearly	Yearly	Yearly	Yearly
Intrinsic mortality	$f(A_{max})$ neg.exptl.	$f(A_{max})$ neg. exptl.	$f(A_{max})$ neg. exptl.	$f(A_{max})$	$f(A_{max})$ neg.exptl.	No
Stress induced mortality	$f(\text{rel. } D_{bh} \text{ increment})$	$f(\text{abs. and rel. } D_{bh} \text{ increment})$	$f(\text{growth efficiency})$	$f(5 \text{ year average growth efficiency})$	$f(\text{abs. and rel. } D_{bh} \text{ increment})$	$f(\text{integral C budget})$
Disturbances	Generic	Generic	Generic	Optional	Bark beetle	Fire (not used)
Fertility	Yes (not used)	Yes (not used)	Yes	No	Yes	Not yet included
Topography	No	No	No	No	Yes	Yes (not used)
Sunshine duration	No	No	Yes, daily	Yes	No	Yes, daily
Precipitation, temperature	Monthly	Monthly	Daily	Daily	Monthly	Daily
Evapotranspiration	Thornthwaite	Bugmann and Cramer (1998)	Jarvis and McNaughton	Jarvis and McNaughton	Thornthwaite	Penman
Soil water balance	1 layer bucket	1 layer bucket	Multi layer bucket percolation model snow cover	2 layer bucket	1 layer bucket snow cover	3 layer bucket
Drought limitation factor	Whole year	Vegetation period	Whole year	Intrinsic to coupled carbon and water balance model	Vegetation period	Daily $f(\text{soil water potential})$
Competition for	Light	Light	Light	Light, water	Light, water	Light, water

The model version used in the present study is FORCLIM V2.9.2. It differs from the version described by Bugmann and Solomon (2000) by implementing a stress-related mortality rate based on an approach similar to the one in FIRE-BGC (Keane et al., 1996). The simulations in the present paper were conducted without the submodel for belowground carbon and nitrogen turnover; nitrogen availability for plant growth was set to a high 100 kg/ha, thus effectively minimizing nitrogen limitation in the simulations.

2.1.2. *DISCFORM*

DISCFORM (Distribution based Climate driven Forest Model, Lischke et al., 1998b; Löffler and Lischke, 2001) is an aggregated version of FORCLIM 2.4 (Bugmann, 1996). It uses the same allometric and process functions, and parameters. DISCFORM is a distribution-based population model, rather than an individual-based stochastic model as the traditional gap models. It does not calculate numerous replicates of the stochastic processes occurring in one gap, but determines at each time step the frequency distributions of the tree densities in all gaps, i.e. in the whole stand. The vertical structure is depicted by tree densities in discrete tree height classes. Another difference between FORCLIM and DISCFORM is in the allometric function relating biomass to diameter, which has been calibrated based on tariff functions derived from the second Swiss National Forest Inventory (Kaufmann, 1999). The resulting correction factor of 0.5 is multiplied to the FORCLIM biomass function.

2.1.3. *FORSKA*

FORSKA was originally developed to simulate dynamics in the boreal forests of Scandinavia (Prentice and Leemans, 1990; Prentice et al., 1993). It was used in north-east Germany and on a transect across Central Europe with modified parameters (Lasch and Lindner, 1995; Lindner et al., 1996). An additional environmental factor, nitrogen availability, was introduced by a fertility response function that modified tree growth (Lindner et al., 1997a) using the approach of Aber et al. (1979). The original soil water model of FORSKA was replaced by a multi-layer percolation model analogous to the FORSANA approach (Grote and Suckow, 1998) and species sensitivity to distance to groundwater table was taken into account. Moreover, the model was modified to work with a daily resolution of the climatic driving forces, leading to more realistic species composition at dry sites (Lasch et al., 1998). The version of FORSKA used for the following applications also includes a modified height growth function, which takes into account the effect of competition on height growth (Lindner et al., 1997b).

2.1.4. *GUESS*

The General Ecosystem Simulator (*GUESS*) combines modeling of individual-level establishment, competition, and mortality with process-oriented representations of photosynthesis, respiration, allocation of assimilated carbon and water exchange between soil, plant and atmosphere (Smith et al., 2001). The biological entities modeled are individuals (for trees) or populations (grasses) belonging to different plant functional types (PFTs). Overall dynamics for a given site or region are derived by sampling from a number of replicate patches, corresponding in size to the maximum area of influence of one large adult individual on its neighbors. The model includes a coupled photosynthesis and water balance module derived from the *BIOME3* global equilibrium biosphere model (Haxeltine and Prentice, 1996). The amount of carbon fixed by each individual each year is influenced by PAR absorption and stomatal conductance, the latter being reduced under conditions of water stress. PAR absorption is affected by shading from neighboring individuals within a patch. Allocation of assimilated carbon to the compartments leaves, fine roots, and sapwood follows a set of allometric relationships, which may differ by PFT. Allocation to leaves versus roots is influenced by water stress.

Establishment of new individuals is based on a PFT-specific maximum establishment rate, on the density of adult individuals of a given PFT over the area modeled and PAR level at the forest floor. Mortality is stochastic and based on the sum of a background rate, inversely related mean non-stressed longevity, and a much higher rate, imposed only if the five-year average growth efficiency falls below a PFT-specific threshold. In contrast to the traditionally site-oriented gap models, *GUESS* is optimized for producing predictions of vegetation and biogeochemical cycling at regional to continental scales.

2.1.5. *PICUS*

PICUS was originally developed to simulate forest succession in the complex topography of the Eastern Alps in central Europe. Special emphasis in this spatially-explicit model was placed on (1) the re-evaluation of the environmental response functions used to model the effects of temperature and soil moisture based on the combined network of forest inventory, soil and meteorological data (Lexer and Hönninger, 1998a), (2) the implementation of a radiation submodel considering both, direct and diffuse radiation, (3) linking indicators of site nutrient status to vegetation development by means of a fuzzy logic control unit (Lexer and Hönninger, 2001), (4) the integration of bark beetle-induced mortality of Norway spruce by coupling the patch model with a stand-level risk model (Lexer and Hönninger, 1998b), (5) the consideration of seed production and dispersal, and (6) the reformulation of the soil moisture submodel. The spatial range of interactions between adjacent patches depends on the characteristics of the simulated stand (tree heights), site characteristics (orientation, slope, latitude) and solar altitude, angle and direction. For the present study, version 1.2 of *PICUS* was used (Lexer and Hönninger, 2001).

2.1.6. SIERRA

SIERRA is a process-based, stand-level model for water limited ecosystems built on three main assumptions (Mouillot et al., 2001): (1) Water and solar radiation are the overriding factors limiting primary production. The availability of water varies spatially according to soil depth and texture and all stages in the life cycle of the plants are related to their water availability and their carbon budget; (2) The germination of seedlings depends on the surface soil water content; and (3) Regeneration is determined by light and soil evaporation, both of which depend on LAI, that is calculated based on the carbon budget and constant throughout a given year. Survival, growth and seed production depend on the carbon budget. Two types of interactions between individuals are simulated: the simultaneous use of the same soil water, depending on plant life form, which determines root depth and their lateral extension, and the extinction of solar radiation with a hierarchy depending on their heights. SIERRA is applied only at the sites where conifers dominate, since up to date it has been parameterized for only two species: *Picea abies* and *Pinus sylvestris*.

As shown in Table I, the models comprise a diversity of approaches (see Bugmann (2001) for a detailed discussion of the rationale of model lineages). The entities described are individuals or cohorts. Number and objects of the state variables vary substantially. The calculation of bioclimatic effects range from a daily to a monthly basis. Some of the models address specific processes in greater detail. For example, PICUS explicitly describes seed dispersal where the seed shadow of each adult tree is modeled as a function of the size of the parent tree and the species' seed characteristics. In spite of these dissimilarities, the species-based models (DISCFORM, FORCLIM, FORSKA and PICUS) that use an aggregated growth function (see Norby et al., 2001) share some important features: Temperature regime and site water balance exert a strong control on the individual species growth rate. Intra and interspecific competition is mainly competition for light. There also is a high degree of similarity between these models in as much as the factors that modify regeneration and growth are mostly the same (Table I) although the algorithms and parameterization differ in many respects. These differences will be addressed in those instances where they appear to explain differences in model behavior.

2.2. SITE DESCRIPTIONS, CURRENT VEGETATION AND SOILS

General site data are given in Table II, and mean monthly temperature and precipitation for the five sites are shown in Figure 1.

2.2.1. Site Descriptions and Current Vegetation

Fågelmyrkölen (central Sweden) is characterized by a cold-oceanic boreal climate with humid summers (Figure 1). The boreal forest is dominated by Norway spruce, *Picea abies* (Linder et al., 1997). After disturbance by large fires, this forest type

Table II
 Site characteristics. (Where sample plot area and forest area are different, forest area is given in parentheses.)

	Fågelmyrkölen	Fontainebleau	Białowieża	Scatlé	Derborence
Latitude	65° 15' N	48° 26' N	52° 45' N	46° 47.5' N	46° 16' N
Longitude	19° 6' E	2° 41' E	23° 50' E	9° 3' E	7° 13' E
Altitude	340	135–140	165	1680–1780	1445–1625
Areal extent (ha)	0.1257 (5–10)	34	1.25	2.68 (9.13)	6.9 (22.3)
Soil	Iron podsol, sandy loam	Calcium carbonate with sand	Brown earth, rich in organic matter, imperfectly drained	Nutrient rich, high water permeability, skeleton rich	Calcium carbonate
Bucket size (cm)	9.3	9.9	12.7	16.4	20.7
pH	4.3	5.2	4.9	4.5	6.6
C/N 0–30 cm	13.7	9.7	29.6	8.9	8.9
C/N 30–100 cm	8.3	4.9	8.7	4.5	4.5
Phytosociological characterization	Piceetum myrtillosum	Melico-Fagetum Fago-Quercetum	Tilio-Carpinetum	Piceetum myrtillosum	Abietetum albae
Dominant species	<i>Picea abies</i>	<i>Fagus sylvatica</i>	<i>Carpinus betulus</i> <i>Tilia cordata</i> <i>Picea abies</i>	<i>Picea abies</i>	<i>Abies alba</i> <i>Picea abies</i>

Table II
(continued)

	Fågelmyrkölen	Fontainebleau	Biatowieża	Scatlé	Derborence
Other tree species	<i>Betula pubescens</i> <i>Pinus sylvestris</i>	<i>Quercus petraea</i> <i>Salix caprea</i> <i>Acer campestre</i> <i>Carpinus betulus</i> <i>Fraxinus excelsior</i> <i>Betula pendula</i>	<i>Betula</i> <i>Pinus sylvestris</i> <i>Quercus robur</i> <i>Acer platanoides</i> <i>Alnus glutinosa</i>	<i>Alnus viridis</i> <i>Sorbus aucuparia</i>	<i>Larix decidua</i>
Trees ha ⁻¹	1585	1983	692	450	
Aboveground biomass (t ha ⁻¹)	60	234		168	309
Data for comparison by dbh-class	Basal area tree number	Basal area tree number	Basal area tree number	Biomass	Biomass
Lower threshold of dbh measurements (cm)	10	4.5	5	8	8

follows a succession through stages initially dominated by birches and pines and finally by spruce. For the site under consideration, no traces of large fires could be detected back to the 17th century. The current dominance of spruce has been promoted by increased browsing during the 20th century (Linder et al., 1997). The inventory data (Table II) are adopted from Linder et al. (1997).

The forest of Fontainebleau (southeast of Paris) has a temperate-oceanic climate with precipitation evenly distributed throughout the year. The stand is dominated by European beech, *Fagus sylvatica* (Lemée, 1978, 1990). The structure of this forest depends on the frequency of big storms (Pontailler et al., 1997), which leads to a heterogeneous regeneration mosaic on relatively small scales (average gap size 175 m²). Regeneration proceeds through beech thickets in the understorey and in canopy gaps. The current dominance of beech may be traced to events over 400 years ago, when forest uses other than royal hunting were stopped. The inventory data (Table II) are adopted from Lemée (1978).

The Białowieża National Park (eastern Poland) has a temperate-continental climate with summer rain. The site is located in the central zone of the park (established in 1921) in which direct human intervention has been excluded since 1929. The plots chosen for long-term studies by the Department of Silviculture of Warsaw University in 1936 did not show any visible traces of harvesting activities at that time (Bernadzki et al., 1998a,b). They cover a gradient from dry to humid and from nutrient-poor to nutrient-rich sites. We compare model results to the inventory data on the site of medium fertility and medium soil water storage capacity (called MDF, mixed deciduous forest, site by Bernadzki et al., 1998a).

Scatlé (eastern Swiss Alps) has a lower subalpine climate with high precipitation distributed evenly through the year. It is located on a remote, steep slope, which is nearly inaccessible for humans and covered by a pure spruce forest (Hillgarter, 1971). There has been little human impact except for some goat grazing, and a constant vegetation composition is documented from pollen analysis back to the 13th century (Hillgarter, 1971). The inventory data (Table II) are adopted from Hillgarter (1971).

Derborence is located in the upper montane zone of the central part of the Swiss Alps, on a steep slope of a largely inaccessible valley (Leibundgut, 1993). It has a montane climate with high precipitation distributed evenly through the year. The site is covered by a spruce-fir forest. In the lower portions of the forest, some single tree harvesting had been practiced before the mid 18th century, when landslides blocked the access to the forest (Leibundgut, 1993). The inventory data (Table II) are adopted from Leibundgut (1993).

2.2.2. Soil Data

For Fågelmyrkölen and Białowieża, soil types were assigned according to the FAO/UNESCO soil map (FAO, 1995) and available water storage capacity and pH were adopted from the values tabulated in the soil map. Available water storage capacity and pH for Fontainebleau were calculated as averages over values for the

soil profile reported in Pontauiller (1979). For Fågelmörkölen, Fontainebleau and Białowieża, the calculation was based on the implicit assumption that soil depth was 1 m. At the Swiss sites, plant available water storage capacity was derived from the Swiss soil suitability map (Frei, 1980) combined with measurements at 20 representative soil profiles covering a wide range of Swiss forest soils (Richard et al., 1978, 1981; Richard and Lüscher, 1983, 1995). In these measurements, the lower limit of soil moisture tension was pF 1.9, and the maximum soil depth was assumed to be 1.5 m. For Scatlé and Derborence pH was adopted from Hillgarter (1971) and the soil suitability map, respectively. The C/N ratio for soil layers 0–30 cm and 30–100 cm were determined following the procedure developed by Batjes (1996) from the FAO soil type for all sites.

2.3. DERIVATION OF CLIMATE SCENARIOS

Our study is based on the assumption that the current vegetation at the study sites is in equilibrium with the current climate (cf. Bugmann, 2001). Hence, to test the models, we ran them from bare ground using a current climate scenario, i.e., a 1000 year synthetic weather series corresponding to the current climate (Bugmann, 2001), which is sufficient for the simulated vegetation to reach an equilibrium. This synthetic series does not describe climate fluctuations during the last 1000 years, nor does it represent the time course of weather during the 20th century (see Section 4.5 for a discussion of the limitations imposed by this simplification). The simulated equilibrium vegetation is then compared to observed (current) vegetation. In addition to this baseline scenario under current climate, six climate change scenarios were defined to analyze model sensitivity to a changing environment. The construction of the current and future climate scenarios (Sections 2.3.2 and 2.3.3) is based on weather station data and additional data sources as described below.

2.3.1. *Climate and Weather Data Sources*

We utilize data of varying detail from weather stations close to the five sites. For all sites, climatic means (monthly means of precipitation and temperature averaged over at least 30 years, Figure 1) are available. Due to disparities in available weather data, different methods were used to construct a weather record for the Swiss sites vs. the other sites as detailed below. These time series of weather were then used for the construction of a synthetic 1000-year time series of weather.

The climate for the Swedish site, Fågelmörkölen was derived from the weather station Gunnarn (1965–1995, courtesy of Swedish Meteorological and Hydrological Institute). Temperatures were corrected for differences in elevation ($-0.65\text{ }^{\circ}\text{C}/100\text{ m}$), but no attempt was made to adjust the precipitation data. Data for Fontainebleau were taken from Lemée (1978). The climate record provides temperature and precipitation measured in Fontainebleau town during the period 1883–1970, and insolation for the period 1929–1973 measured in Versailles. For

Białowieża, mean monthly temperature and precipitation for 1926–1996 were taken from Bernadzki et al. (1998b). For the two Swiss sites, interpolated long-term mean monthly temperature and precipitation values were available for the grid of the Swiss National Forest Inventory (NFI; Kienast, 1997). The NFI-gridpoints closest to the test sites were used. For the temperature at Scatlé, an additional correction of 0.65 °C/100 m was applied, since the closest NFI-gridpoint was located considerably lower than the forest site. For the sites Fågelmyrkölen and Białowieża, sun-shine duration is taken as the average of the data of the nearest grid cells in the Climate Research Unit (CRU) data (Hulme et al., 1995, updated version) for the period 1961–1990 and for the Swiss sites from the stations Chur-Ems and Sion.

To obtain long time series of monthly temperature and precipitation, we calculated anomalies of the NFI gridpoint climate relative to the long-term monthly means of observational data (1931–1970) from the climate stations closest to the sites, i.e. from Chur-Ems (9.531 W, 46.872 N, 555 m asl) for Scatlé, and from Sion (7.36 W, 46.239 N, elevation 542 m) for Derborence. These anomalies were added to the monthly weather time series of the two climate stations, resulting in a 40 year site-specific weather record.

For the other three sites, anomalies relative to the long-term monthly means were calculated using the Climate Research Unit (CRU) data base (Hulme et al., 1995, updated version, 0.5 × 0.5 degree). The difference between the station climatology and the climatology were calculated for the nearest CRU grid. These values were added to the time series of monthly temperature and precipitation of the CRU data set for the years 1901–1970. Thus for these three sites, a 70 year weather series was derived.

For monthly sun-shine duration, climatological means were used, i.e. interannual variation was not taken into account.

2.3.2. *Current Climate Scenarios*

For each site, a 1000-year weather record corresponding to current climate was generated. For the Swiss sites, this was achieved by repeating the 40-year weather records 25 times without changes in the order of consecutive years. For the other three sites, individual years were randomly selected from the 70-year record (cf. Bugmann, 2001). Three of the models require daily input data. For Fågelmyrkölen, Fontainebleau and Białowieża, daily input data sets were generated from the monthly resolution data sets using a weather generator (Bürger, 1997). At Scatlé and Derborence daily weather series were available for the two climate stations Chur-Ems and Sion for the period 1931–1970. For these two sites the daily weather series were produced by adding the anomalies between site climate and station data to the daily station time series.

Table III

Changes of long-term average climatic parameters relative to current climatic conditions (annual mean temperature and annual precipitation sum) used to define six climate change scenarios

Scenario	Temperature change (°C)	Precipitation change (%)
0	0	0
1	+1.5	0
2	+1.5	-20
3	+1.5	+20
4	+3.0	0
5	+3.0	-20
6	+3.0	+20

2.3.3. *Climate Change Scenarios*

Six climate change scenarios were developed for each site. They are defined by addition of either 1.5 °C or 3 °C to every monthly temperature value and by augmenting or decreasing every single monthly precipitation value by 20% (cf. Table III).

The models were run for the 1000 years of current climate, then a transition period of 100 years was added, followed by another 1000 years of a hypothetically constant future climate. During the transition period the values for augmentation or decrease in temperature and precipitation were linearly interpolated between zero and the change signals prescribed for the 1000 year scenarios, thus yielding a transient of climate change of 100 years. Interannual variability in the future climate was prescribed in the same way as for the current climate scenario, i.e. by adding the change signals to individual years of the weather series. The daily series were produced in analogy to the current climate scenarios, i.e. by augmenting or decreasing directly the variables of the daily series for the stations Scatlé and Derborence and by using the weather generator to produce daily series from the monthly climate change scenarios.

2.4. METHODS FOR COMPARISON OF MODEL RESULTS TO DATA

We compare simulated stand-level species composition, basal area, aboveground biomass, and tree numbers per species with the inventory data available at each site (Table II). These observational data include stand totals as well as information by species and diameter (size) class. Model results were recorded for every tenth year and averaged across a model-specific number of simulations (patches; cf. Table I

and Bugmann, 2001). For the comparison with stand inventory data, we averaged the results for the last 100 simulation years in the current climate run. We also recorded simulated annual actual evapotranspiration (AET) to compare the fraction of precipitation which is returned to the atmosphere via evapotranspiration.

At each site, simulated species abundances were divided into three groups, depending on their relative share of total stand biomass, basal area or stem number (i.e., <1%, 1–10%, >10%, respectively). In several cases, no observational data were available for the <1% group. From model outputs and the observed species composition, we defined species of high abundance (subsequently called dominant species) as those species that contribute >10% of either total biomass, basal area or total stem number on the plot. Different variables had to be used for this classification since no single variable was available from all models and all sites. For this reason the percentages of abundance calculated for DISCFORM, FORCLIM, and PICUS are only indicative at sites Fågelmyrkölen, Fontainebleau and Białowieża (see legend of Table IV). The GUESS model contains functional groups rather than species. For comparison to GUESS, the observed species were assigned to functional groups according to the classification that is underlying GUESS (i.e., *Betula* and *Populus* = shade intolerant, all other broadleaved species = shade tolerant).

A similarity index, S , between measured and observed variables was calculated from the differences of simulated and observed share of species in the total tree number, biomass or basal area as follows:

$$S = 1 - \frac{\sum_{i=1}^n |f_{obs,i} - f_{sim,i}|}{200}$$

where $f_{obs,i}$ and $f_{sim,i}$ ($i \leq n$) are the percentage for observed and simulated species abundance and n is the total number of species either observed or simulated. S has a value of 1 if the match is perfect and a value of zero if there is no match.

When comparing basal area or biomass in diameter classes, the similarity index we used was calculated as the geometric mean of $f_{1,i}/f_{2,i}$, where $f_{1,i} = f_{obs,i}$ and $f_{2,i} = f_{sim,i}$ if $f_{obs,i} < f_{sim,i}$, and vice versa.

We analyzed the model predictions for the climate change scenarios (1 through 6) with respect to changes in the abundance of species or life forms and calculated the percent change in stand biomass relative to the current climate run (scenario 0). We used only those models that reproduced the species composition at a given site under current climatic conditions with a similarity index $S > 0.5$.

Table IV

Comparison of observed and predicted dominant species. The abundances of the species and functional types are evaluated as percent of either biomass (Scatle and Derborence) or tree number (Fågelmjyrkölen, Fontainebleau and Białowieża). The relative abundances for FORSKA are calculated from the same variables while for DISCFORM, FORCLIM and PICUS biomass is used at all sites. Only species with an abundance >10% are reported in this table. Functional types noted as: NE = needle leaved evergreen, SI BL SG = shade intolerant, broad-leaved, summer-green, ST BL SG = shade tolerant, broad-leaved, summer-green. The value for functional types given in parentheses in the columns for observed refer to the sums of all species, species of minor abundance included

Site	Species	OBSERVED	DISCFORM	FORCLIM	FORSKA	PICUS	GUESS	SIERRA
Fågelmjyrkölen	<i>Betula pubescens</i>	15			13			
	<i>Picea abies</i>	82			60			33
	<i>Pinus cembra</i>		17	82				
	<i>Pinus montana</i>			13				
	<i>Pinus sylvestris</i>		69		18	98		67
	NE	82(85)	86	95	78	98	99	
Fontainebleau	SI BL SG	15			13			1
	<i>Castanea sativa</i>		19	52				
	<i>Carpinus betulus</i>					12		
	<i>Fagus sylvatica</i>	99			64			
	<i>Pinus sylvestris</i>		44					
	<i>Quercus petraea</i>				15			
	<i>Quercus robur</i>		15	27	13	78		
	<i>Taxus baccata</i>		59					37
	NE							
	SI BL SG							
Białowieża	ST BL SG	99(100)	19	79	92	90	64	
	<i>Abies alba</i>			14				20
	<i>Acer platanoides</i>							

Table IV
(continued)

Site	Species	OBSERVED	DISCFORM	FORCLIM	FORSKA	PICUS	GUESS	SIERRA
Białowieża	<i>Castanea sativa</i>		35	15				
	<i>Carpinus betulus</i>	42			12	26		
	<i>Fagus sylvatica</i>			13		17		
	<i>Picea abies</i>	19						
	<i>Quercus robur</i>		21	18		20		
	<i>Tilia cordata</i>	25			80			
	<i>Ulmus glabra</i>			12				
	NE	19(22)		14			45	
	SIBL SG	0(3)						
	STBL SG	67(75)	56	58	92	83	55	
Scatlé	<i>Betula pendula</i>				19			
	<i>Picea abies</i>	100	70	89		97		72
	<i>Pinus cembra</i>		20					
	<i>Pinus sylvestris</i>				43			28
	<i>Populus trem.</i>				34			
	NE	100	90	89	43	97	100	
	SIBL SG				53			
Derborence	<i>Abies alba</i>	58	21	24	53	48		
	<i>Fagus sylvatica</i>		18	24		30		
	<i>Picea abies</i>	39	35	37	47	21		72
	<i>Pinus sylvestris</i>							28
	NE	97(100)	66	61	100	69	96	
	SIBL SG						4	
	STBL SG		18	24		30		

Table V

Index of similarity (see Section 2.4) between observed and simulated species composition for species based models (first number) and similarity index for stand structure (second number). Underlined numbers: model has originally been developed for application in a region that comprises climatic conditions at the site. Italicized numbers: model has been modified for applications in regions with climatic conditions similar to the site climate. None of the models has been parameterised for application at a specific site

	DISCFORM	FORCLIM	FORSKA	PICUS
Fågelmyrkölen	0.03/0.07	0.03/0.29	<u>0.76/0.70</u>	0.03/0.45
Fontainebleau	0.01/0.23	<i>0.01/0.29</i>	<i>0.65/0.04</i>	0.01/0.08
Białowieża	0.21/0.33	<i>0.14/0.44</i>	<i>0.46/0.15</i>	0.38/0.38
Scatlé	<u>0.70/0.40</u>	<u>0.89/0.38</u>	0.00/0.27	<u>0.97/0.56</u>
Derborence	<u>0.58/0.41</u>	<u>0.64/0.45</u>	0.93/0.39	<u>0.70/0.79</u>

3. Results

3.1. CURRENT CLIMATE: ABUNDANCE OF SPECIES

All models generally predict the correct dominant life form: conifers or broad-leaved deciduous trees. The presentation of simulation results is structured according to these broad categories.

3.1.1. Coniferous Forests

Fågelmyrkölen in central Sweden currently is dominated by spruce with some co-occurring birch. The model results are summarized in Table IV and the corresponding similarity indices for the species based models are shown in Table V. FORSKA predicts a forest dominated by spruce ($S = 0.76$) with some pine and birch (*B. pendula*, since it is not parameterized for *B. pubescens*). FORCLIM, DISCFORM and PICUS all predict pine forests, with *P. sylvestris* dominating in the PICUS results, and *P. cembra* in FORCLIM and DISCFORM ($S = 0.03$). SIERRA also predicts a forest dominated by pine, but with considerable amount of spruce present.

The measured species composition at Scatlé, a spruce-dominated stand, is predicted by FORCLIM and PICUS ($S > 0.8$). DISCFORM predicts that *Pinus cembra* contributes 20% to the total aboveground biomass. FORSKA simulates a mixed pine-poplar-birch forest ($S = 0$). SIERRA, which has *Picea* and *Pinus* as the only species, predicts a mixture of both, with dominance of spruce.

Derborence, which is a mixed spruce-fir forest, is predicted by FORCLIM and DISCFORM as a spruce-fir-beech forest, while FORSKA predicts a mixed spruce-

fir stand. PICUS projects a fir-beech-spruce forest and SIERRA a mixture of *Picea* and *Pinus*.

3.1.2. Broadleaved Forests

For the pure beech stand of Fontainebleau, FORSKA predicts a beech stand with a considerable share of oaks mixed with pine ($S = 0.65$), while FORCLIM and PICUS predict stands dominated by oaks ($S = 0.01$) mixed with *Castanea* (FORCLIM) or *Carpinus* (PICUS, Tables IV and V). DISCFORM simulates a pine forest with *Castanea* and *Taxus* for this site. DISCFORM, FORCLIM and PICUS predict beech regeneration, but this species contributes less than 2% to total biomass in these models.

Białowieża is a mixed forest dominated by broadleaved deciduous species. All the species-based models project mixed deciduous forests, but with significant differences in species composition ($S \leq 0.5$, Table V). None of the dominating species simulated by FORCLIM and DISCFORM grow in the forest, while FORSKA and PICUS predict either *Tilia cordata* or *Carpinus betulus* correctly, mixed with other species. All four models agree that *Quercus robur* should occur with more than 10% of the biomass at the site. *Q. robur* is currently present with 8% of the trees at the site.

At all five sites, GUESS predicts the correct dominant plant functional type, i.e. either needleleaved evergreen or broadleaved deciduous trees. SIERRA, which is parameterized for *Picea abies* and *Pinus sylvestris* only, simulates the correct dominant species at the alpine sites, while it results in *P. sylvestris* having a higher abundance than *P. abies* in Fågelmörkölen. Thus, for the latter site it shares the pine bias of FORCLIM, DISCFORM and PICUS.

In terms of the total number of species occupying a site at the end of the simulation period under current climate, a marked ranking of models can be observed (Figure 2). DISCFORM predicts the highest total number of species on all five sites, closely followed by FORCLIM. PICUS and FORSKA arrive at a substantially lower number of species, with PICUS always having the higher number of the two. The same ranking is observed when only the number of species that contribute more than 1% to total biomass or tree number are taken into account, except at sites Fågelmörkölen and Scatlé where FORSKA predicts a higher number than PICUS and a higher number than all the other models, respectively. In comparison to the observations, DISCFORM and FORCLIM consistently show higher numbers of species contributing more than 1%, while PICUS and FORSKA are characterized by both over- and underestimations.

Thus, in general DISCFORM and FORCLIM allow for regeneration of many more species than PICUS and FORSKA. Yet, a considerable fraction of these species grows with little success in the models. Consequently, in terms of number of species with high biomass and tree numbers, the four models produce results that are similar, although even at this level a trend persists for more diverse stands to be predicted by DISCFORM and FORCLIM. In this context it must be kept in

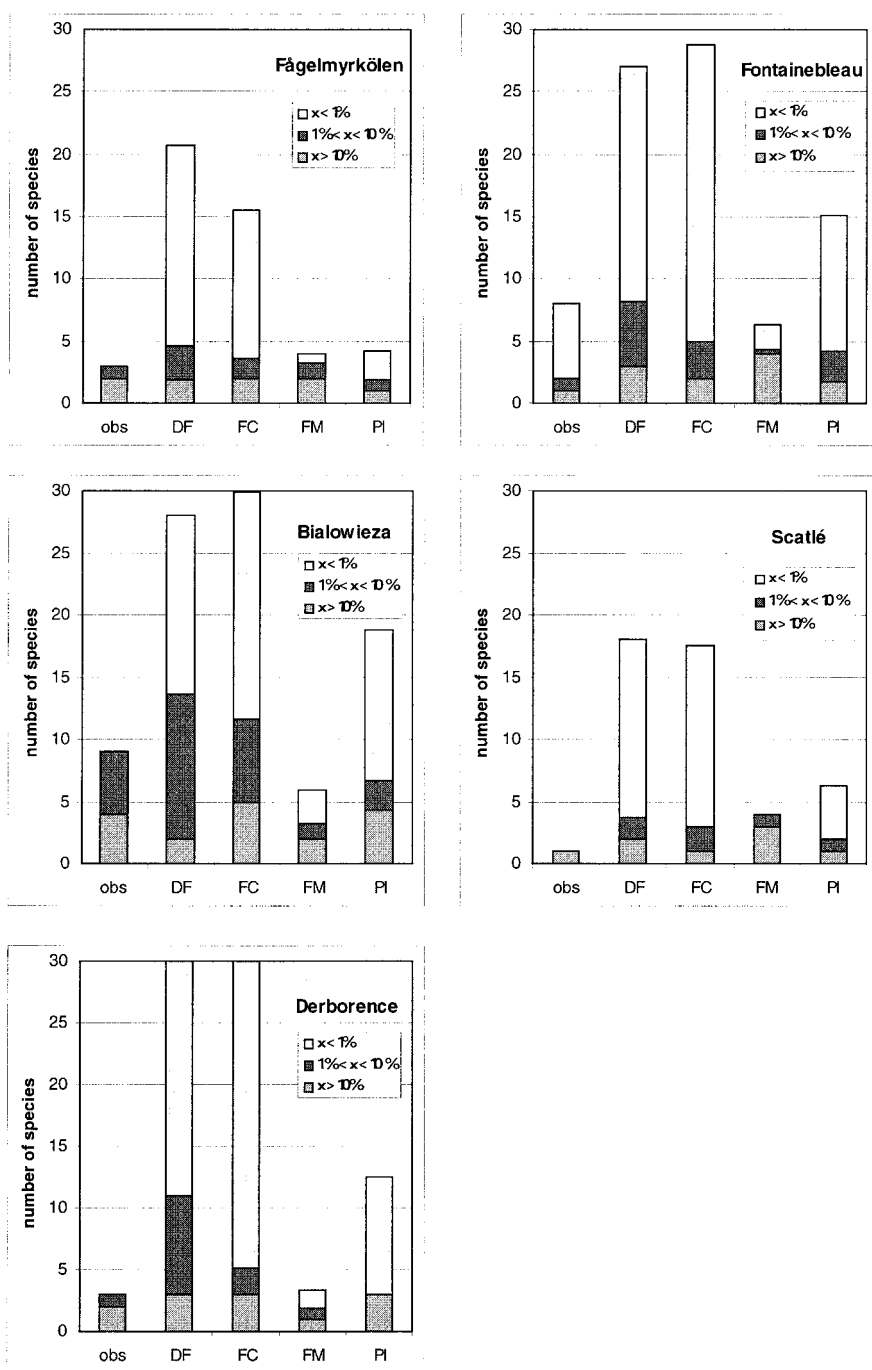


Figure 2. Number of species present during the last hundred years of the standard, current climate simulation run and the number of species observed at the time of inventory. obs = observed, DF = DISCFORM, FC = ForCLIM, FM = FORSKA, PI = PICUS.

Table VI

Percentage deviation of predicted from observed values for aboveground woody biomass, tree number per unit area and number of species with biomass/or tree number >10% of the total. The number correctly predicted is compared to the number observed ([predicted of the observed]/observed). x = No observational data

Model	Fågelmörkölen	Fontainebleau	Białowieża	Scatlé	Derborence
Biomass, % of observed					
DISCFORM	44	94	x	77	53
FORCLIM	72	168	x	163	108
FORSKA	128	79	x	191	211
GUESS	559	194	x	288	173
PICUS	110	126	x	183	135
SIERRA	126	NA	NA	128	92
Tree number, % of observed					
DISCFORM	43	72	158	88	x
FORCLIM	16	26	90	55	x
FORSKA	158	126	709	970	x
Dominant species (>10%)					
DISCFORM	0/2	0/1	0/3	1/1	2/2
FORCLIM	0/2	0/1	0/3	1/1	2/2
FORSKA	1/2	1/1	1/3	0/1	2/2
PICUS	0/2	0/1	1/3	1/1	2/2
Dominant functional groups (>10%)					
GUESS	2/2	1/1	2/2	1/1	1/1

mind that FORSKA has a lower number of species in the seedbank (17 versus 29 or 30 in the other models).

3.2. BIOMASS AND DENSITY

All models except DISCFORM overestimate aboveground woody biomass (Table VI). The underestimation of biomass by DISCFORM is coupled with an underestimation of stand density. FORCLIM also underestimates stand density, but this is coupled with an overestimation of biomass. In FORSKA, both biomass and density are overestimated except at Fontainebleau.

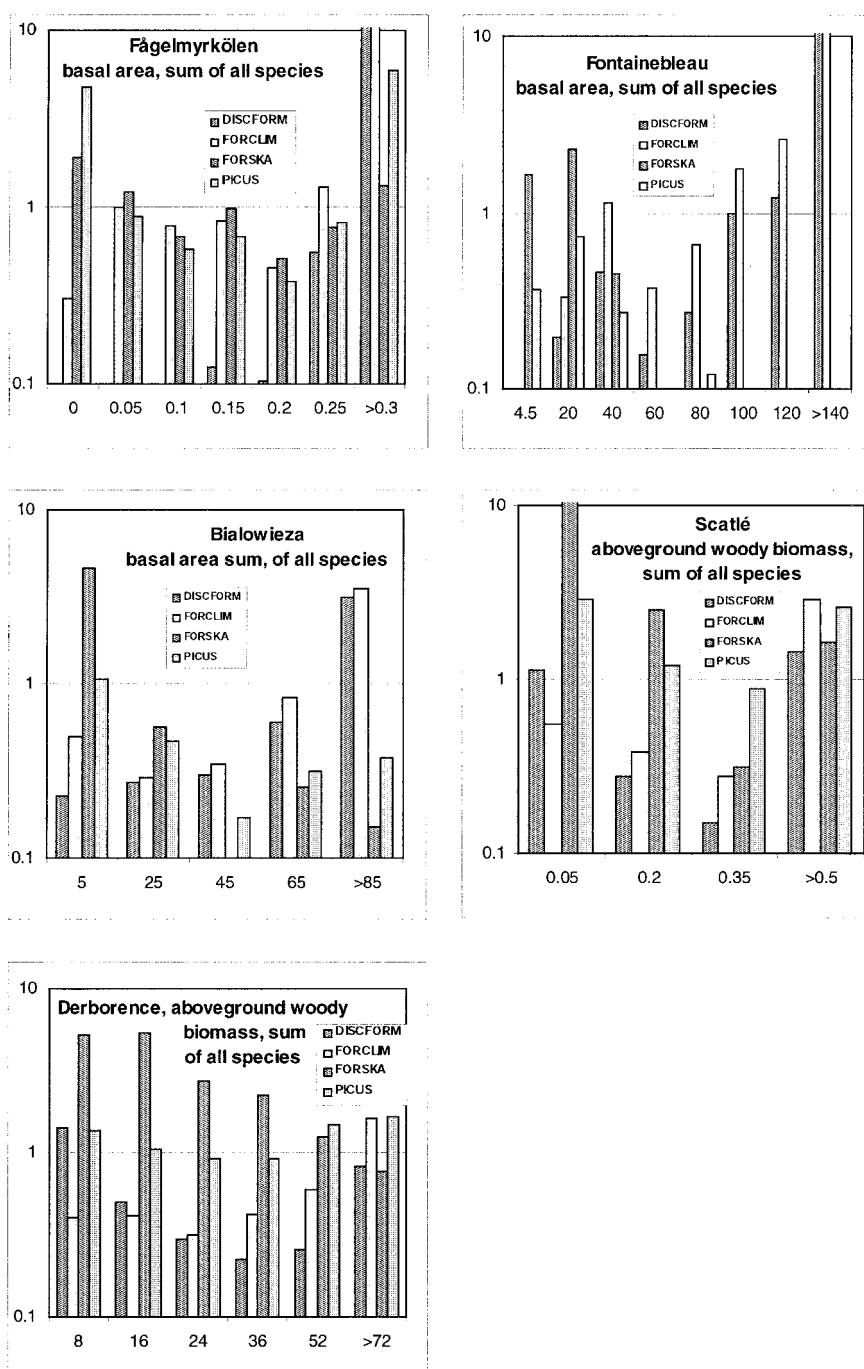


Figure 3. Stand structure, given as simulated/observed basal area sum of all species or sum of above-ground woody biomass of all species per diameter class. Class values indicate the lower dbh-class boundary in cm. For sites Fontainebleau and Białowieża the number of classes has been reduced by combining two classes in one.

Table VII

Predicted percentage change in stand biomass in scenarios 1 through 6 relative to the current climate (scenario 0) for models with $S > 0.5$ (Table V). FORSKA was not run under climate change scenarios at Derborence

Site	Model	Scenario					
		1	2	3	4	5	6
Fågelmjärkölen	FORSKA	-4.4	-8.6	+46.7	-28.4	-61.1	+8.3
Fontainebleau	FORSKA	-17.8	-39.2	-33.2	-40.5	-54.9	-41.1
Scatlé	DISCFORM	+14.2	+14.2	+14.2	+36.7	+36.7	+36.7
Scatlé	FORCLIM	+6.2	+7.3	+9.3	+26.7	+18.6	+26.2
Scatlé	PICUS	+4.2	+1.9	+4.5	+35.2	+33.0	+40.3
Derborence	DISCFORM	+20.9	+20.9	+20.9	+34.6	+34.6	+34.6
Derborence	FORCLIM	+6.8	+7.6	+8.3	+16.1	+15.5	+18.1
Derborence	PICUS	+11.3	+8.0	+10.1	+14.7	+13.2	+16.3

3.3. STAND STRUCTURE

In Figure 3 the ratio of simulated to observed basal area or biomass in individual diameter size classes is shown. The corresponding similarity index is reported in Table V.

FORCLIM and DISCFORM results are in all cases or with one exception, respectively, biased towards higher diameters, i.e. the share of tree numbers as well as basal area and biomass is underestimated for the low diameter classes and overestimated for the high diameter classes. FORSKA shows a trend for opposite results. Here, with two exceptions, the lower classes are over-represented and too few trees are simulated in the higher classes. At Fontainebleau, the bias of FORSKA towards lower classes is due to the fact that no trees with diameters greater than 60 cm are simulated. At Scatlé, FORSKA and PICUS over-estimate biomass in the lowest as well as the highest classes. Similar to the similarity index of species composition, the similarity index of measured vs. simulated stand structure is generally higher at sites for which the model has been developed and tested. At these sites (Table V) FORSKA and PICUS yield $S > 0.5$, while FORCLIM and DISCFORM yield $S < 0.5$ due to a strong bias towards over-estimation of basal area and biomass in the high diameter classes.

3.4. CLIMATE CHANGE SCENARIOS

Results from the species-based models under the scenarios of climatic change are presented in Table VII. Only those models that yielded $S > 0.5$ under the current climate scenario are included. We discuss at the same time the changes in abun-

dance of dominant species which were evaluated as for the current climate (data not shown).

At Fågelmyrkölen, FORSKA predicts that *Picea* remains the dominant species under all climate change scenarios. Total stand biomass increases under the scenarios of higher precipitation (3 and 6) and decreases in all other scenarios (Table VII). Biomass of *Picea* is higher in scenarios 1, 3, and 6 as compared to the current climate (scenario 0). When temperature is 1.5 °C higher and precipitation 20% lower, *P. sylvestris* which had a share of 18% in total stand biomass under current climate, gains relative to *Picea*, while in all other scenarios it is reduced to very low levels of abundance (results not shown). GUESS predicts that the dominant life form, needleleaved evergreen trees, stays dominant for all climate change scenarios.

At Fontainebleau, FORSKA predicts that *Pinus sylvestris* disappears from the stand in all scenarios except under scenario 2 where it is reduced to a very low level of abundance. *Fagus sylvatica* attains the highest abundance in the stand compared to the other species in the scenarios with increased precipitation (3 and 6). Stand biomass is lower than under current climate for all scenarios (Table VII). Remarkably, stand biomass is lower in scenario 3 compared to scenario 1 and in scenario 6 compared to scenario 4. GUESS predicts that shade tolerant broadleaved trees stay dominant in all the climate change scenarios and gain relative to needleleaved evergreen trees.

At Białowieża, GUESS predicts decreased abundance of shade tolerant broadleaved summergreen trees and increased abundance of needleleaved evergreen trees in scenarios 2 and 4 through 6. The inverse result is obtained for scenario 1 whereas in scenario 3 both functional types have a slightly increased abundance.

At Scatlé and Derborence, FORCLIM and PICUS predict only marginal effects of changes in precipitation on biomass while DISCFORM obtains fully identical results for scenarios 1 through 3 and 4 through 6, respectively, i.e. a pure temperature response, with increases in temperature leading to increases in biomass (Table VII).

At Scatlé, PICUS simulates marginal increases in biomass in scenarios 1 through 3 and strong increases in scenarios 4 through 6. This threshold effect corresponds to a complete replacement of *Picea* by *Abies* and *Fagus* in scenarios 4 through 6 (see Figure 4 for results on scenario 4), while the species composition stays essentially unchanged in scenarios 1 through 3. Similar trends for replacement of species are predicted by DISCFORM and FORCLIM, but in both models *Abies* is simulated to occur already at +1.5 °C, and *Picea* does not disappear completely in any of the scenarios (see Figure 4 for results on scenario 4). *Fagus* is a part of the forest in scenarios 4 through 6 in the DISCFORM and FORCLIM simulation results. GUESS predicts needleleaved evergreen trees to remain dominant in all climate change scenarios. In scenarios 4 through 6, some shade tolerant broadleaved trees can establish at the site (<20% of stand total biomass).

Also at Derborence, DISCFORM, FORCLIM and PICUS predict reduced abundance of *Picea* and increased abundance of *Fagus*. In all climate change scenarios,

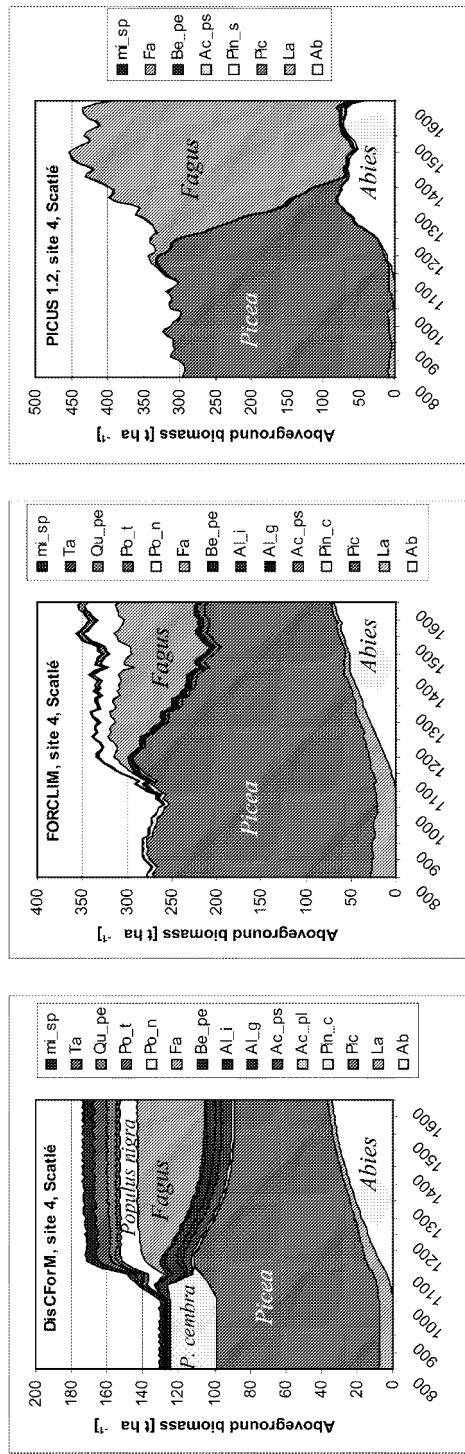


Figure 4. Change in species composition from last 200 years of current climate scenario (years 800 through 1000) into first 500 years of scenario 4 (years 1100 to 1600) expressed as species composition of total aboveground biomass. Years 1000 through 1100 corresponds to the transition period from current to changed (+3 °C) climate. Ab = *Abies alba*, La = *Larix decidua*, Ptc = *Picea abies*, Pin_c = *Pinus cembra*, Pin_s = *Pinus sylvestris*, Ac_pl = *Acer platanoides*, Ac_ps = *Acer pseudoplatanus*, Al_g = *Alnus glutinosa*, Al_i = *Alnus incana*, Be_pe = *Betula pendula*, Fa = *Fagus sylvatica*, Po_n = *Populus nigra*, Po_t = *Populus tremuloides*, Qu_pe = *Quercus petraea*, Ta = *Taxus baccata*, mi_sp = species with minor contribution to biomass (<1 t ha⁻¹).

Carpinus betulus gets established in PICUS simulations, while DISCFORM and FORCLIM show establishment of higher numbers of deciduous tree species. PICUS and FORCLIM predict a reduction of the abundance of *Abies alba*. GUESS predicts an increase in abundance of shade tolerant broadleaved summergreen trees in all scenarios. Yet, this functional type does not attain dominance at the site in any of the climate change scenarios. Needleleaved evergreen trees stay at equal level in scenarios 1 and 3, decrease in abundance in scenarios 4 and 6 and increase in scenarios 2 and 5.

4. Discussion

With the current study, we present the first attempt of model testing for forest succession models by combining a model intercomparison and a comparison of model results with forest stand data that include detailed information on stand structure. The stand data are collected from some of the rare European forests with low levels of human impact. This subjects the models to more detailed tests with respect to stand structure (cf. Section 4.3) than those that were made in the past. Below we discuss the causes of disagreement between model results and observed species composition (Section 4.1), biomass (Sections 4.2 and 4.3), model behavior in the changed climates (Section 4.4) and limitations in the climate and vegetation data (Section 4.5).

4.1. ABUNDANCE OF SPECIES

While all models predict at least one of the dominant functional types at all the sites, the results on species composition are less satisfactory. DISCFORM, FORCLIM and PICUS results at Fågelmyrkölen and Fontainebleau as well as FORSKA results at Scatlé show a set of species completely different from the observed set ($S < 0.04$). Yet, all the observed dominant species are predicted correctly with similarity indices, $S > 0.5$, by DISCFORM, FORCLIM and PICUS at Scatlé and Derborence, and by FORSKA at Derborence and Fågelmyrkölen (if prediction of *Betula pendula* is counted as correct prediction at the latter site). Thus, when comparing the success at different sites, a distinct pattern emerges: models developed and already tested in a specific biome generally show better results in the same biome and fail more often under different environmental conditions (Table V). Thus, in spite of significant model development over the last years there is still a lack of general applicability of the models to the whole of Europe.

Our analysis of specific reasons for discrepancies between model results and observed species composition revealed that in many cases they are related to simulated drought limitations (note the similar findings in the parallel comparison studies on American and Chinese forests, Bugmann et al. (2001) and Shao et al. (2001)). Therefore, we examine the related model traits in greater detail.

4.1.1. *Causes for Differences in Model Performance: The Water Balance*

In FORCLIM, PICUS and DISCFORM, *Picea* is prevented from growing at Fågelmyrkölen because of the simulated strong drought limitation. In these models, drought indices are calculated from actual and potential evapotranspiration. They vary between 0 (no drought) and 1 (no available water). The drought index is then used to determine a growth reduction factor. When the drought index is equal to 0 a growth reduction factor of 1 results, equivalent to no limitation of growth. When the drought index is equal to a species specific maximum, the growth reduction factor is equal to 0 and no growth occurs. In FORCLIM, the average simulated drought index for Fågelmyrkölen is 0.224 and thus higher than the model-specific maximum species limit for *Picea* (0.15). In PICUS, the average drought index and the species limit are about equal (0.3), while in FORSKA the average simulated drought index of 0.108 is much lower than the species limit for *Picea* (0.4).

The climate change scenarios taken as a sensitivity analysis to changes in temperature and precipitation add further evidence for the different importance of drought limitations in the different models. In FORCLIM, DISCFORM and PICUS, *Picea abies* can not establish in substantial numbers in any of the scenarios at Fågelmyrkölen. FORCLIM generally predicts Fågelmyrkölen to be close to the dry treeline under current climate. Hence, the simulated response in the climate change scenarios is dominated by the effects of precipitation changes: decreased precipitation leads to a breakdown of the forest, whereas increased precipitation leads to increases in biomass by a factor of up to 5. In contrast, a mixed response is predicted in DISCFORM with only moderate differences between the unchanged and increased precipitation scenarios, but strong effects for decreased precipitation. At +3.0 °C, a decrease in precipitation leads to biomass losses, while higher growth rates are realized in all the other scenarios. PICUS also shows a mixed response to changes of temperature and precipitation, but combined with increases in production under all climate change scenarios.

For the deciduous forest of Fontainebleau, the drought limits of the tree species play an important role in determining the predicted forest composition. All species-based models predict dominance of species that are more drought tolerant than beech (*Quercus spp.*, *Castanea sativa*, *Pinus sylvestris*). These species usually are outcompeted on mesic sites by beech and attain dominance only when beech is hampered by frost, drought or other reasons. The results obtained under the climate change scenarios corroborate these findings. The drier the conditions, the more FORCLIM and DISCFORM reduce predicted growth for the species in the order of their susceptibility to drought and even in those scenarios with increased precipitation beech cannot gain a dominant or codominant position. As opposed to this, PICUS predicts a beech forest in scenario 3 as does FORSKA in scenarios 3 and 6.

In summary, the predicted species spectrum at Fontainebleau in all models is shifted towards more drought tolerant species compared to the spectrum observed at the site. Thus, for the species-based models the site conditions impose higher

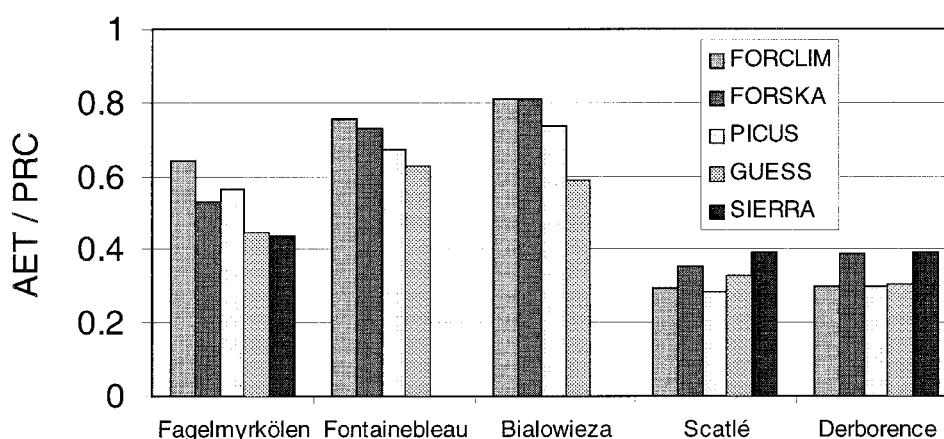


Figure 5. Comparison of the model-specific ratio of average annual actual evapotranspiration over precipitation at the five sites.

drought limitations than they do in reality. In fact, the site is close to the drought limit of beech in the Paris region (Pontauiller et al., 1997). Exploratory simulations (not shown here) revealed that higher soil water holding capacity or an increase in beech drought tolerance lead to more realistic species compositions. For example, an increase of the maximum tolerable drought index for beech from 0.25 to 0.35 in FORSKA leads to simulation of a pure beech forest.

The above results indicate the need to reconsider the methods for parameter estimation and to improve the estimates of specific parameter values. This can be illustrated for drought effects, where a cascade of elements that determine the effective limitation of a species by drought relative to its competitors needs to be considered. The individual elements are: (a) calculation of PET, (b) calculation of AET, (c) determination of a drought index based on AET, PET and related variables (e.g. interception, snow melt), (d) parameterization of species-specific drought limits, (e) calculation of drought limitation as a function of c and d, and (f) combination of drought limitation with other limiting factors. At each step of this cascade, the models discussed here can and often do differ.

The comparison of the simulated ratio of actual evapotranspiration and precipitation (AET/PRC, Figure 5) reveals that there is considerable variation in the predicted AET/PRC ratio. The span of the difference in annual AET is between 9 and 22% of annual precipitation, with the smallest differences close to 10% occurring at the alpine sites. This result is similar to the inter-model variability found in the Project for Intercomparison of Landsurface Schemes (Pitman and Henderson-Sellers, 1998). In this study the comparison of 22 models at a site in the Netherlands revealed the span between highest and lowest predicted AET to be equal to 32.4% of the annual precipitation sum.

A comparison of the other elements of the cascade of factors described above for some selected cases (results not shown) revealed degrees of variation between models similar to the variation in AET/PRC. Thus, an in-depth comparison of these factors is needed if the causes of divergent model results are to be understood fully, based on a step-by-step comparison of the elements of the cascade. Such an analysis should include comparison of simulated AET to AET measured at eddy flux sites. New gap models which are based on a more detailed description of physiological and water balance processes should be included in these comparisons, even if they are not yet operational with respect to processes such as regeneration and do not yet include a larger number of species (for example GUESS simulates functional types, and the model 4C is currently parameterized for 4 species only, cf. Price et al., 2001). Finally, the consequences of the use of different parameterization procedures for the ranking of species with respect to bioclimatic factors should be examined.

4.1.2. Causes for Differences in Model Performance: Temperature Effects

As opposed to FORCLIM, DISCFORM and PICUS, growing degree days (GDDs) are used in FORSKA only to prescribe a lower limit of thermal requirements during the growing season. The GDD sum is used as a step function that yields zero when the GDD sum is below a species specific threshold, and equal to one (i.e., non-limiting) when it is above the threshold. There are only small differences in the threshold values assigned to *Pinus sylvestris* (500), *Populus tremula* (400), *Picea abies* (600) and *Betula pendula* (500). When the step function attains a zero value it excludes photosynthesis and establishment. In FORSKA, none of the boreal species is excluded by the degree day limits at Fågelmörkölen, and therefore the shade-tolerant *Picea* dominates the stand in the long run. Contrary to this situation, the temperature regime at Scatlé discriminates between *Picea* and the other boreal species in terms of FORSKA's GDD limit in many years (average GDD sum = 525 during the 1000 years of current climate). Thus, *Picea*, which is dominating in the real stand, is kept at a low level of abundance in the FORSKA simulation results.

In all climate change scenarios at Fågelmörkölen, *P. cembra* is excluded in DISCFORM, while it can continue to co-dominate in FORCLIM. This difference is due to the fact that DISCFORM imposes an upper temperature limit for tree growth by applying a parabolic GDD dependence (cf. Bugmann, 2001), while FORCLIM is based on an asymptotic relationship. At Fågelmörkölen, the average GDD sum increases from a value of about 100 GDD above the lower GDD limit (619) of *P. sylvestris* in DISCFORM under the current climate to a value above the upper limit of *P. cembra* (1124) under the +3 °C scenarios.

Hence, the examination of temperature effects reveals differences between the models which are related to the model structures. The GDD sum is used to describe thresholds for growth and establishment in FORSKA and for calculation of growth modifiers with either parabolic (DISCFORM) or asymptotic (FORCLIM) functions. Since the relevance of these different model structures for the prediction

of species composition is high, the realism of the divergent approaches needs to be re-examined.

4.1.3. *Causes for Differences in Model Performance: Other Factors*

There are other causes of disagreement between model behaviour and observed species composition that deserve to be mentioned here:

First, the simulation experiments are based on the assumption that the current geographical distribution of the species is in equilibrium with current climate. In reality, a species that is predicted to have a high abundance but does not grow in the real forest (e.g., *P. cembra* in the case of FORCLIM at Fågelmörkölen) may be absent because of migration lags or the lack of immigration routes from glacial refuges. In the special case of *P. cembra*, there is empirical evidence that the species could grow and reproduce in Scandinavia, but that it is competitively excluded by other conifers. The species was introduced to Finland during the 1860s; it produces seeds and regenerates in experimental plots, but seems to be unable to succeed in the competition with local species (Anonymous, 1995).

Second, if a model is parameterized for a specific provenance (locally adapted population, e.g. of *Pinus sylvestris* and *Picea abies* in Fennoscandia) that differs in terms of drought and temperature requirements as compared to other provenances which grow in other regions (e.g. alpine), then failure of a model in the latter region could be due to the difference of the provenances' traits. In such cases, different sets of parameters would be needed for different provenances. Given the number of known ecotypes of *Picea abies* and *Pinus sylvestris* and their wide distribution range, autecological differentiation with respect to their bioclimatic requirements cannot be ruled out and requires further investigation.

4.2. BIOMASS

Model estimates of stand biomass depend on the one hand on the allometric relationships used to calculate tree dimensions (as height or diameter at breast height) and biomass from one another and on the other hand on the distribution of trees into the size classes. The comparison of FORCLIM and DISCFORM provides an important clue to the separation of the two components. While the results produced by the two models are similar in many respects including stand structure (see Section 3), the simulated biomass differs roughly by a factor of two. This is mainly due to the use of an additional empirical correction factor by DISCFORM in the algorithm for calculation of biomass from stem dimensions (see description of DISFORM in Section 2.1). Generally, the assumptions about stem form and wood density implicit in the model relationships between stem dimensions and biomass can and should be compared to large data sets on individual tree stems and empirical relationships used in forestry.

Substantial differences in predicted biomass can arise from differences in the parameterisation of the allometric relationships between diameter, height and bio-

mass. However, they are not closely linked to the core of the simulation model. For example, consider the case of a model that calculates biomass from diameter and height but biomass as such does not have any impact on the subsequent stand dynamics. In this case the relationship used for calculation of biomass from diameter and height can be changed without any impact on the modelled stand dynamics, but with big changes in the derived biomass values. Therefore the distribution of trees and biomass into size classes needs to be taken into account in order to distinguish between errors in the estimation of (1) single tree biomass, (2) the number of old big trees and (3) stand density.

4.3. STAND STRUCTURE AND BIODIVERSITY

The examination of the results on stand structure shows a consistent bias in FORCLIM, FORSKA and DISCFORM. FORCLIM and DISCFORM underestimate tree numbers, basal area and biomass in the low diameter classes and overestimate them in the high diameter classes. Hence, too many big trees persist in the simulation for too long, either because too many patches are dominated by big trees or because big trees can persist with too high density. FORSKA consistently overestimates tree numbers, basal area and biomass in the low diameter classes. Such a bias is likely to be related to the algorithms for mortality, regeneration and growth. For instance, an underestimation of the intrinsic mortality would lead to a bias towards big, old trees. Also, high regeneration rates in combination with an underestimation of growth rates can lead to a bias towards many small trees. These factors and relationships, which were beyond the scope of the present paper, should be analyzed in follow up studies.

The models FORCLIM and DISCFORM allow for establishment of more species than do PICUS and FORSKA (Figure 2). While FORSKA and PICUS exert a stronger selection at the time of establishment, for most of the numerous species which get established in FORCLIM and DISCFORM, few individuals grow into high diameter classes (data not shown). As opposed to this, in PICUS most of the regenerating species die in the sapling stage. These different patterns affect the share in biomass and basal area that is ascribed to the dominating species (Table IV). The overestimation of regenerating species in DISCFORM and FORCLIM can arise either because they miss environmental limitations of regeneration (see Price et al., 2001), because they underestimate the effect of light competition, or because seed availability is restricted in reality due to high distances to potential seed trees. In the latter case, the algorithms for regeneration can be correct but a module for seed production and dispersal, such as the one included in PICUS needs to be added. An elegant way to examine this topic would be to run PICUS with unlimited seed availability.

4.4. MODEL BEHAVIOR UNDER CLIMATE CHANGE SCENARIOS

The FORSKA climate change scenario runs for Fågelmyrkölen show that the simulated changes in production are due to the strong interactions between higher temperatures, which increase production, and drought risk. Neither FORSKA nor GUESS predict establishment of more southern broadleaved deciduous trees for the full range of scenarios. Drought acts on the relative abundance of *Picea abies* and *Pinus sylvestris*. Thus, the model scenarios suggest that the expected changes in forest composition do not imply migration of species since the boreal tree species that are already growing locally would be able to persist. Insofar as expected changes in biomass (Table VII) are concerned, the results pinpoint a high uncertainty as long as the prediction of precipitation changes are uncertain.

For the two alpine sites, the simulation results of the four models agree with each other to a high degree. Generally, they predict increases in biomass and a shift in forest composition towards a species spectrum which can currently be found at lower elevations. DISCFORM, FORCLIM and PICUS predict similar relative changes in biomass (Table VII). At these sites with high precipitation and therefore ample water supply in all climate change scenarios, temperature is the major limiting factor for simulated tree growth and also for establishment. In future studies, drier sites (e.g. in central alpine valleys with a more continental climate) should be included in model comparisons to assess scenario results under conditions where a mixed temperature and moisture response can be expected. The predicted change in forest composition and increase in biomass is monotonous with time, without a transient reduction in biomass under any scenario (see e.g. Figure 4). The differences between the changes in forest composition predicted by FORCLIM and DISCFORM compared to PICUS are again related to the trends in the number of species which can coexist. Once deciduous species are simulated to grow at the sites, DISCFORM and FORCLIM predict a higher biodiversity than PICUS.

For Fontainebleau, which is close to the ecoclimatic limit of beech, the FORSKA results under the climate change scenarios corroborate the high sensitivity of forest composition to changes in precipitation. When precipitation increases (scenarios 3 and 6), beech dominates the forest; when it decreases, oaks and pines replace beech. Increasing evaporative demand and drought stress decrease total standing biomass in all scenarios. Interesting results are the lower simulated biomass in the beech forests growing in scenarios 3 and 6 than in the oak-pine forests which are simulated to grow in scenarios 1 and 4. This might be realistic for the limiting situation where beech is still close to its drought limit, but just vigorous enough to outcompete the other species by shading. GUESS results are compatible with FORSKA's predictions.

4.5. LIMITATIONS OF THE MODEL-DATA COMPARISON

There are three groups of factors that have to be taken into account when evaluating gap model simulation results against stand data from pristine forests (cf. also Bug-

mann, 2001): (1) accuracy and representativity of the environmental driving variables provided for the study; (2) possible directional changes and non-equilibrium conditions effective at the sites under consideration; and (3) representative nature of the inventory data. These issues will be discussed in turn.

First, with the exception of Białowieża, no on-site measurements of weather variables were available. Therefore measurements at places close to or in some cases fairly far away from the site (71 km at Fågelmörkölen) were used. The uncertainty related to this information can not be quantified at present. The uncertainty related to extrapolation of precipitation data is generally high, which led us to discard one site (Pfinwald in Switzerland).

Soil data were also not available for all sites. Thus, there is uncertainty related to the estimation of soil properties (Lexer and Hönninger, 1998c). Even for sites where measurements of soil properties were available (e.g. Fontainebleau), the well known micro-site heterogeneity of soil characteristics might limit the usefulness of the data. A central question in this context is the determination of water holding capacities. If greater rooting depths are important for water supply during dry periods (see Wullschleger et al., 2001), then an information on rooting depth is crucial for the parameterization of specific sites.

We used a synthetic weather record constructed from current climate information. Hence, known trends in chemical and physical elements of climate on time scales relevant to forest succession were not taken into account, including the medieval climate optimum, the little ice age, the 20th century global warming trend, nitrogen deposition, and CO₂ fertilization. The impact of these factors, which are thought to be of importance for changes in forest composition at some sites, e.g. at Białowieża (see Bernadzki et al., 1998) should be examined in future studies based on reconstructed long term weather records. Such data sets covering several centuries of weather patterns are increasingly becoming available, particularly for Europe (cf. Bugmann and Pfister, 2000).

Second, disturbance history also poses a potential problem. For instance, at the Swedish site exclusion of big fires played an important role in the dominance of *Picea*. In Białowieża, management of game levels is one of the main factors explaining the shifts in species composition observed since 1936 (Bernadzki et al., 1998a). The historical retreat and recolonisation patterns correlated with glacial-interglacial cycles may be a factor responsible for the exclusion of species that are simulated to be present at some sites (such as *Pinus cembra* and *Castanea sativa*), when unlimited seed availability is assumed. In some cases, the possible non-equilibrium between climate and plant distribution might even introduce a bias in parameter values estimated from overlays of bioclimatic and geographical maps.

Third, to arrive at a representative sample of forest composition, a minimal area is required for the inventory. The size required varies as a function of the disturbance regime relevant at the site and many inventory plots are quite small or otherwise non-representative. For instance, at Fågelmörkölen the data are representative for one possible state only which is dominant after long fire free periods.

For Fontainebleau the plot data are limited for minor species (e.g. single specimens of *Ulmus* and *Carpinus* have been reported to grow in the forest).

Some of the above limitations to the use of stand data for model evaluation purposes can be relaxed to some extent in the future by extension of the forest inventory, site properties, and the climate data bases. Some other limitations, especially those related to the history of non-climatic site conditions, are more difficult to relax.

Thus, there are several potential causes for discrepancies between model results and observed stand data that are not indicative of model failure. Is the comparison of model outputs to plot data under these circumstances a useful exercise or does it lead to arbitrary results? Certainly, a discrepancy between a simulation result of a single model and site data can not be interpreted as successful model falsification. Yet, we compared several models to each other and to site data in order to reveal systematic patterns of model-specific (as opposed to data-specific) problems. For example, the analysis of stand structure data revealed different types of bias for different models across all sites. Thus, the probability that the disturbance history of a specific site is the cause of the discrepancies between observed and simulated stand structure is minimized, suggesting a need to analyze the model-specific causes for diverging patterns of stand dynamics. The example of drought limitations shows that the implications of several sources of error can be identified with the approach we took. For example, an insufficient data base for the parameterization of soil water holding capacities was identified as one potential problem that can be verified in future studies. At the same time, the model comparison demonstrated that the different ranking of species' susceptibilities to drought in the individual models contributed to the divergence of model results and requires further investigation. Therefore, we conclude that the combination of several methods for model testing should be pursued further, and that an iterative process of model testing and improvement is most likely to increase the trustworthiness of model behavior (see also Bugmann, 2001).

5. Conclusions

All models predicted at least one of the dominating functional types, and with two exceptions (2 out of 20 cases) they also correctly predicted the functional type with the highest abundance. With respect to these predictions, the classic species-based models as well as the functional type-based model, which includes more physiological detail, yielded similar results. In about 50% of the simulations, the species-based models failed to predict the correct species composition. In these cases, the deviation between modelled and observed species composition typically represented a shift of the simulated forest towards neighboring systems along an environmental gradient, such as soil water availability.

The performance of the six models at several European sites demonstrates inherent limitations of the current model formulations. As expected, there was a clear trend for an enhanced performance of the models when applied in the subspace of environmental conditions for which they were originally developed. We propose the hypothesis that this is related to the main climatic factors that determine changes in forest composition within these subspaces. On the one hand, the elevational temperature gradient is the dominant factor in the Alps and its effects appear to be simulated correctly by DISFORM, FORCLIM and PICUS. FORSKA failed at one of the alpine sites because its parameters apparently do not correctly describe the low temperature limit of *Picea abies*. On the other hand, when soil water availability plays a dominant role in the competition balance of tree species, FORSKA yielded higher similarity indices than the other models. This model had been modified to project the success of boreal tree species at ecotones determined by drought. Based on this hypothesis, we conclude that DISFORM, FORCLIM and PICUS can be used for climate impact studies in the alpine forests, and FORSKA in boreal forests. In contrast, though the models correctly predict the deciduous forest type, the application of any of the models for prediction of the species composition of these temperate deciduous forests can only be recommended after thorough revision of the models.

At those sites where the models provided reasonably accurate results under current climate, we also obtained close agreement under the scenarios of climatic change (Section 4.4). The climate change scenarios used here do not carry the forests far away from their current ecoclimatic location relative to the ecoclimatic differences between the sites (cf. Figure 1). Yet, the strongest climate scenarios, used in the present study imply climate change signals similar to the changes expected during the 21st century (e.g., Kattenberg et al., 1996). Thus, if models are selected based on their performance under current climate, we can expect similar trends in their predictions of change in species composition under future climates. We interpret this as an indication of applicability of the models for prediction of responses to climatic change for the selected cases that were examined here. Yet, an extension of the range of applicability across sites which are ecoclimatically very different (cf. Figure 1) requires improvements of the forest succession models. We suggest the following priorities for further model testing, which should serve to identify the necessary changes in model structure and parameterization.

- Our analyses clearly demonstrated strong effects of the different water balance submodels that are used in gap models. Hence, we recommend to analyze and improve the submodels on water balance and drought impact by comparison to measured flux and soil water data.
- The analyses of stand structure (Section 4.3) indicated a consistent bias in the simulated rates of regeneration or mortality, or in the simulated competition. Given the design of our study, the respective process formulations and their effects could not be examined in detail here, but should be addressed in follow-

up studies. We suggest that systematic sensitivity studies should be conducted to highlight the effects of specific algorithms for recruitment, mortality, growth and light competition on the simulated stand structure.

- In our study, the comparison of results was hampered by the use of different sets of species by different models. Hence future model comparison studies should be based on unified sets of species.
- Some tree species, particularly those with a wide climatic distribution range, may differ significantly in their autecological properties from one region to another. The use of one single parameter set for a given species, as done in our study, may not reflect such differences. Hence, we recommend to evaluate if provenances (ecotypes) require different parameterizations in forest gap models.
- With our simulation protocol, the effect of historical climate anomalies and particularly extreme events on the present structure and composition of a real forest cannot be represented. Thus, future model-data comparisons should be based on several centuries of reconstructed weather patterns instead of relatively short time series from the instrumental record. Such long data sets are increasingly becoming available, particularly for Europe.

The present study demonstrated a high sensitivity of model predictions to the parameterisation of soil properties in drought prone forests. Hence, we conclude that there is a need to improve the databases of input variables on physical and chemical soil properties and rooting depth.

A new generation of physiology-based succession models operating at the species level that would comprise a balanced treatment of production, growth, establishment and mortality will not be available for application in the near future (GUESS e.g. simulates functional types, the model 4C is currently parameterized for 4 species only as reported by Price et al., 2001). Yet, these new models as well as existing forest growth models should play an important role in detailed studies of specific causal relationships in forests, such as drought limitations or competition for light, water and nutrients. The aim would then be to derive simplified, but robust formulations from the more detailed, physiology-based approaches that can be incorporated in gap models.

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