

Assessing impacts of climatic change on forests in the Alps

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Abstract. This paper presents a method to project quantitatively the possible impacts of climatic change on mountain forests at high temporal (annual cycle), spatial, and qualitative resolution. It allows linkage from global scenarios simulated by climate models through local climatic scenarios to stand-specific forest models. The method was applied to four representative sites in the Alps using the CCC-GCMII climate model, a statistical procedure to downscale GCM-output to the regional scale, and the forest patch model FORCLIM. Sharply contrasting forest responses were observed within short distances under the same $2\times\text{CO}_2$ scenario of radiative forcing. While some forest simulations produced only small changes in tree species

composition, others produced major changes even to the point of a complete disappearance of the forest. In some cases new species assemblages emerged without any analogue under present conditions. The results suggest that some mountain forests are sensitive to a $2\times\text{CO}_2$ global change, and that human assistance may be required to help forests to adapt. The proposed method made good use of existing data, integrated current understanding, and appears sufficiently flexible and general to assess impacts of climatic change on any mid to high latitude forests in accordance with IPCC guidelines.

Key words. Climate change impacts, mountain forests, statistical downscaling, patch models, Alps.

INTRODUCTION

In a world subject to global change, mountain forests may play an increasingly important role. They moderate the water cycle, stabilize soils, protect human settlements, shape the landscape, provide wood and other products, and begin playing a key role in preserving biodiversity while current trends of low-elevation deforestation continue. Assessing possible impacts of climate change on these important ecosystems poses a particular scientific challenge, owing to the complex effects of mountainous topography both on local climates and on their forests.

Neither ecological theory (e.g. Solomon, 1988) nor experimental approaches (e.g. Körner, 1993) enable us to predict precisely the consequences of particular climatic changes on ecosystems. On the other hand carefully designed simulation models (e.g. Fischlin, 1991), which embrace what is known from theory and experiments, not only make it possible to trace the consequences of a given set of assumptions, but also render the underlying theory and experimental data accessible for scrutiny. Thus it may be argued that models currently provide the most comprehensive

means to assess impacts of climatic change on ecosystems and are likely to remain so for some time.

Simulation models are also essential tools for impact assessments according to the IPCC Guidelines (Carter *et al.*, 1994), which distinguish these basic methods: experimentation; impact projections; empirical analogue studies; and expert judgement. In the case of forests, experimentation is often impractical due to the longevity of the dominant tree species; to follow conventional experimental approaches, forests would need to be investigated over several centuries. Forest ecosystem models are therefore essential, although the question remains 'How much can they actually accomplish?'

Several modelling approaches are currently available to assess the impact of climatic changes (e.g. Shugart, 1990; Kirschbaum & Fischlin, 1996), offering varying advantages or disadvantages, depending on emphasis plus resolution in time, space, and structure.

In the first of these approaches, climate and vegetation are empirically correlated by assuming equilibrium conditions (Holdridge, 1947, 1967; Box, 1978, 1981). If such relationships can be quantified, efficient tools to project vegetation responses in space

result (e.g. Emanuel, Shugart & Stevenson, 1985; Kienast, Brzeziecki & Wildi, 1987; Box & Meentemeyer, 1991; Brzeziecki, Kienast & Wildi, 1993, 1995; Cramer & Leemans, 1993). This approach assumes a static relationship between climate and climax vegetation, however, which may be perfectly adequate to predict a potential natural vegetation in an undisturbed, distant future world, but not necessarily the real, near-future vegetation.

The second approach is to use ecophysiological models (e.g. Schimel *et al.*, 1990; Rastetter *et al.*, 1991; McGuire *et al.*, 1993; Melillo *et al.*, 1993; Parton *et al.*, 1993) which offer the advantages of being dynamic and able to reproduce ecosystem responses to climatic forcings at a high temporal and sometimes relatively high spatial (e.g. Melillo *et al.*, 1996) or qualitative resolution (e.g. Kirschbaum *et al.*, 1994). These models, however, often focus on particular chemical elements such as C or N (e.g. Raich *et al.*, 1991; Raich & Schlesinger, 1992) or on ecophysiological processes that lump together properties, such as species composition (e.g. Schimel *et al.*, 1990; Parton *et al.*, 1993) or canopy structure, hence providing only poor qualitative resolution. The associated up-scaling problems limit the usefulness of these approaches, since feed-backs to the atmosphere by structural changes in an ecosystem must be ignored unless the latter are modelled explicitly. For instance, if the species composition in a mixed-deciduous forest changes, this may greatly affect winter albedo, an effect which can only be modelled if species composition is modelled explicitly. Similar arguments can be put forward for other structural properties of forests, such as age structure, stem density or dispersion, all affecting surface roughness.

Some additional problems often apply to the above approaches. In many instances paleoecological studies of the effects of climatic change on ecosystems have demonstrated that structural properties such as the species composition are of essential relevance (Davis, 1986, 1989, 1990). This has been confirmed particularly for forests (e.g. Davis, 1981; Huntley & Birks, 1983; Huntley, 1990; Overpeck, Bartlein & Webb III, 1991; Prentice, Bartlein & Webb III, 1991; Solomon & Bartlein, 1992; Webb III, 1992; Wright *et al.*, 1993). Since most phytosociological as well as ecophysiological approaches ignore species composition (Perruchoud & Fischlin, 1995), their usefulness for studies of climatic change impacts appears to be limited.

The third and perhaps most promising approach is the use of patch dynamic models, which have already

proved relatively successful in mimicking forest succession (e.g. Shugart, 1984). By operating at an intermediate level (high spatial, medium temporal, and medium qualitative resolution) they allow the relevant time constants of forest dynamics to be included while still simulating important structural characteristics of forests such as species composition or age structure.

Patch models are able to mimic broad characteristics of real forests under a wide range of climates (e.g. West, Shugart & Botkin, 1981; Shugart, Leemans & Bonan, 1992; Smith, Smith & Shugart, 1992) and are thus of relatively high predictive power (Shugart, 1984). Patch models have also been successfully used to study forest responses to: (i) past climatic changes (Solomon *et al.*, 1980; Solomon & Webb III, 1985; Lotter & Kienast, 1992; Solomon & Bartlein, 1992; Fischlin, Guisan & Lischke, 1997; Fischlin, Lischke & Bugmann, 1997); (ii) direct effects of CO₂ (Solomon, 1986; Pastor & Post, 1988; Kienast, 1991); or (iii) possible future climatic changes (Solomon, West & Solomon, 1981; Shugart *et al.*, 1986; Overpeck, Rind & Goldberg, 1990; Botkin & Nisbet, 1992; Smith, Leemans & Shugart, 1994).

With regard to the Alps, several authors have conducted modelling and evaluation studies (FORECE Kienast, 1987; Kienast & Kuhn, 1989; ForClim Bugmann, 1994; FORSUM Kräuchi, 1994) and have studied possible impacts of a changing climate on Alpine forests (Kienast, 1991; Kräuchi, 1993; Kräuchi & Kienast, 1993; Bugmann, 1994; Bugmann & Fischlin, 1994, 1996; Fischlin, 1995).

These studies have shown that Alpine forests may be sensitive to climatic change. However, they have all relied upon relatively coarse climatic scenarios, which may have hampered the internal consistency and potential realism of the results. Indeed, the highly variable topography of the Alps, their location in the transitional zone between the temperate, Mediterranean and continental climatic regimes, the complexity of forests, and the high input and precision requirements of forest patch models render the construction of appropriate climate change scenarios a challenging task.

A simple method often adopted is to adjust climate parameters on an ad hoc basis, e.g. by assuming a temperature increase of 1–4°C within the next, say, 50–100 years (e.g. Houghton, Jenkins & Ephraums, 1990; Ozenda & Borel, 1990). While this approach may be useful for initial sensitivity studies, its main disadvantage is that differences between possible patterns of global climate change, as well as the

regionally differentiated responses to such patterns must be completely ignored. In complex terrain like the Alps, this approach is therefore particularly likely to yield inconsistent results (Gyalistras *et al.*, 1994).

An approach with fewer shortcomings (Carter *et al.*, 1994) is to rely upon simulations with global climate models, in particular three-dimensional, coupled general circulation models of the atmosphere (Washington & Parkinson, 1986) and the oceans (Semtner, 1995) ('AO-GCMs'). At least three different strategies to construct regional climate change scenarios from GCMs have been proposed.

First, GCM-output at a few gridpoints in the vicinity of the region of interest may be used (e.g. Karl *et al.*, 1990; Santer *et al.*, 1990). For instance Bugmann & Fischlin (1996) directly interpolated climatic scenarios from GCM grids to assess the impacts of these scenarios on Alpine forests. However, GCMs typically show very large errors at individual model gridpoints (e.g. Grotch & MacCracken, 1991). This is particularly true over complex topography such as the Alps (Gyalistras *et al.*, 1994).

The second approach is to use a physically-based regional climate model (RegCM) driven by boundary conditions taken from a GCM (e.g. Giorgi, Marinucci & Visconti, 1992). A major limitation is that even if a RegCM is run at very high horizontal resolution (say ~20 km, Marinucci *et al.*, 1995), the simulated climatic changes can only be trusted at a spatial scale above several RegCM-gridpoint distances (cf. von Storch, 1995). Hence, many mountain features (ridges, valleys, slopes), can not be adequately resolved. Further, the huge computational requirements of RegCMs severely restrict the construction of time-dependent scenarios over the time spans needed to assess forest responses, i.e. several centuries.

The third approach is based on interpretation of large-scale climatic changes as simulated by GCMs (or RegCMs) using expert knowledge (e.g. Robock *et al.*, 1993) or statistical models that relate regional climates to the large-scale atmospheric state (e.g. von Storch, Zorita & Cubasch, 1993). The latter approach appears to be practical, offering the potential to satisfy all requirements simultaneously (Gyalistras *et al.*, 1994). Several authors have demonstrated that the application of empirical 'downscaling' relationships can yield physically plausible and internally consistent first-order estimates of possible climatic changes at least at regional scales (for reviews see e.g. Kattenberg *et al.*, 1996; Gyalistras *et al.*, 1997). Bugmann (1994; Bugmann & Fischlin, 1994) and Fischlin (1995) have

used statistically downscaled scenarios to assess forest responses in the Alps, but they have used scenarios (Gyalistras *et al.*, 1994) which considered only winter and summer seasons instead of the entire annual cycle.

This paper presents a general method for estimating the possible impacts of climate change on forests in the complex Alpine terrain by combining global climate models, downscaling techniques, and patch models. For several carefully selected sites, each representing a typical forest ecosystem, it will be shown that: the proposed method provides consistent and plausible (and otherwise unavailable) quantitative projections of possible changes in key structural characteristics such as species composition of mountain forests; many forests in the Alps are sensitive to these down-scaled climate change scenarios given at a monthly resolution, and; forests within a relatively small distance may show a surprisingly wide range of responses to the same pattern of global climatic change.

MATERIALS AND METHODS

Climate change impacts were assessed at four study sites in the Alps (Table 1). For each site CLIMSHELL (Gyalistras *et al.*, 1994; Gyalistras & Fischlin, 1996) was used to define base line climates and to derive climate change scenarios from GCM simulation results, and FORCLIM (Bugmann, 1994; Fischlin, Bugmann & Gyalistras 1995) was used to simulate forest responses to the obtained climate scenarios (Fig. 1).

Each case study site (Table 1) represents a particular ecoregion from North to South: Bern located on the Swiss Plateau is a typical submontane site, Bever represents subalpine forests, Gotthard represents an alpine site, currently above the timberline, and Sion represents colline belt conditions (cf. Ellenberg, 1988).

Baseline climates

The large-scale observations used to fit the downscaling models were gridded (5° × 5° latitude by longitude) anomalies of monthly mean sea-level pressure (SLP, provided by NCAR, see Jessel, 1991) and near-surface air temperature (NST, from the data set of Jones & Briffa, 1992; Briffa & Jones, 1993) over the North-Atlantic/European sector (40°W–40°E and 30°N–70°N). Local climatological observations were extracted from the data base of the Swiss Meteorological Institute (Bantle, 1989).

The forest model FORCLIM uses a stochastic weather

Table 1. Characteristics and major current climate parameters of the case study sites.

Site	Location	Elevation (m above sea level)	Annual mean temperature (°C)	Annual precipitation sum (cm)	Current potential natural vegetation (Ellenberg & Klötzli, 1972)
A Bern	Swiss Plateau (Northern Alps)	570	8.6	99	Submontane mixed deciduous forests dominated by beech (<i>Fagus sylvatica</i> L.) and silver fir (<i>Abies alba</i> Miller)
B Bever	Central/Southern Alps	1712	1.6	82	Subalpine coniferous forests dominated by larch (<i>Larix decidua</i> Miller) and arolla pine (<i>Pinus cembra</i> L.)
C St Gotthard	Transition zone Northern to Southern Alps	2300	-1.0	207	Alpine belt, above current timberline
D Sion	Central Alps	542	9.9	60	Colline mixed-deciduous oak forest

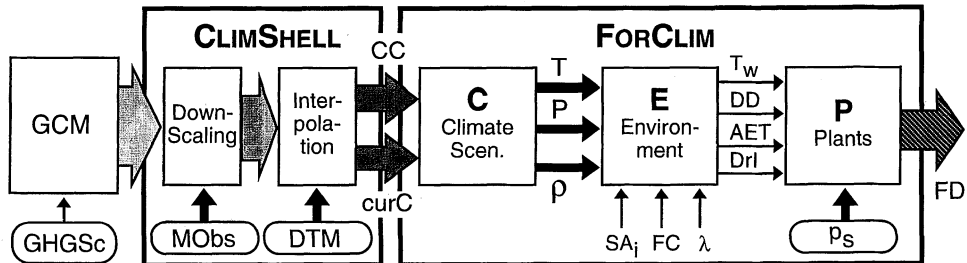


Fig. 1. Method used to derive climate scenarios (CLIMSHELL Gyalistras *et al.*, 1994; Gyalistras & Fischlin, 1996) and simulate forest responses (FORCLIM Bugmann, 1994; Fischlin *et al.*, 1995). Arrows represent data flow: large—vectors or matrices, thin—scalar variable or parameter. GHGSc, Green House Gas Emission scenario (in this study $2 \times \text{CO}_2$ -equilibrium); GCM, General Circulation Model (simulation results used in this study from CCC-GCMII, Boer *et al.*, 1992); MObs, Meteorological large-scale (Jessel, 1991; Jones & Briffa, 1992; Briffa & Jones, 1993) and local (Bantle, 1989) observations; DTM, Digital Terrain Model (in this study ARC/INFO data describing Swiss Alps); curC, current climate data; CC, data describing climate change; T, climatic parameters $E[T_m]$, $\text{VAR}[T_m]$, monthly temperatures; P, parameters for monthly precipitation sums $E[P_m]$, $\text{VAR}[P_m]$; ρ , $\text{COV}[T_m, P_m]$; SA_i , slope-aspect index; FC, field capacity; λ , latitude; T_w , winter temperature; DD, day degrees; AET, actual evapotranspiration; DrI, drought index; Ps, matrix of species parameters; FD, forest dynamics (e.g. age distribution, species composition, leaf area index, etc.). Downscaling is described in Gyalistras *et al.* (1994); Interpolation attempts to make best use of local/regional meteorological measurements and digital terrain model; submodel ForClim-C controls climatic change within FORCLIM; submodel ForClim-E, computes abiotic environment; submodel ForClim-P, simulates tree dynamics.

generator to simulate annual cycles of monthly mean temperature (T) and precipitation totals (P) based on the following set of site-specific, climatic input parameters: expected values of monthly mean temperatures ($E[T]$), monthly precipitation totals ($E[P]$), and monthly 2×2 cross-covariance matrices ($\text{COV}[T, P]$) for each month of the year (Fischlin *et al.*, 1995).

For Bever, Bern and Sion, all climatic parameters were computed from daily measurements for the period 1931–1980 (Bantle, 1989). For St Gotthard, which is

~ 0.6 km away from the nearest climatological station (at 2090 m a.s.l.), $E[T]$ and $E[P]$ were interpolated using a further thirty-nine stations for T (twenty-five for P) up to a distance of 80 km (60 km for P), whereas $\text{COV}[T, P]$ was taken directly from the nearest station. To interpolate we applied a linear regression separately for each month to predict $E[T]$ and $E[P]$ from elevation, and then adjusted the result based upon an inverse distance-weighted (IDW) interpolation of elevation-detrended expected values from the surrounding

stations (cf. Gyalistras & Fischlin, 1995, 1996). We used for E[P] a linear, and for E[T] a piecewise linear, seasonally varying dependency on elevation with a breakpoint at 1450m.

Climate change scenarios

All climate change scenarios were derived from a '2 × CO₂' global climate change experiment simulated by the Canadian Climate Centre CCC-GCMII (Boer, McFarlane & Lazare, 1992). The scenarios were constructed based on the statistical downscaling method of Gyalistras *et al.* (1994, 1995, 1996) as follows.

(a) For each month Empirical Orthogonal Function analysis (EOF, Preisendorfer, 1988) was used to construct a smaller number of new, large-scale variables (so-called EOF-scores), from the 306 variables contained in the SLP- and NST-fields of the period 1931–1980. Between eight (winter months) and fourteen (summer months) EOF-scores were retained, which explained ~90% of the total inter-annual large-scale variability for all months.

(b) Canonical Correlation Analysis (CCA, Barnett & Preisendorfer, 1987), again performed for 1931–1980, was used to establish separately for each location and month a multivariate regression model to predict from the EOF-scores simultaneous anomalies of local monthly mean T and monthly \sqrt{P} from their respective long-term means. The CCA regression parameters define pairs of large-scale patterns and corresponding local responses (see von Storch *et al.*, 1993; Gyalistras *et al.*, 1994), which were all plotted to allow inspection of the statistical relationships.

(c) The monthly downscaling models derived from the CCA were applied to 5 years of monthly mean large-scale anomalies as simulated by the CCC-GCMII under '2 × CO₂' conditions relative to the long-term mean fields from a 5 year control ('1 × CO₂') simulation. Changes in the seasonal (winter = DJF, spring = MAM, summer = JJA, and autumn = SON) mean SLP- and NST-fields were plotted to examine the downscaled scenarios.

(d) Site-specific changes in E[T] and E[P] were estimated by averaging the five downscaled anomalies for each month. Since these changes showed jagged annual cycles at all locations, annual cycles were smoothed using a moving average of the downscaled changes of the month itself and the preceding and subsequent months. The climate change scenario for

St Gotthard was obtained by IDW interpolation of the downscaled monthly changes from the same surrounding stations as were used to derive the present climate. Since the downscaled changes showed no strong dependency on altitude, no correction for elevation was applied. At all sites the covariance matrices COV[T,P] were held constant at present (baseline) values.

Forest model FORCLIM

From the modularized forest model FORCLIM (version 2.4.0.4 Bugmann, 1994; Fischlin *et al.*, 1995) we used three submodels (Fig. 1). FORCLIM-C (climate) simulates location-specific climate changes as discrete events. FORCLIM-E (environment) simulates the abiotic environment of a patch from the climatic parameters as produced by FORCLIM-C. FORCLIM-P (plants) is a discrete time (1 year time step) patch dynamics model simulating the fate of tree cohorts populating a patch of 1/12ha in a species specific manner.

FORCLIM-E contains the stochastic weather generator which simulates interannual variability in monthly temperature and precipitation. From the location-specific parameters SA_i, FC, and λ (Fig. 1) FORCLIM-E then computes the winter temperature T_w, the annual day degree sum DD, and the drought index DrI; for input to FORCLIM-P. T_w is the minimum of the variates of T for December, January, and February. DD is computed by correcting for biases and discretisation errors (Fischlin *et al.*, 1995) according to the method developed by Bugmann (1994). Following a simple bucket-model approach, actual (AET) and potential (PET) evapotranspiration are computed according to Thornthwaite & Mather (1957), where calculations depend not only on the usual site-specific parameters, field capacity FC (in this study at all sites 30cm) and latitude λ (site A: 46.9°N; B, C: 46.6°N; and D: 46.2°N), but also on the slope-aspect index SA_i. The latter was used to correct the PET for the slope and aspect dependent radiation plus wind effects (cf. Bugmann, 1994). The drought index DrI is the difference between PET and AET divided by the PET (Prentice & Helmisaari, 1991; Bugmann, 1994; Fischlin *et al.*, 1995).

FORCLIM-P simulates three basic processes, which determine annual changes in the tree cohorts currently existing within a patch: (i) establishment of saplings; (ii) death of individual trees (both (i) and (ii) formulated as Poisson processes), and; (iii) tree growth, formulated

deterministically based on an improved growth equation (Moore, 1989; Bugmann, 1994), which mimics explicitly inter- and intraspecific competition for light and implicitly for water and nutrients. Establishment and growth are directly affected by weather. However, since slow growth lasting over a series of years increases the probability of tree deaths, weather may also contribute indirectly to mortality.

Full definitions of all equations forming FORCLIM can be found in Bugmann (1994, ForClim-P) and Fischlin *et al.* (1995, ForClim-E).

Simulation results were obtained according to the Monte-Carlo technique by sampling for each site 200 variates (Bugmann, Fischlin & Kienast, 1996). Always assuming an empty patch as the initial condition, each variate was obtained by sampling the state vector every twentieth year within the simulation period 800 to 3200. FORCLIM-C simulated climatic changes as a step change in the year 2050. All simulations were performed on Macintosh computers (68040 CPU) and Sun workstations using the interactive RAMSES* simulation environment (Fischlin, 1991; Fischlin *et al.*, 1994) and the RAMSES simulation server RASS (Thoeny, Fischlin & Gyalistras, 1994, 1995).

Steady state estimates under current and future climates were computed from the 200 variates by averaging species abundances from biomasses over 400-year periods, under the base-line climate (1840–2040), and under future equilibrium conditions assumed to be reached after 2800 (cf. Bugmann *et al.*, 1996).

To summarize, effects of climatic change on species composition similarity indices, S_i , were computed between pairs of steady state estimates (see above) according to the formula $S_i = 1 - \sum |x_i - y_i| / \sum (x_i + y_i)$ where x_i and y_i are abundances of species i in the current (x_i) and the future (y_i) climate, respectively.

RESULTS

Climatic change scenarios

At all four study sites (Table 1) the GCM-based future scenarios showed an increase in annual mean

temperature and a tendency towards wetter conditions compared to the present climate. The direction and magnitude of the changes (Fig. 2) differed from site to site. Annual mean temperatures increased by 2.4°C at Sion and St Gotthard, by 2.5°C at Bern, and by 2.6°C at Bever. Precipitation showed no significant change at Sion (+0.9 cm or +1%), whereas increases of 8.6 cm (+11%), 18 cm (+31%), and 42 cm (+20%) were obtained at Bern, Bever and St Gotthard, respectively.

The downscaling models provided plausible linkages between observed inter-annual variability of the local climate variables and large-scale anomalies in: (i) the strength of the westerlies in winter; (ii) the intensity of more meridional (i.e. north-south) flow patterns in the transition seasons, and; (iii) the strength of large-scale subsidence in summer (cf. Gyalistras *et al.*, 1994, 1997). The proportions of total variances of the local variables explained in the fitting interval 1931–80 averaged over all locations for the winter half-year (October–March) amounted to 58% for temperature and 36% for precipitation. For the summer half-year (April–September), the mean variances were 65% and 32% for temperature and precipitation, respectively.

Comparison of the annual cycles of temperature and precipitation under present-day and the simulated future climate shows (Fig. 3) that the shifts in the annual means (Fig. 2) were not equally distributed throughout the year and that the seasonal patterns vary from site to site. Averaged over all locations warming was smallest in spring and autumn (+2.2°C) and largest in summer (+2.8°C) and precipitation increased in all seasons (+9% to +30%) except for summer (–5%). Among sites the warming differed the least in autumn (0.3°C) and the most in summer (0.9°C) and the changes in precipitation differed again the least in autumn (20%) and the most in spring (44%).

These results conform to the underlying circulation changes simulated by the CCC-GCM. In winter the GCM-projected enhanced mean westerly flow over Europe would produce stronger temperature changes at the more north-westerly sites (Bern and Sion) and a general precipitation increase. The smaller warming at all locations during spring is associated with a distinct strengthening of the northerly flow component simulated by the GCM. In summer, increased anticyclonic activity over central Europe in combination with strong mid-continental heating produced greater temperature increases at the more easterly locations (St Gotthard, Bever). A strengthening of the northeasterly flow in autumn was associated with a smaller warming and a slight increase in

*RAMSES is an acronym for Research Aids for Modelling and Simulation of Environmental Systems. RAMSES is available as freeware from the anonymous ftp host 'ftp.ito.umnw.ethz.ch' (Internet address 129.132.80.130) and detailed information can be obtained via the World-Wide-Web at the netsite <http://www.ito.umnw.ethz.ch/SysEcol>.

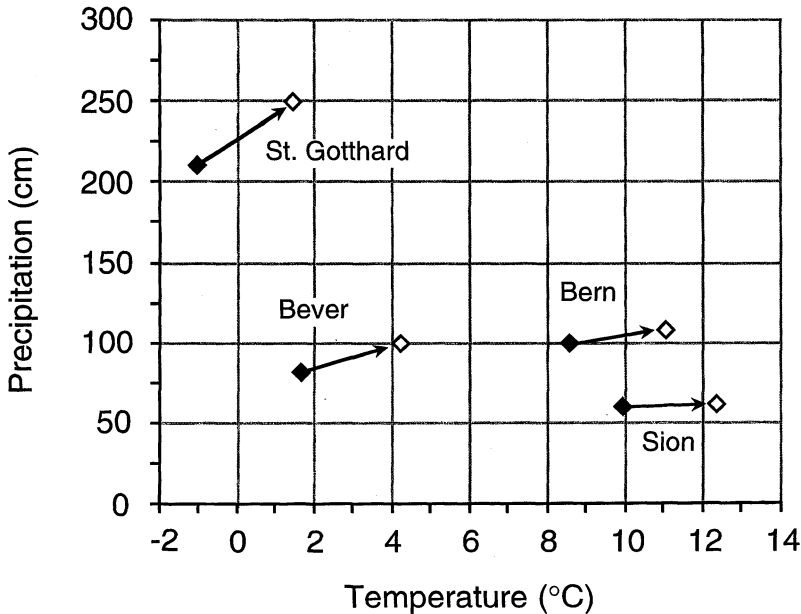


Fig. 2. Comparison of annual mean temperatures and annual precipitation sums under the present (◆) and the assumed scenario climates (◇) at the case study sites (Table 1). ◆, means for 1931–80 computed from daily measurements (Bantle, 1989); ◇, scenario values derived by statistical downscaling (Gyalistras *et al.*, 1994; Gyalistras & Fischlin, 1996) from a '2 × CO₂'-experiment with the CCC-GCMII (Boer *et al.*, 1992).

precipitation at all sites, except for the more sheltered location at Sion.

Forest responses

A general response to climatic change, probably typical for many mountain forests in the Alps (Bugmann, 1994; Bugmann & Fischlin, 1994), is that observed at the Bever site (Fig. 4). The primary succession starting in year 800 lasts about six centuries, after which European larch (*Larix decidua* MILL.), a pioneer species, is substantially replaced by the late-successional species arolla pine (*Pinus cembra* L.). The climax community is the larch-arolla pine forest often found in the central subalpine belt of the Alps (Table 1). At this site the simulated step change in climate (cf. Figs. 2,3) produced a sharp transient response in the forest. It then initiated a secondary succession resembling a primary one, which eventually lead to a completely new climax community containing none of the previously dominant species. Only larch and Scots pine (*P. sylvestris* L.) from the earlier climax community appear as early successional species.

The steady-state biomass densities for all four sites (Table 1) are depicted for current climate in Fig. 5 and for the projected future equilibrium climates (Figs. 2, 3), in Fig. 6. At Bern (A) the climatic change caused no significant changes in the climax communities ($S_i = 0.92$). Contrastingly, the steady states at Bever (B) differ sharply ($S_i = 0.07$). A similar dramatic change ($S_i = 0.002$) was obtained at St Gotthard (C) where a forest appears above the current timberline (cf. Fig. 7 bottom). At Sion (D) we obtained a quite different response, i.e. the collapse of the forest canopy. Only very low tree biomass remains in the climax community under the changed climate ($S_i = 0.07$).

The flexibility of the new technique (CLIMSHELL combined with FORCLIM, cf. Fig. 1) is demonstrated in Fig. 7. The technique makes it possible to simulate the behaviour of forests at locations different from those at which weather records are available, for instance along an altitudinal gradient. This is possible not only for current, but also for down-scaled, future projected climatic scenarios (Fig. 7 top, middle, bottom; steady-states from bottom simulation also shown in Figs 5 and 6).

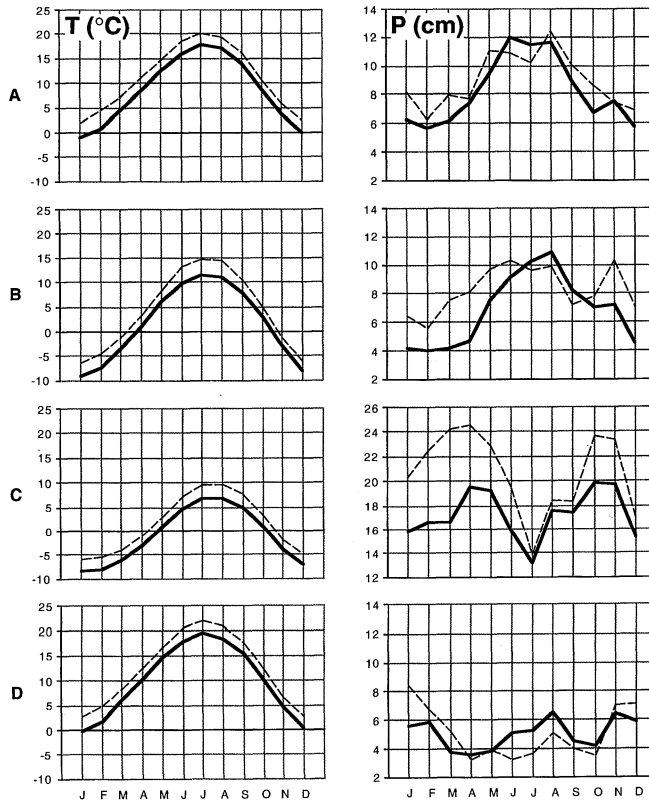


Fig. 3. Comparison of observed 1931–1980 (thick lines) annual cycles for monthly mean temperature (left) and total precipitation (right) (Bantle, 1989) with the climatic scenarios (broken lines) derived by statistical downscaling (Gyalistras *et al.*, 1994; Gyalistras & Fischlin, 1996) from a $2 \times \text{CO}_2$ -experiment with the CCC-GCMII (Boer *et al.*, 1992) at the four case study sites (A, Bern; B, Bever; C, Gotthard; D, Sion; see also Table 1). Note the different scale for precipitation at site C.

DISCUSSION

For a far-future $2 \times \text{CO}_2$ equilibrium world, the CCC-GCMII projects a warming in the mean annual global near-surface air temperature of 3.5°C (Boer *et al.*, 1992), approximately at the centre of the 2.1 – 4.6°C range projected by state-of-the-art GCMs (Kattenberg *et al.*, 1996). Transient experiments with coupled GCMs (with climatic sensitivities in the range noted above), under steadily increasing concentrations of greenhouse-gases at the time of doubled CO_2 showed a warming of 1.3 – 3.8°C , with an average of only 2.0°C . Such a delay was not considered in our simple, step-like scenarios, but, as has been shown by Bugmann (1994), it is probably of minor relevance for the mid- and long-term response of forests.

Several reasons indicate that the regional scenarios

of climatic change used here are plausible and spatially consistent. (i) The scenarios plausibly reflect the effects of changes in the spatial distributions of large-scale monthly mean sea-level pressure and near-surface temperature as projected by the CCC-GCMII (analysis of CCA model response). (ii) The projected warming is to be expected, since it seems unlikely that any changes in regional climate forcings (which could lead to e.g. increased frequency of thermal inversions or of cold air drainage) could override the strong, general warming prescribed by the CCC-GCM. (iii) The projected increases in precipitation are consistent with the general increases in globally averaged precipitation of *c.* 2–15% projected by GCMs under a CO_2 -doubling (Houghton *et al.*, 1990; Houghton, Callander & Varney, 1992), as well as with indications from an experiment with a regional climate model (Schär *et al.*, 1996). (iv)

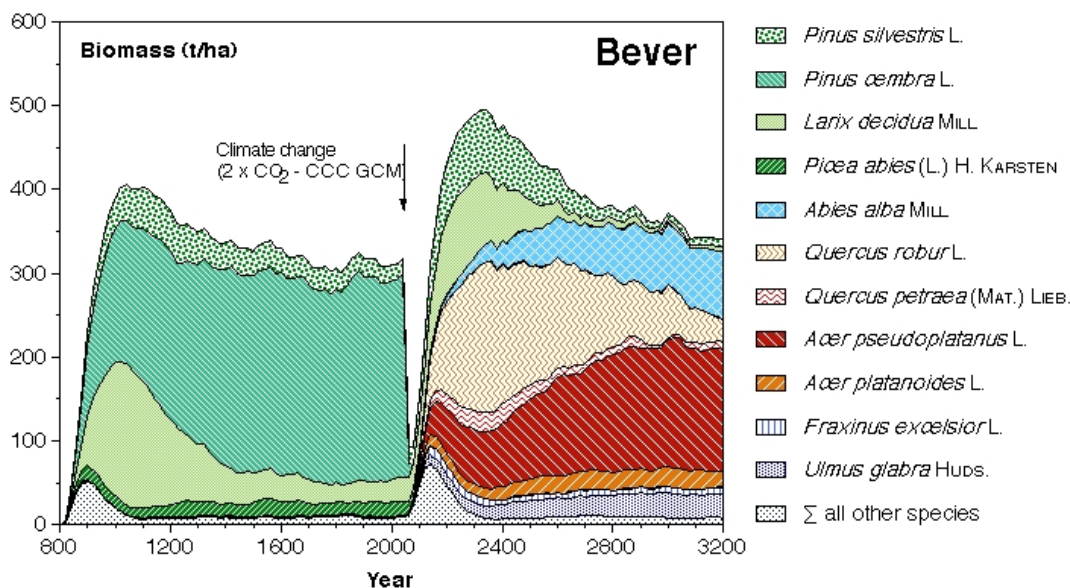


Fig. 4. Simulated species compositions at the case study site Bever (B, Table 1) in the Swiss Alps for current climate (800–2040) and a possible, future $2 \times \text{CO}_2$ climate (2060–3200) as down-scaled (Gyalistras *et al.*, 1994) from the CCC-GCMII (Boer *et al.*, 1992). All simulations were made with the forest model FORCLIM (Bugmann, 1994; Fischlin *et al.*, 1995). Accumulatively shown mean species abundances in t/ha were averaged from 200 variates sampled according to the Monte-Carlo technique from the stochastic process described by FORCLIM (cf. Fig. 5 and 6). ‘ Σ all other species’ is total of the following low abundance species: *Salix alba* L., *Sorbus aria* (L.) CRANTZ, *S. aucuparia* L., *Tilia cordata* MILLER, *T. platyphyllos* SCOP., *Quercus pubescens* WILLD., *Populus tremula* L., *Corylus avellana* L., *Betula pendula* ROTH, *Carpinus betulus* L., *Alnus glutinosa* (L.) GAERTNER, *A. incana* (L.) MOENCH, *A. viridis* (CHAIX) DC., *Taxus baccata* L., *Acer campestre* L., and *Pinus montana* MILLER.

The average ratio between projected changes in annual temperature and precipitation ($5.4\%/^{\circ}\text{C}$) is consistent with the theoretical value (e.g. Roedel, 1992, p. 65) obtained under the assumption that the relative humidity of the atmosphere would remain unaltered (e.g. Mitchell & Ingram, 1992). (v) The variability in the regionalized patterns of change appears realistic, in view of the seasonally and spatially strongly varying link between Alpine and large-scale climate (e.g. Schüepp, 1968; Fliri, 1974; Gensler & Schüepp, 1991; Gyalistras *et al.*, 1994; Schär *et al.*, 1997). (vi) The projected changes were spatially more uniform for temperature than for precipitation, in agreement with patterns observed in the Alpine region (Fliri, 1974; Ehrendorfer, 1987; Auer & Böhm, 1994; Beniston *et al.*, 1994). (vii) The scenarios are consistent with climatic changes obtained at a coarser spatial scale from physically-based regional climate models (for a detailed comparison of model-based and empirically-downscaled scenarios for the Alpine region, see Gyalistras *et al.*, 1997).

In present climates FORCLIM normally produces

realistic species compositions as is shown not only by the present results (cf. Table 1 with Figs 4–7), but also by other studies, which have analysed and validated the behaviour of this model in Europe, North America, present, and past (e.g. Bugmann, 1994; Bugmann & Fischlin, 1994; Bugmann & Solomon, 1995; Fischlin, 1995; Fischlin *et al.*, 1997). From all this evidence we claim that the model FORCLIM has considerable predictive power and is generally capable of projecting ‘realistic’ results.

Similarly, sensitivity analyses at the four study sites (not shown), agree with results from former studies (e.g. Bugmann, 1994) and suggest that the projected new equilibria for the species compositions are relatively robust, i.e. that small changes in the climatic scenarios of the order of $\pm 0.5^{\circ}\text{C}$ or $\pm 5\%$ for precipitation would show only little effect (Fischlin *et al.*, 1995).

Although all study sites were affected by the same global pattern of climatic change, the projected forest responses differed significantly, ranging from enhanced growing conditions, to no effect, to complete

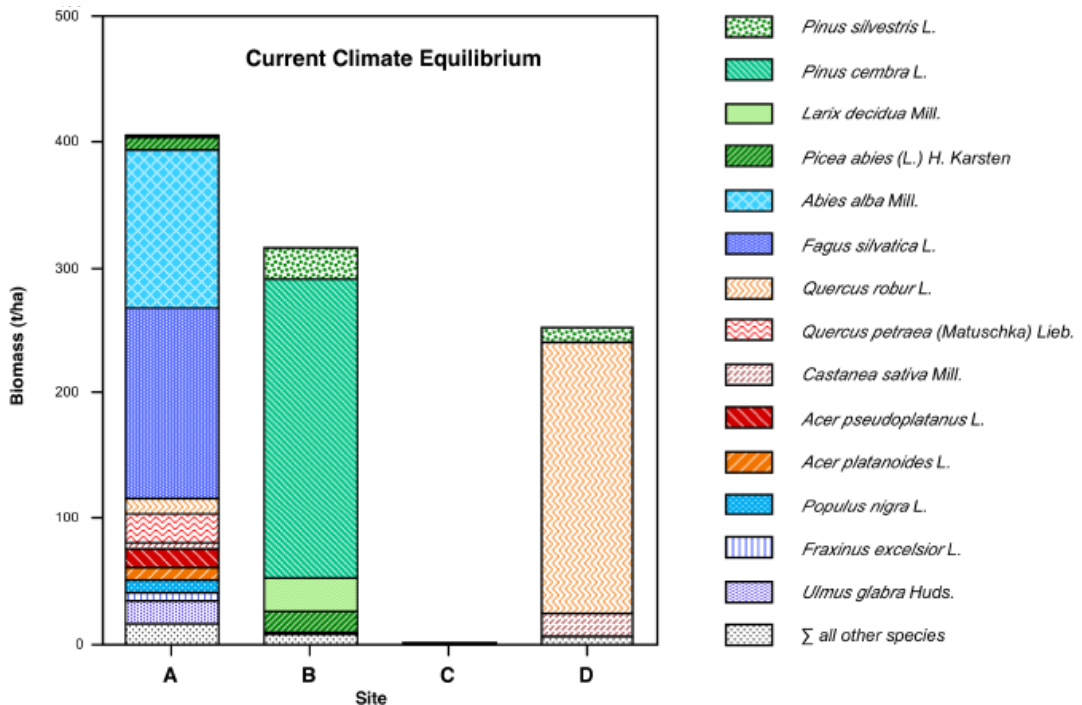


Fig. 5. Simulated equilibrium species compositions at the case study sites (A, Bern; B, Bever (cf. Fig. 4), C, Gotthard (cf. Fig. 7 bottom); D, Sion; see also Table 1) in the Alps for current base-line climate (800–2040). All simulations made with FORCLIM (Bugmann, 1994; Fischlin *et al.*, 1995). Depicted mean species abundances averaged from 200 variates sampled according to a Monte-Carlo technique from the stochastic process described by FORCLIM. (cf. Fig. 6). All other settings as described under Fig. 4.

disappearance of the forest (cf. Figs 5 and 6). All simulations assumed an identical species pool disregarding any phytogeographic history. Thus, observed differences among the sites can be explained, at least partly, by the site specific climatic parameters for monthly temperature and precipitation. Since the scenarios of local climatic change contained also a strong shared component, however, the dramatic differences found in the forest responses cannot be explained only by the physical environment. To fully understand the obtained patterns, we have to consider also the intrinsic mechanics of the ecosystem model, which form a complex network of non-linear, interdependent causes behind the projected forest responses.

Forest responses at the case study sites

Site A—Bern

Bern shows a remarkable insensitivity to the projected changes. It is the only site where the similarity index

is close to one, whereas all other sites show very small, near zero indices, indicating sharp changes in species compositions under current *v.* new equilibrium conditions. Although other studies (e.g. Nilsson & Pitt, 1991) have projected similarly small changes for this zone (Swiss Plateau) our result contrasts with that obtained by Brzeziecki, Kienast & Wildi (1995), who have applied a statistical, steady-state model based on correlations between zonal forest communities, temperature, and edaphic factors (Brzeziecki *et al.*, 1993, 1995). Their model uses temperature as the only climatic factor determining plant communities. Although temperature may serve in some instances as a useful indicator for the water balance regime, this can not be expected to be the case in general (Holdridge, 1947, 1967; Box, 1981; Woodward, 1987; Box & Meentemeyer, 1991), which may explain some of the differences between their and our results.

Moreover, the Bern site is currently characterized by few periods of drought stress, whereas in the southern Alpine areas (which Brzeziecki *et al.* have used as an

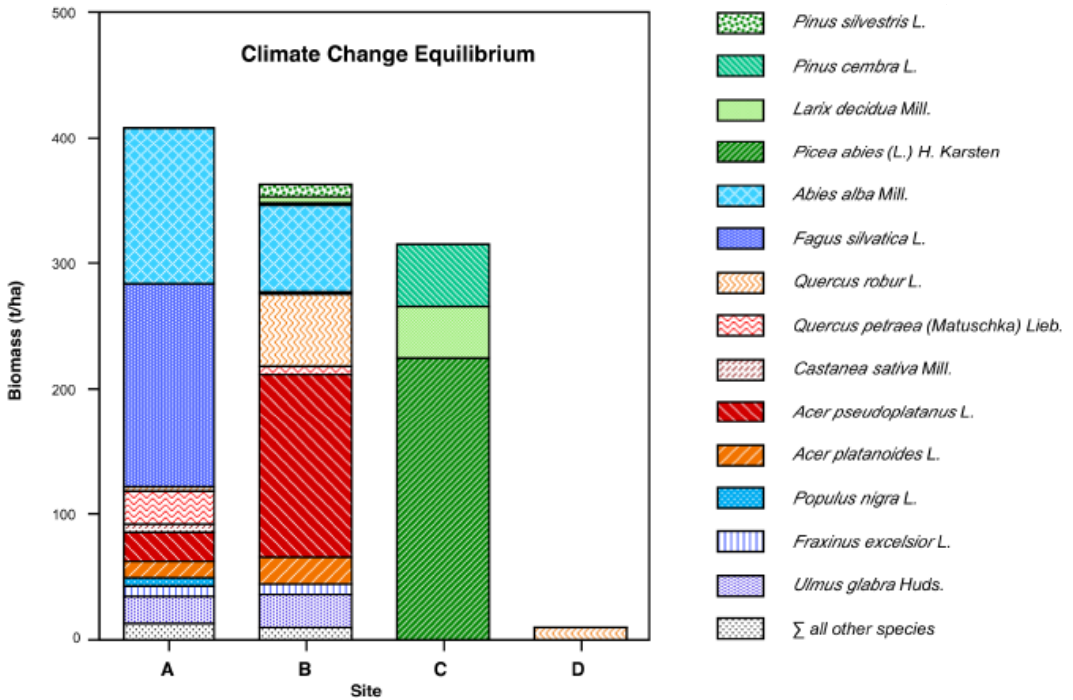


Fig. 6. Simulated equilibrium species compositions at the case study sites (A, Bern; B, Bever (cf. Fig. 4), C, Gotthard (cf. Fig. 7 bottom), D, Sion; see also Table 1) in the Alps for a possible, future $2 \times \text{CO}_2$ climate (2060–3200) as down-scaled (Gyalistras *et al.*, 1994) from the CCC-GCMII (Boer *et al.*, 1992). All other settings as described under Fig. 4 and 5.

analogue for the future conditions on the Swiss Plateau) precipitation and, hence, drought stress, show greater intra- and interseasonal variability. For example, Bern receives under present climate in summer (winter) a mean precipitation sum of 35 cm (18 cm) distributed over 35 (28) days, whereas at the southern Alpine location of Lugano a far larger amount of 55 cm (23 cm) falls within only 32 (20) days.

A further explanation for this difference lies in our use of seasonal climate change scenarios, which projected the strongest warming at Bern during winter, which has only a minor effect on the vegetation. Moreover, Brzeziecki *et al.* have assumed no changes in precipitation, whereas the down-scaled scenarios showed increased precipitation during winter, spring, and fall, partly compensating for the projected increases in temperature.

Unless the insubrian climate typical of the Southern Alps should really prevail on the Swiss Plateau, the projections by FORCLIM appear to be more plausible for the given climate change scenario. The small

sensitivity at Bern to warming is further corroborated by the temperature requirements of the presently dominant tree species, since the projected climate changes do not push any of these species far from their ecophysiological optima, allowing them to remain within the centre of their realized niches. However, the statistical model by Brzeziecki *et al.* might again become superior, in cases of extreme warming scenarios, where patch models like FORCLIM—e.g. due to the use of simplified schemes to compute the local water balance (Thorntwaite & Mather, 1957; Fischlin *et al.*, 1995)—tend to underestimate the sensitivity of forest responses (Kienast, 1991; Bugmann, 1994; Bugmann & Fischlin, 1994).

Site B—Bever

At the subalpine site Bever, the projected climatic changes cause major changes in species composition (Fig. 4), also expressed in the extremely low similarity index. The new forest composition simulated under a

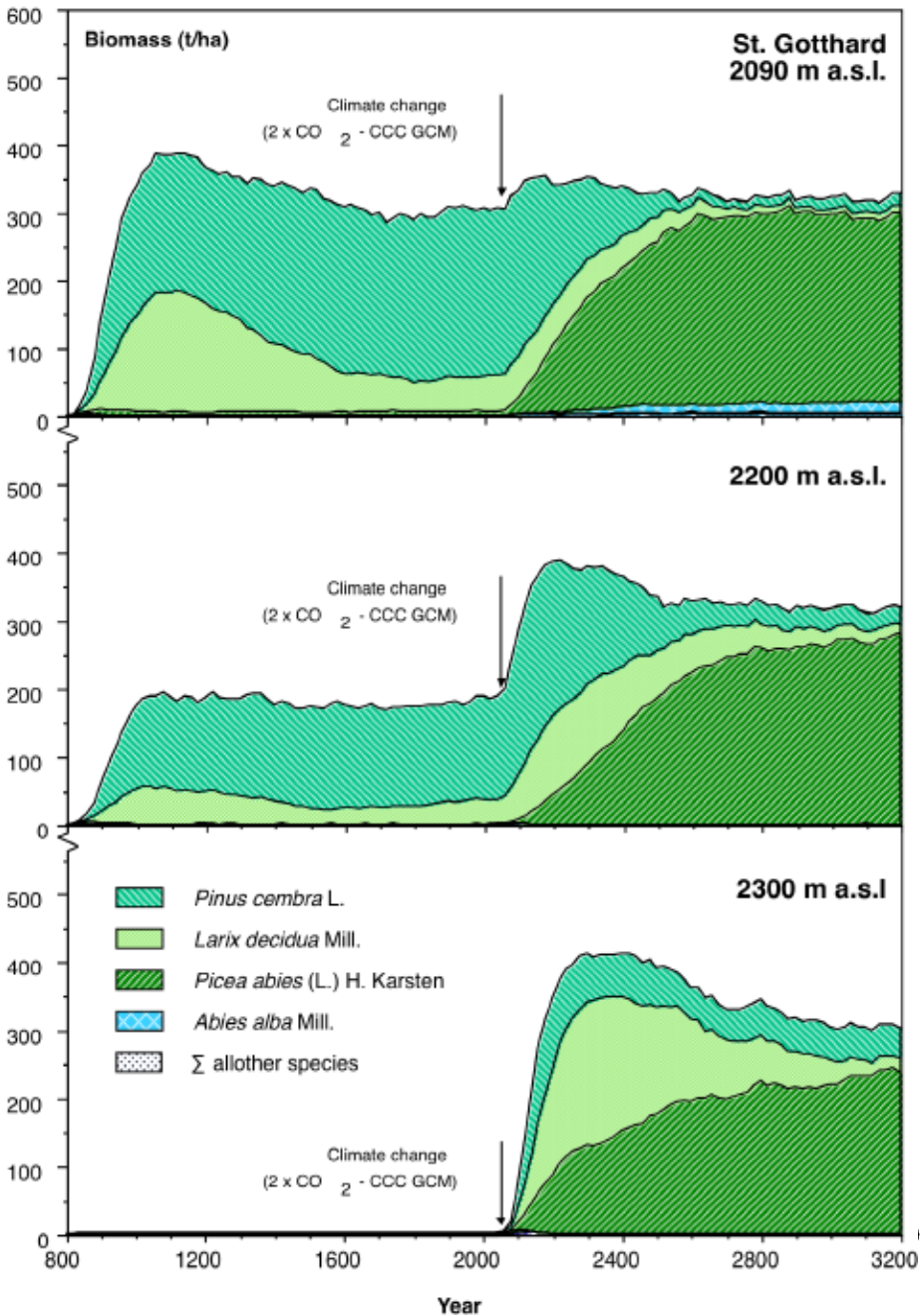


Fig. 7. Using the CLIMSHELL (Gyalistras & Fischlin, 1996) to explore forest dynamics where there are no measurements available (top, 2090; middle, 2200; bottom, 2300 m a.s.l.). The applied technique allows interpolation of base-line climates and climate scenarios by combining measurements from climatic base stations (this study: station of St Gotthard at 2090 m a.s.l.), with measurements from auxiliary climatological stations (this study: up to additional thirty-nine stations), a digital terrain model, and regionalized GCM-output (for bottom cf. Figs. 5 and 6). All other settings as described under Figs. 4 and 5.

changed climate represents a completely new community with no present analogue (Ellenberg & Klötzli, 1972; Ellenberg, 1988). This result conforms with the individual species responses postulated by several authors to explain the patterns found during past climatic changes (e.g. Davis, 1981; Huntley & Birks, 1983; Davis, 1990; Huntley, 1990).

The climatic changes projected for Bever vary considerably with season. For instance, summer warms by $\sim 0.7^\circ\text{C}$ more than winter, while precipitation in summer remains unchanged, but increases 12–55% in other seasons.

Not surprisingly, the annually averaged changes in climate at Bever (Fig. 3B), distributed equally over all months, cause a forest response (results not shown here) which differs significantly in its transient as well as equilibrium species compositions ($S_i = 0.62$). Consistent with increased water availability and less warming during summer, *Acer pseudoplatanus* was found to be less abundant in the non-seasonal scenario than under our original, monthly resolved scenario (Fig. 4). Instead, *Picea abies* produces c. 30% of the total biomass. The high abundance of *P. abies* moves this new forest composition closer to that found under present conditions. Hence, we conclude that using annually averaged scenarios may lead to an overestimation of such a forest's ability to adapt to potential climatic change.

Bever is located in the centre of the Alps and the omnipresence of species, e.g. of sweet chestnut (*C. sativa*) or European beech (*Fagus sylvatica*), as assumed in the model, cannot be expected to be the case in reality. Therefore, the transition to a new equilibrium, is likely to be further hampered by the migrational barriers posed by mountains. This inference is corroborated by phytogeographic evidence from the past, which shows that the Alps have functioned as an insurmountable barrier for slow-migrating species in the present-day climate (Huntley & Birks, 1983; Huntley, 1990; Ozenda & Borel, 1990).

Site C—Gotthard

At Gotthard tree growth is completely suppressed under the current climate, whereas in the projected new climate trees can form a forest canopy (cf. Figs 5C, 6C, and 7). This site is located just above the current tree line (cf. Figs 7A, 7B v. 7C) where forests are believed to be mainly limited by temperature, since precipitation is abundant (Woodward, 1987; Ellenberg, 1988).

The forest responses projected by FORCLIM are consistent with ecological expectations, which require particular temperature regimes for tree growth, i.e. a growing season of at least 30 days with daily mean temperature above 10°C and fewer than 8 months with mean daily minima below 0°C (Walter & Breckle, 1986, 1991). At St Gotthard the present climate is characterized by no months with a daily mean temperature above 10°C , but in the projected climate (cf. Fig. 3C) there are more than 30 days exceeding this threshold. Furthermore, the period with daily minima below freezing decreases from almost 8 months under the present climate to less than 7 months under the projected, future climate.

Hence, the forest establishment projected by the model appears plausible, although some details of the initial succession may not be realistic. Firstly, existing soils may not be fully colonizable (Renner, 1982), requiring a long phase of development. Secondly, growth at the tree line may be reduced because of adverse local conditions such as diseases, strong winds, browsing by cattle and game, or physical instability on steep slopes. Thirdly, the models ignore the form of the precipitation (tree growth might also be hampered by mechanical or drought stress due to snow and ice), and changes in incoming solar radiation and in the duration of snow cover. For instance, increases in temperature and/or its variance during spring may produce warm periods which can melt the snow cover earlier than at present. Since occasional invasions of cold air into central Europe during spring can be expected to occur also in the future, an early retreat of the protective snow cover may increase the exposure of plants to frost damage. The strengthening of the northerly flow component over Europe, as projected by the CCC-GCM during spring (mainly April), even suggests the possibility for an increase of this risk under a ' $2 \times \text{CO}_2$ '-climate.

Even though high latitude tree lines can not be compared directly with high altitude Alpine tree lines (e.g. because of the different radiation regime), some recent observations from boreal tree lines (Taubes, 1995) appear to suggest similar effects of at least transiently reduced growth under warming conditions.

Site D—Sion

The Sion site presents an opposite case from that of St Gotthard: the current climate allows for tree growth, whereas in the projected new climate, trees can no longer form a forest canopy (cf. Figs 5D, 6D). The

disappearance of the forest vegetation appears to be plausible, considering the present-day low mean annual precipitation of 600 mm (cf. Table 1), which places this xeric site close to the drought tree line (Holdridge, 1967; Walter & Breckle, 1983, 1984, 1986, 1991; Woodward, 1987). Using the FORECE model (Kienast, 1987; Kienast *et al.*, 1987; Kienast & Kuhn, 1989) Kienast (1991) has obtained similar results for this site.

An analysis of the growth factor that quantifies the effect of soil moisture deficits in FORCLIM (Bugmann, 1994; Fischlin *et al.*, 1995) revealed that the simulated degradation of growth conditions was due to enhanced drought stress. In the projected climate, growth was reduced to a range between 4% and 10% (upper and lower 95% confidence limits) of the maximum growth potential. This increased drought stress was caused not only by the general rise in temperature, but also by the simultaneous 28% decrease in summer precipitation. The downscaled changes for summer precipitation are particularly uncertain (e.g. Gyalistras *et al.*, 1994), but it is worth-noticing that other experiments with FORCLIM (not shown here)—where we assumed only warming and no changes in annual precipitation—still lead to a collapse of the forest canopy.

Sensitivities and uncertainties

The sensitivity of Alpine forests to human interference with the climate system depends directly on the underlying sensitivities of the global and regional climate. We note that in this study, we used a global climate model with an intermediate sensitivity to increased concentrations of greenhouse gases, and that the downscaling procedure adopted may over- or under-estimate the response of the local climates to the simulated changes in global climate (Gyalistras *et al.*, 1997). The forest responses obtained then revealed a potential for greatly differing sensitivities to the same global scenario of climatic change, a result which must be interpreted carefully. Despite many recent efforts to improve FORCLIM (e.g. Bugmann & Fischlin, 1992, 1994; Fischlin *et al.*, 1995; Bugmann *et al.*, 1996), this model may not always adequately reflect the sensitivities of the real forests.

For instance, the disappearance of the forest at Sion may overestimate the true sensitivity, since this result depends, amongst others, on the particular and limited pool of species used in the simulations. Olive trees (*Olea europaea* L.), oaks such as the cork oak (*Q. suber* L.), holly oak (*Q. ilex* L.), or Pyrenean oak (*Q. pyrenaica* Willd.) could probably produce higher tree

biomasses than those simulated by FORCLIM. Similarly, if we were to accept the oak species now included in FORCLIM, i.e. *Q. robur* L., *Q. petraea*, and *Q. pubescens*, could possess the characteristics of Mediterranean provenances of these species, we would obtain a similar effect (Fischlin *et al.*, 1997). Without human assistance, however, it is unlikely that such provenances could quickly migrate to Sion, leaving the site vulnerable to a transitory, yet long-lasting forest disappearance.

Moreover, FORCLIM may have overestimated the sensitivity at all sites, since, the greater the genetic plasticity of today's tree species in terms of tolerance to abiotic forcings such as drought, the lower is their expected sensitivity to a given climatic change. Such a buffering effect, now completely ignored by FORCLIM, might be further enhanced if climatic change were to trigger novel selection and thus alter the gene pools of the tree species by affecting gene frequencies. Considering such effects would require additional simulations which include new species or adjustments of the corresponding species parameters within FORCLIM.

Conversely FORCLIM may over-estimate the robustness of forest compositions at the Bern site, since various simulations under even stronger warming (not shown here) still showed little effect. Nevertheless, as already discussed, for the ranges of climatic change used in this study, the low sensitivity obtained at Bern is likely to be generally realistic.

FORCLIM may also underestimate the sensitivity close to the timberline limited by temperature. This is because it ignores possible additional effects resulting from decreases in the duration of the snow cover, from increases in photosynthetic efficiency, or from improved nutrient allocation (cf. e.g. Körner, 1995).

The projections represent no forecasts: they merely describe the forest succession if all prescribed assumptions hold or become actually true. Consequently, many unavoidable and in some instances eventually irreducible uncertainties accompany the projections. For instance, the arbitrary selection of particular reference points in a large space of abiotic and other environmental parameters like the selection of the $2 \times \text{CO}_2$ radiative forcing scenario, the CCC-GCMII, the 1931–80 base line climate, the species parameters, etc. all generate uncertainties.

Thanks to the modular structure of our method it is easy to explore uncertainties, because modules can simply be exchanged for others: e.g. the CLIMSHELL can be switched to any other GCM, or FORCLIM can easily be simulated with any combination of submodels (Fischlin, 1991; Fischlin *et al.*, 1994). In some cases

this allows quantification of uncertainties. For instance, based on a random resampling procedure (Efron, 1979) we obtained $c. \pm 0.5^\circ\text{C}$ for temperature and $\pm 20\%$ for precipitation relative to the 'best estimate' scenario values obtained from the $2 \times \text{CO}_2$ experiment with the CCC-GCMII (averaged over twenty-two Alpine locations and all months of the year by determining 95% percentiles, for details see Gyalistras & Fischlin, 1995).

CONCLUSIONS

This study has demonstrated the feasibility and viability of a new method for assessing possible transient responses and equilibrium states of forests in a topographically complex region such as the Alps. In combining results from a GCM-experiment with a downscaling technique and a forest patch model (Fig. 1) we obtained regionally differentiated, integrated, reproducible, quantitatively consistent assessments of climatic change and their associated impacts on mountain forests at a relatively high temporal and spatial resolution. The method is spatially flexible and general and has the potential to be applied directly without modification in the mid- and high-latitudes of the Northern Hemisphere (Bugmann & Solomon, 1995) at every location of ecological interest. Finally, it conforms to the IPCC guidelines for impact assessments (Carter *et al.*, 1994), is modular and efficient. The latter is important for exploring sensitivities and uncertainties and provides a basic framework for replacing modules with better variants or enhancing the method as new procedures or submodels become available.

The climatic change scenarios obtained and the associated forest responses appeared reasonable in light of current knowledge of the climate system and the local ecology. It mattered for the forest responses that we used climatic change scenarios resolving the annual cycle, indicating that annually averaged scenarios may yield misleading results. The models produced obtained highly variable forest sensitivities within close vicinity. Insensitivity was found for low-altitude deciduous forests, whereas high sensitivities were found at the water- and temperature-tree lines. These results indicate that mountain forests will be highly sensitive to climatic change. At present little is known about the proportions of sensitive vs. insensitive forests in a region such as the Alps. Consequently, the relative importances of critical forest responses (e.g. temporary die-back during

phases of major changes in species composition or even complete disappearance) versus beneficial effects (e.g. establishment above the current timber-line) remain to be studied further. If climatic change should occur in the patterns suggested here, it is likely to result in severe local damage, even if the total area affected is relatively small. Once more the results of this study indicate that tree populations respond individually and not as a community and that without human assistance new steady states are reached only after several centuries or millennia, especially in the presence of migrational barriers.

The results ought not to be confused with actual forecasts: they represent mere projections which give possible answers to 'what if' scenarios. The validity of some of these projections may hold, only the future can reveal. We believe that they represent valid first-order estimates of possible impacts of climatic change on forests in the Alps if greenhouse gas forcing doubles.

ACKNOWLEDGMENTS

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REFERENCES

- Auer, I. & Böhm, R. (1994) Combined temperature-precipitation variations in Austria during the instrumental period. *Theor. Appl. Climatol.* **49**, 161–174.
- Bantle, H. (1989) *Programmdokumentation Klimadatenbank am RZ-ETH Zurich*. Schweizerische Meteorologische Anstalt (SMA), Zurich, Switzerland.
- Barnett, T. & Preisendorfer, R. (1987) Origins and levels of monthly and seasonal forecast skills for the United States surface air temperatures determined by canonical correlation analysis. *Mon. Weather Rev.* **115**, 1825–1850.
- Beniston, M., Rebetez, M., Giorgi, F. & Marinucci, M.R. (1994) An analysis of regional climate change in Switzerland. *Theor. Appl. Climatol.* **49**, 135–159.

- Boer, G.J., McFarlane, N.A. & Lazare, M. (1992) Greenhouse gas-induced climate change simulated with the CCC second-generation general circulation model. *J. Clim.* **5**, 1045–1077.
- Botkin, D.B. & Nisbet, R.A. (1992) Forest response to climatic change: effects of parameter estimation and choice of weather patterns on the reliability of projections. *Clim. Change* **20**, 87–111.
- Box, E. (1978) Geographical dimensions of terrestrial net and gross productivity. *Radiat. Environ. Biophys.* **15**, 305–322.
- Box, E.O. (1981) *Macroclimate and plant forms: an introduction to predictive modelling in phytogeography*. 258pp. Junk, The Hague.
- Box, E.O. & Meentemeyer, V. (1991) Geographic modelling and modern ecology. *Modern ecology*. (ed. by G. Esser and D. Overdieck), pp. 773–804. Elsevier Science, Amsterdam.
- Briffa, K.R. & Jones, P.D. (1993) Global surface air temperature variations during the twentieth century—Part 2: implications for large-scale, high-frequency paleoclimatic studies. *The Holocene* **3**, 77–88.
- Brzeziecki, B., Kienast, F. & Wildi, O. (1993) A simulated map of the potential natural forest vegetation of Switzerland. *J. Veg. Sci.* **4**, 499–508.
- Brzeziecki, B., Kienast, F. & Wildi, O. (1995) Modelling potential impacts of climate change on the spatial distribution of zonal forest communities in Switzerland. *J. Veg. Sci.* **6**, 257–268.
- Bugmann, H. (1994) *On the ecology of mountainous forests in a changing climate: a simulation study*. Diss. ETH No. 10638, Swiss Federal Institute of Technology: Zürich, Switzerland, 258 pp.
- Bugmann, H. & Fischlin, A. (1996) Simulating forest dynamics in a complex topography using gridded climatic data. *Clim. Change*, **34**, 201–211.
- Bugmann, H., Fischlin, A. & Kienast, F. (1996) Model convergence and state variable update in forest gap models. *Ecol. Model.* **89**, 197–208.
- Bugmann, H.K. & Fischlin, A. (1992) Ecological processes in forest gap models—analysis and improvement. *Responses of forest ecosystems to environmental changes* (ed. by A. Teller, P. Mathy, & J.N.R. Jeffers), pp. 953–954. Elsevier Applied Science, London & New York.
- Bugmann, H.K. & Fischlin, A. (1994) Comparing the behaviour of mountainous forest succession models in a changing climate. *Mountain environments in changing climates* (ed. by M. Beniston), pp. 237–255. Routledge, London.
- Bugmann, H.K.M. & Solomon, A.M. (1995) The use of a European forest model in North America: a study of ecosystem response to climate gradients. *J. Biogeogr.* **22**, 477–484.
- Carter, T.R., Parry, M.L., Harasawa, H. & Nishioka, S. (1994) *IPCC technical guidelines for assessing climate change impacts and adaptations*, 59 pp. Department of Geography, University College London, National Institute for Environmental Studies, Japan.
- Cramer, W.P. & Leemans, R. (1993) Assessing impacts of climate change on vegetation using climate classification systems. *Vegetation dynamics and global change* (ed. by A.M. Solomon & H.H. Shugart), pp. 190–219. Chapman and Hall, New York.
- Davis, M.B. (1981) Quaternary history and the stability of forest communities. *Forest succession: concepts and application* (ed. by D.C. West, H.H. Shugart & D.B. Botkin), pp. 132–153. Springer Verlag, New York.
- Davis, M.B. (1986) Climatic instability, time lags and community disequilibrium. *Community Ecology* (ed. by J. Diamond & T. Case), pp. 269–284. Harper & Row, Cambridge.
- Davis, M.B. (1989) Lags in vegetation response to greenhouse warming. *Clim. Change* **15**, 75–82.
- Davis, M.B. (1990) Biology and palaeobiology of global climate change: Introduction. *Trends Ecol. Evol.* **5**, 269–270.
- Efron, B. (1979) Bootstrap methods: another look at the jackknife. *The Annals of Statistics*, **7**, 1–26.
- Ehrendorfer, M. (1987) A regionalization of Austria's precipitation climate using principal component analysis. *J. Climatol.* **7**, 71–89.
- Ellenberg, H. (1988) *Vegetation ecology of Central Europe* 4th edn; 731 pp. Cambridge University Press, Cambridge.
- Ellenberg, H. & Klötzli, F. (1972) Waldgesellschaften und Waldstandorte der Schweiz. *Eidg. Anst. Forstl. Versuchswes.*, **48**, 589–930.
- Emanuel, W.R., Shugart, H.H. & Stevenson, M.P. (1985) Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Clim. Change* **7**, 29–43.
- Fischlin, A. (1991) Interactive modelling and simulation of environmental systems on workstations. *Analysis of dynamic systems in medicine, biology and ecology* (ed. by D.P.F. Möller), pp. 131–145. Springer, Berlin.
- Fischlin, A. (1995) Assessing sensitivities of forests to climate change: experiences from modelling case studies. *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains* (ed. by A. Guisan, J.I. Holten, R. Spichiger & L. Tessier), pp. 145–147. Conserv. Jard. Bot., Genève.
- Fischlin, A., Bugmann, H. & Gyalistras, D. (1995) Sensitivity of a forest ecosystem model to climate parametrization schemes. *Environ. Pollut.* **87**, pp. 267–282.
- Fischlin, A., Guisan, A. & Lischke, H. (1997) A glance to the future: modelling the response of vegetation in the Alps to climate change. *Views from the Alps: regional perspectives on climate change* (ed. by P. Cebon, U. Dahinden, H.C. Davies, D. Imboden and C. Jäger), pp. 28 (in press). MIT Press, Cambridge, Mass.
- Fischlin, A., Gyalistras, D., Roth, O., Ulrich, M., Thoeny, J., Nemecek, T., Bugmann, H.K. & Thommen, F. (1994) *ModelWorks 2.2: an interactive simulation environment for personal computers and workstations*. Systems Ecology Report No. 14, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology ETH, Zurich, Switzerland, 324 pp.
- Fischlin, A., Lischke, H. & Bugmann, H. (1997) The

- dynamic approach: Evaluating the fate of forests. *Views from the Alps: regional perspectives on climate change* (ed. by P. Cebon, U. Dahinden, H.C. Davies, D. Imboden and C. Jäger), pp. 22 (in press). MIT Press, Cambridge, Mass.
- Fliri, F. (1974) *Niederschlag und Lufttemperatur im Alpenraum*, 111 pp. Wissenschaftl. Alpenvereinshefte, Innsbruck.
- Gensler, G. & Schüepf, M. (1991) Witterungsklimatologie von Graubünden. *Beiträge zur Geographie Graubündens* (ed. by H. Elsasser and M. Boesch), pp. 7–17. *Bundesamt für Landestopographie, Wabern*.
- Giorgi, F., Marinucci, M.R. & Visconti, G. (1992) A 2 × CO₂ climate change scenario over Europe generated using a limited area model nested in a general circulation model—Part II: climate change scenario. *J. Geophys. Res. D*, **9**, 10011–10028.
- Grotch, S.L. & MacCracken, M.C. (1991) The use of general circulation models to predict regional climate change. *J. Clim.* **4**, 286–303.
- Gyalistras, D. & Fischlin, A. (1995) Downscaling: applications to ecosystems modelling. *Proc. of the 6th International Meeting on Statistical Climatology* (ed. by I.O. Muircheartaigh), Galway, Ireland; June 19–23, pp. 189–192. University College, Galway, Ireland.
- Gyalistras, D. & Fischlin, A. (1996) *Derivation of climate change scenarios for mountainous ecosystems: a GCM-based method and the case study of Valais, Switzerland*. Systems Ecology Report No. 22, Swiss Federal Institute of Technology ETHZ, Zurich, Switzerland.
- Gyalistras, D., Schär, C., Davies, H.C. & Wanner, H. (1997) Future Alpine climate. *Views from the Alps: regional perspectives on climate change* (ed. by P. Cebon, U. Dahinden, H.C. Davies, D. Imboden and C. Jäger), pp. 22 (in press). MIT Press, Cambridge, Mass.
- Gyalistras, D., von Storch, H., Fischlin, A. & Beniston, M. (1994) Linking GCM-simulated climatic changes to ecosystem models: case studies of statistical downscaling in the Alps. *Clim. Res.* **4**, 167–189.
- Holdridge, L.R. (1947) Determination of world plant formations from simple climatic data. *Science*, **105**, 367–368.
- Holdridge, L.R. (1967) *Life zone ecology*, 206 pp. Tropical Science Center, San Jose, Costa Rica.
- Houghton, J.T., Callander, B.A. and Varney, S.K. (1992). *Climate Change 1992—The Supplementary Report to the IPCC Scientific Assessment*, 200 pp. Cambridge University Press, Cambridge.
- Houghton, J.T., Jenkins, G.J. and Ephraums, J.J. (eds) (1990) *Climate change—the IPCC scientific assessment*, 365 pp. Cambridge University Press, Cambridge.
- Huntley, B. (1990) European post-glacial forests: compositional changes in response to climatic change. *J. Veg. Sci.* **1**, 507–518.
- Huntley, B. and Birks, H.J.B. (1983). *An atlas of past and present pollen maps for Europe: 0–13,000 years ago*, 667 pp. Cambridge University Press.
- Jessel, I. (1991) *Inventory of available observed data sets*. Tech. Report No. 1, Deutsches Klimarechenzentrum GmbH, Hamburg.
- Jones, P.D. & Briffa, K.R. (1992) Global surface air temperature variations during the twentieth century—Part I: spatial, temporal and seasonal details. *The Holocene*, **2**, 165–179.
- Karl, T.R., Wang, W.-C., Schlesinger, M.E., Knight, R.W. & Portman, D. (1990) A method relating general circulation model simulated climate to the observed local climate. Part I: seasonal statistics. *J. Clim.* **3**, 1053–1079.
- Kattenberg, A., Giorgi, F., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stouffer, R.J., Tokioka, T., Weaver, A.J. and Wigley, T.M.L. (1996) Climate models—projections of future climate. *Climate Change 1995—The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell), pp. 289–357. Cambridge University Press, Cambridge.
- Kienast, F. (1987) *FORECE—A forest succession model for southern central Europe*, 69 pp. Report ORNL/TM-10575, Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Kienast, F. (1991) Simulated effects of increasing atmospheric CO₂ and changing climate on the successional characteristics of Alpine forest ecosystems. *Landscape Ecol.* **5**, 225–238.
- Kienast, F., Brzeziecki, B. and Wildi, O. (1987) Computergestützte Simulation der räumlichen Verbreitung naturnaher Waldgesellschaften in der Schweiz. *Schweiz. Z. Forstwes.* **145**, 293–309.
- Kienast, F. and Kuhn, N. (1989) Simulating forest succession along ecological gradients in southern Central Europe. *Vegetatio*, **79**, 7–20.
- Kirschbaum, M. and Fischlin, A. (1996) Climate change impacts on forests. *Climate change 1995—Impacts, adaptations and mitigation of climate change: scientific-technical analysis. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel of Climate Change* (ed. by R. Watson, M.C. Zinyowera and R.H. Moss), pp. 95–129. Cambridge University Press, Cambridge.
- Kirschbaum, M.U.F., King, D.A., Comins, H.N., McMurtrie, R.E., Medlyn, B.E., Pongracic, S., Murty, D., Keith, H., Raison, R.J., Khanna, P.K. and Sheriff, D.W. (1994) Modelling forest response to increasing CO₂ concentration under nutrient-limited conditions. *Plant Cell Environ.* **17**, 1081–1099.
- Körner, C. (1993) CO₂ fertilization: the great uncertainty in future vegetation development. *Vegetation dynamics and global change* (ed. by A.M. Solomon, and H.H. Shugart), pp. 53–70. Chapman & Hall, New York.
- Körner, C. (1995) Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains* (ed. by A. Guisán, J.I. Holten, R. Spichiger and L. Tessier), pp. 113–120. Conserv. Jard. Bot., Genève.

- Kräuchi, N. (1993) Potential impacts of a climate change on forest ecosystems. *Eur. J. For. Pathol.* **23**, 28–50.
- Kräuchi, N. (1994) *Modelling forest succession as influenced by a changing environment*, 271 pp. Diss. ETH No. 10479, Swiss Federal Institute of Technology, Zürich.
- Kräuchi, N. and Kienast, F. (1993) Modelling subalpine forest dynamics as influenced by a changing environment. *Water Air Soil Pollut.* **68**, 185–197.
- Lotter, A. and Kienast, F. (1992) Validation of a forest succession model by means of annually laminated sediments. *Laminated sediments* (ed. by M. Saarnisto and A. Kahra), Proceedings of the workshop laminated sediments, 4–6, June 1990, pp. 25–31. Geological Survey of Finland, Lammi Biological Station.
- Marinucci, M.R., Giorgi, F., Beniston, M., Wild, M., Tschuck, P. and Bernasconi, A. (1995) High resolution simulations of January and July climate over the Western Alpine region with a nested regional modeling system. *Theor. Appl. Climatol.* **51**, 119–138.
- McGuire, A.D., Joyce, L.A., Kicklighter, D.W., Melillo, J.M., Esser, G. and Vorosmarty, C.J. (1993) Productivity response of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. *Clim. Change*, **24**, 287–310.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore III, B., Vorosmarty, C.J. and Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.
- Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.-D. and Sala, O.E. (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. *Climate Change 1995—The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell), pp. 445–481. Cambridge University Press, Cambridge.
- Mitchell, J.F.B. and Ingram, W.J. (1992) On CO₂ and climate: mechanisms of changes in clouds. *J. Clim.* **5**, 5–21.
- Moore, A.D. (1989) On the maximum growth equation used in forest gap simulation models. *Ecol. Model.* **45**, 63–67.
- Nilsson, S. and Pitt, D. (1991) Climate change and mountain forests. *Mountain world in danger: climate change in the mountains and forests of Europe*, pp. 57–81. Earthscan Publications, London.
- Overpeck, J.T., Bartlein, P.J. and Webb III, T. (1991) Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science*, **254**, 692–695.
- Overpeck, J.T., Rind, D. and Goldberg, R. (1990) Climate-induced changes in forest disturbance and vegetation. *Nature*, **343**, 51–53.
- Ozenda, P. and Borel, J.-L. (1990) The possible responses of vegetation to a global climatic change—Scenarios for western Europe with special reference to the Alps. *Landscape-ecological impact of climatic change—Proceedings of a European conference* (ed. by Boer, M. & Degroot, R.S.), pp. 221–249. IOS Press, Amsterdam.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.-C., Garcia Moya, E. and Apinan Kamnalrut, Kinyamario, J.I. (1993) Observation and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cycles* **7**, 785–809.
- Pastor, J. and Post, W.M. (1988) Response of northern forests to CO₂-induced climate change. *Nature*, **334**, 55–58.
- Perruchoud, D. and Fischlin, A. (1995) The response of the carbon cycle in undisturbed forest ecosystems to climate change: A review of plant-soil models. *J. Biogeogr.* **22**, 759–774.
- Preisendorfer, R.W. (1988). *Principal component analysis in meteorology and oceanography*, 425 pp. Elsevier, Amsterdam.
- Prentice, I.C., Bartlein, P.J. and Webb III, T. (1991) Vegetation and climate changes in eastern North America since the last glacial maximum. *Ecology*, **72**, 2038–2056.
- Prentice, I.C. and Helmisaari, H. (1991) Silvics of North European trees: compilation, comparisons and implications for forest succession modelling. *For. Ecol. Mgmt.* **42**, 79–93.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore III, B. and Vorosmarty, C.J. (1991) Potential net primary production in South America: application of a global model. *Ecol. Appl.* **1**, 399–429.
- Raich, J.W. and Schlesinger, W.H. (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus—Series B: Chemical and physical meteorology* **44B**, 81–99.
- Rastetter, E.B., Ryan, M.G., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Hobbie, J.E. and Aber, J.D. (1991) A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition. *Tree Physiol.* **9**, 101–126.
- Renner, F. (1982) *Beiträge zur Gletschergeschichte des Gotthardgebietes und dendroklimatologische Analysen an fossilen Hölzern*, 180 pp. Diss. Univ. of Zurich University Zürich, Department of Geography: Zurich.
- Robock, A., Turco, R.P., Harwell, M.A., Ackerman, T.P., Andressen, R., Chang, H.S. and Sivakumar, M.V.K. (1993) Use of general circulation model output in the creation of climate change scenarios for impact analysis. *Clim. Change*, **23**, 293–335.
- Roedel, W. (1992). *Physik unserer Umwelt—Die Atmosphäre*, 457 pp. Springer, Berlin.
- Santer, B.D., Wigley, T.M.L., Schlesinger, M.E. and Mitchell, J.F.B. (1990) *Developing climate scenarios from equilibrium GCM-results*. Report no. 47, Max-Planck-Institut für Meteorologie, Hamburg.
- Schär, C., Frei, C., Lüthi, D. and Davies, H.C. (1996)

- Surrogate climatic change scenarios for regional climate models. *Geophys. Res. Lett.* **23**, 669–672.
- Schär, C.T.D., Frei, C., Wanner, H., Widmann, M., Wild, M. and Davies, H.C. (1997) Current Alpine climate. *Views from the Alps: regional perspectives on climate change* (ed. by P. Cebon, U. Dahinden, H.C. Davies, D. Imboden, and C. Jäger), pp. 16 (in press). MIT Press, Cambridge, Mass.
- Schimel, D.S., Parton, W.J., Kittel, T.F.G., Ojima, D.S. and Cole, C.V. (1990) Grassland biogeochemistry: links to atmospheric processes. *Clim. Change* **17**, 13–25.
- Schüpp, M. (1968) Kalender der Wetter- und Witterungslagen im zentralen Alpengebiet. *Veröffentl. Schweiz. Meteorol. Z. anstalt*, **11**, 1–43.
- Semtner, A.J. (1995) Modeling ocean circulation. *Science* **269**, 1379–1385.
- Shugart, H.H. (1984). *A theory of forest dynamics—The ecological implications of forest succession models*, 278 pp. Springer, New York.
- Shugart, H.H. (1990) Using ecosystem models to assess potential consequences of global climatic change. *Trends Ecol. Evol.* **5**, 303–307.
- Shugart, H.H., Antonovsky, M.Y., Jarvis, P.G. and Sandford, A.P. (1986) CO₂, climatic change, and forest ecosystems. *The greenhouse effect, climatic change, and ecosystems* (ed. by B. Bolin, B.R. Döös, J. Jäger, and R.A. Warrick), pp. 475–522. Wiley, Chichester.
- Shugart, H.H., Leemans, R. and Bonan, G.B. (eds) (1992) *A systems analysis of the global boreal forest*, 565 pp. Cambridge University Press, Cambridge.
- Smith, T.M., Leemans, R. and Shugart, H.H. (1994). *The application of patch models of vegetation dynamics to global change issues—a workshop summary*, pp. 1–22. Kluwer, Dordrecht.
- Smith, T.M., Smith, J.B. and Shugart, H.H. (1992) Modelling the response of terrestrial vegetation to climate change in the tropics. *Tropical forests in transition—ecology of natural and anthropogenic disturbance processes* (ed. by J.G. Goldammer), pp. 253–268. Birkhäuser Verlag, Basel-Boston.
- Solomon, A.M. (1986) Transient response of forests to CO₂-induced climate change: simulation modelling experiments in eastern North America. *Oecologia*, **68**, 567–579.
- Solomon, A.M. (1988) Ecosystem theory required to identify future forest responses to changing CO₂ and climate. *Ecodynamics: contributions to theoretical ecology* (ed. by W. Wolff, C.-J. Soeder, and F.R. Drepper), pp. 258–274. Springer, Berlin.
- Solomon, A.M. and Bartlein, P.J. (1992) Past and future climate change: response by mixed deciduous-coniferous forest ecosystems in northern Michigan. *Can. J. For. Res.* **22**, 1727–1738.
- Solomon, A.M., Delcourt, H.R., West, D.C. and Blasing, T.J. (1980) Testing a simulation model for reconstruction of prehistoric forest-stand dynamics. *Quat. Res.* **14**, 275–293.
- Solomon, A.M. and Webb III, T. (1985) Computer-aided reconstruction of late-quaternary landscape dynamics. *Ann. Rev. Ecol. Syst.* **16**, 63–84.
- Solomon, A.M., West, D.C. and Solomon, J.A. (1981) Simulating the role of climate change and species immigration in forest succession. *Forest succession: concepts and application* (ed. by D.C. West, H.H. Shugart, and D.B. Botkin), pp. 154–177. Springer, New York.
- Taubes, G. (1995) Is a warmer climate wilting the forests of the North? *Science*, **267**, 1595.
- Thoeny, J., Fischlin, A. and Gyalistras, D. (1994) RASS: Towards bridging the gap between interactive and off-line simulation. *CISS—First Joint Conference of International Simulation Societies, August 22–25, 1994; Zurich, Switzerland* (ed. by J. Halin, W. Karplus and R. Rimane), pp. 99–103. The Society for Computer Simulation International, P.O. Box 17900, San Diego.
- Thoeny, J., Fischlin, A. and Gyalistras, D. (1995) *Introducing RASS—the RAMSES simulation server*. 32 pp. Systems Ecology Report No. 21, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology ETH, Zurich.
- Thornthwaite, C.W. and Mather, J.R. (1957) Instructions and tables for computing potential evapotranspiration and the water balance. *Publ. Climatol.* **10**, 183–311.
- von Storch, H. (1995) Inconsistencies at the interface of climate impact studies and global climate research. *Meteorol. Z.* **4**, 72–80.
- von Storch, H., Zorita, E. and Cubasch, U. (1993) Downscaling of global climate change estimates to regional scales: an application to Iberian rainfall in wintertime. *J. Clim.* **6**, 1161–1171.
- Walter, H. and Breckle, S.W. (1983, 1984, 1986, 1991) *Ökologie der Erde, Band 1–4*. Gustav Fischer: Stuttgart.
- Washington, W.M. and Parkinson, C.L. (1986) *An introduction to three-dimensional climate modelling*, 422 pp. Oxford University Press, Oxford.
- Webb III, T. (1992) Past changes in vegetation and climate: lessons for the future. *Global warming and biological diversity* (ed. by R.L. Peters, and T.E. Lovejoy), pp. 59–75. Yale University Press, New Haven.
- West, D.C., Shugart, H.H. and Botkin, D.B. (eds) (1981) *Forest succession: concepts and application*, 517 pp. Springer, New York.
- Woodward, F.I. (1987). *Climate and plant distribution*, 174 pp. Cambridge University Press, Cambridge.
- Wright, H.E.J., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A. and Bartlein, P.J. (eds.) (1993) *Global climates since the last glacial maximum*, 569 pp. University of Minnesota Press, Minneapolis.