

Simulated effects of increasing atmospheric CO₂ and changing climate on the successional characteristics of Alpine forest ecosystems

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Abstract

Possible effects of changing climate and increasing CO₂ on forest stand development were simulated using a forest succession model of the JABOWA/FORET type. The model was previously tested for its ability to generate plausible community patterns for Alpine forest sites ranging from 220 m to 2000 m a.s.l., and from xeric to mesic soil moisture conditions. Each model run covers a period of 1000 yrs and is based on the averaged successional characteristics of 50 forest plots with an individual size of 1/12 ha. These small forest patches serve as basic units to model establishment, growth, and death of individual trees. The simulated CO₂ scenario assumes linear climate change as atmospheric CO₂ concentration increases from 310 $\mu\text{l/l}$ to 620 $\mu\text{l/l}$ and finally to 1340 $\mu\text{l/l}$. Direct effects of increasing CO₂ on tree growth were modeled using tree-ring and growth chamber data. The simulation experiment proved to be a useful tool for evaluating possible vegetation changes that might occur under CO₂-induced warming. On xeric sites from the colline to the high montane belt, the simulated climate change causes drastic soil water losses due to elevated evapotranspiration rates. This translates into a significant biomass decrease and even to a loss of forest on xeric low-elevation sites. Biomass gains can be reported from mesic to intermediate sites between 600 and 2000 m a.s.l. Increasing CO₂ and warming alters the species composition of the simulated communities considerably. In today's montane and subalpine belt an invasion of deciduous tree species can be expected. They outcompete most conifers which in turn may migrate to today's alpine belt. Some of these changes occur as early as 40 yrs after climate begins to change. This corresponds to a mean annual warming of 1.5°C compared with today's mean temperatures.

Introduction

Since the middle of the 19th century global atmospheric CO₂ concentrations are increasing. A gradual increase to 310 $\mu\text{l/l}$ from a preindustrial mean of about 280 $\mu\text{l/l}$ in the mid-19th century was followed by an increase of more than 30 $\mu\text{l/l}$ in atmospheric CO₂ after 1950 (Gammon *et al.* 1985). It is undisputed that the burning of immense amounts of fossil fuels for energy production is the major

reason for this increase. The hypothesized change in the global climatic pattern is expected to alter the successional characteristics of plant communities significantly and cause drastic shifts in the vegetation zonation. General circulation models (GCM's) indicate a global warming of the magnitude of 3" to 4°C with a CO₂ doubling and suggest that the temperature response to be strongly dependent on latitude and season (MacCracken and Luther 1985; Manabe and Stouffer 1980; Wigley and Jones

1988). The poles are more likely to experience greater warming than the equator, and the winter months are expected to show greater warming than the summer months (Manabe and Wetherald 1980). The precipitation projections of GCM models are not in close agreement and the regional patterns vary substantially depending on local orographic conditions. Various authors suggest an increase of 7–11% in the averaged global precipitation rate (MacCracken and Luther 1985).

In addition to the hypothesized climate change, direct effects of increasing CO₂ on the biomass of woody plants are postulated. Numerous experimental studies have shown increased photosynthetic rate, water-use efficiency, and growth caused by elevated CO₂ concentrations (Carlson and Bazaz 1980; Conroy *et al.* 1986; Gates 1985; Kienast and Luxmoore 1988; Kramer 1981; Luxmoore *et al.* 1986). However most studies were conducted for exposure periods shorter than one year, and it is unclear if the observed growth responses can be sustained in the long term (Bjorkman and Pearcy 1983). Long-term exposure experiments will be necessary to address this issue. Since the beginning of the 1980's attempts have been made to detect CO₂-induced changes on plants growing under outside conditions. One of the key indicators utilized has been annual growth represented in tree-ring chronologies (Graybill 1987; Hari *et al.* 1984; Jacoby 1986; LaMarche *et al.* 1984). Up to present only vage relationships between positive growth responses and the historically documented CO₂ increase have been established (Kienast and Luxmoore 1988; Stockton 1984).

In the present study, we attempt to combine the knowledge acquired from forest succession models, GCM models and tree-seedling experiments to simulate potential responses of Alpine forest stands to elevated CO₂ levels and subsequent warming. It is undisputed that these explanatory simulation approaches are simplistic representations of reality. The combination of such systems has a danger of amplifying errors and generating system behaviours which are inaccurate projections of the real world. However, in the absence of empirical data on the long-term responses of vegetation to climate change and increased atmospheric CO₂, this

approach reflects a welcome methodology to generate a set of possible responses that can be used either as hypotheses for further experimental studies or as scenarios for political decision makers. Similar studies were conducted by Shugart and Emanuel (1985) and Solomon (1986) for North American conditions. By using a similar simulation technique, the present modeling experiment aims to generate compatible results for other environmental and phytogeographical conditions.

Methods

Forest stand simulation model

The forest simulator used for the present study is a gap model of the JABOWA/FORÉT type (Shugart and West 1980). It is based on previous models of Botkin *et al.* (1972), Dale and Hemstrom (1984), Shugart and West (1977), and Pastor and Post (1985). A detailed description of the model is given in Kienast (1987) and Kienast and Kuhn (1989). The simulator runs on a basis of 1/12 ha plots, which is equivalent to forest succession models for the Appalachian region of the Eastern United States. Stand development on each forest plot is simulated by calculating establishment, growth, and death of individual trees as a mixture of deterministic and stochastic processes. To obtain forest development on a regional level, the successional patterns of all plots of one run are averaged. This concept is supported by different plant succession studies which show that a forest ecosystem may be described by the average growth dynamics of a multitude of gaps with different successional ages (Bray 1956; Curtis 1959; Forman and Godron 1981; Watt 1947).

Forest succession is driven by extrinsic and intrinsic variables of the species or the stand, respectively. Extrinsic variables to the stand are summer warmth, spring frost, soil moisture, and browsing. Intrinsic variables to the species are maximum potential growth rate and mortality, while shading and crowding are intrinsic variables to the stand. Each model starts with a randomly selected cohort of seedlings in a gap to simulate tree establishment. Unfavorable environmental factors and site condi-

tions control the exclusion of species from the seed pool. Growth of each individual tree is simulated by decreasing the maximum potential growth rate at its respective age by factors that are less than optimum. To do so growth multipliers for each limiting factor are calculated. The growth curve for optimum diameter growth of each species was obtained by fitting a theoretical growth equation to data from yield tables. For details see Kienast (1987). The theoretical growth equation has a logistic form and is based on the assumption that biomass increment in one year is proportional to the amount of sunlight the leaves receive (Botkin *et al.* 1972).

Death of individual trees is determined with a mortality function, that allows only 1% of all trees to reach the maximum physiological age. Also trees are 'killed' if they are growing slower than specified by the user. The individual species data for light, soil moisture requirements, maximum age etc. were derived from silvics books and phytosociological vegetation descriptions (Amann 1954; Bernatzky 1978; Ellenberg 1982; Mitscherlich 1970). The conventional data base to run a JABOWA-type model was not always readily available for European tree species and some input parameters had to be omitted or modified, *i.e.*, minimum and maximum diameter for sprouting, dry days per growing season, and minimum January temperature tolerated. However, the basic input parameters such as maximum diameter, maximum height, maximum age of a species, degree day range, sprouting tendency, and shade tolerance could be provided.

The incorporation of the soil humidity indicator value (Ellenberg 1979) is the major modification of the model compared with previous simulators for eastern forests in North America. This indicator value is a non-measurable number on a scale from 1 (extremely xeric) to 12 (flooded). It is assigned to each species according to its ecophysiological behaviour and is based largely on observations of the botanist in the field. The level of precision is well-suited for the forest simulator FORECE. The fact that a broad spectrum of plants are incorporated in this system makes it an important information source for modeling purposes. However, the indices do not simply express the physiological possibilities of the plant but are rather a mixture between

physiologically possible niches and realized niches. Species competition may alter the values remarkably. These interpretation limits have to be considered for all model runs presented in this paper.

Simulation conditions

In accordance with Solomon and West (1987), Solomon (1986) and Gammon *et al.* (1985), a scenario for elevated CO₂ concentrations (referred to as 'CO₂ scenario') and a control scenario were designed each covering a 1000 yr period. The climatic changes in the CO₂ scenario were derived from GCM runs of Mitchell (1983), Mitchell and Lupton (1984) and Wigley and Jones (1988). During the first 400 yrs both scenarios are identical. CO₂ concentration is assumed to be 310 $\mu\text{l/l}$ which is representative for the early 1950's (Gammon *et al.* 1985). Monthly temperature and precipitation values vary stochastically around the measured long-term mean of the climatological station considered (data on tape, Swiss Meteorological Institute). We simply refer to 'today's climate' to express this climatic pattern. For the control run, climate and CO₂ concentrations are assumed to stay constant for the remaining 600 yrs of the simulation. For the CO₂ scenario, however, carbon dioxide concentrations are assumed to increase linearly to 620 $\mu\text{l/l}$ between 400 and 500 yrs of the simulation. Simultaneously the average temperature for December, January and February rises linearly by 3.5°C. For all other months an increase of 3°C is assigned. Precipitation is assumed to rise by 10% between 400 and 500 yrs and subsequently stays constant. According to Gammon *et al.* (1985) a doubling of atmospheric CO₂ within 100 yrs is quite plausible since the current growth rates ($\sim 1.5 \mu\text{l/l}$ per year) are expected to rise in the next decades with increasing burning of fossil fuels (Hulme *et al.* 1990; Tabalka 1985). Between 500 and 700 yrs CO₂ concentration is assumed to rise to 1340 $\mu\text{l/l}$ which is about four times the CO₂ concentration of the 1980's, while temperatures of the winter months (December, January, February) increase by 4°C, temperatures of the spring months (March, April, May) by 3.5°C, and temperatures of the remaining

months increase by 2.5°C. The scenario for CO₂ doubling is considered realistic if no emission controls are achieved (Hulme *et al.* 1990). The quadrupling of CO₂ and the corresponding climatic warming mark the upper range of potential changes that might occur. However, there is no basis for suggesting when, if ever, this concentration will be reached. It is possible that unknown feedback mechanisms between oceans, CO₂, and temperature will cause the temperature to rise less drastic than assumed or that strict emission controls become effective after clear signs of a warming have been perceived by policy makers.

Direct effects of increasing CO₂ on the photosynthetic rate of woody plants were simulated using empirical data presented by Kienast and Luxmoore (1988). A parameter often used to express the responses of various species to CO₂ enrichment is the biotic growth factor β (Bacastow and Keeling 1973). The productivity (P) of vegetation at a CO₂ concentration C is related to productivity P₀ at a lower CO₂ level (C₀) by the following formula:

$$P/P_0 = 1 + \beta \ln(C/C_0) \quad \text{or} \\ \beta = ((P - P_0)/P_0)/(\ln C - \ln C_0) \quad (1)$$

For more details about the use of the β factor see Kienast and Luxmoore (1988). The β factor is strongly dependent on the species considered. Since only a few experiments have been conducted for Central European species, we simply assigned a β factor of 0.30 to coniferous trees and a value of 0.35 to deciduous trees.

In the model implementation, CO₂ fertilization affects the potential growth rate of each species at a given diameter. To do so maximum growth rate is increased according to formula (2):

$$GMax_C = GMax_{C_0} (1 + \beta \ln(C/C_0)) \quad (2)$$

where GMax_C = maximum growth rate of a given species at a given dbh under elevated CO₂ concentrations
 GMax_{C₀} = maximum growth rate under ambient concentrations (310 μ l/l)
 (all other parameters are explained under formula (1))

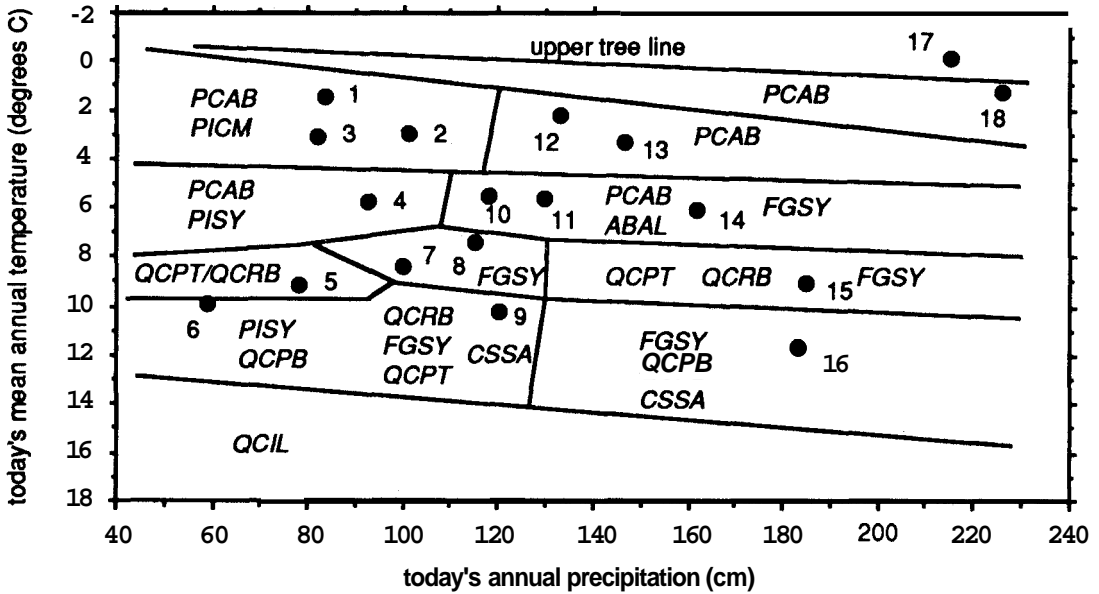
Direct fertilization effects result in an approximately 20% increase of the potential growth rate with CO₂ doubling and a 40–50% increase with CO₂ quadrupling. Compared with other authors (Solomon 1986; Shugart 1984) this potential increase is considered moderate.

Results

The simulation experiment was conducted for 18 climatic stations in the Central part of the Alps, thus generating 36 model runs (18 CO₂ scenarios, 18 control runs). All simulations cover a period of 1000 yrs and are conducted for 50 replicates (plots) each. Stand, species, and tree specific data are provided through time in intervals of five years. Figure 1 compares the climatological conditions of the stations considered. According to Ellenberg (1982) each temperature/precipitation combination is characterized by a typical vegetation pattern with specific tree species dominating the stand under natural conditions. In a previous investigation (Kienast and Kuhn 1989) we showed that the forest model FORECE is reasonably valid for simulating these vegetation communities. Since the model only distinguishes between soils of different water storage capacity, the simulations aggregate forest plots with different soil properties such as acidity or nitrogen supply. Commensurate with the Swiss forest inventory (EAFV 1988) and the map of the potential vegetation of Switzerland (Schmid 1949) the site types simulated are a representative set of stands in terms of site quality and vegetation belt.

Species-specific responses to CO₂-induced warming

The nature of model output is exemplified in Fig. 2 which depicts biomass estimates for the major species on a high montane station in the Swiss Alps. The site has a relatively high amount of precipitation. Under today's climatic conditions and no forest management (control scenario, Fig. 2a) the simulator generates a stand that is dominated by *Picea abies*, *Abies alba* and *Acer pseudoplatanus*.



Climatic stations:

- 1: Bever 2: Davos 3: Saas Fee 4: Montana 5: Basel 6: Sion 7: Bern 8: Langenbruck
 9: Montreux 10: Chaumont 11: Engelberg 12: Arosa 13: Andermatt 14: Airolo
 15: Monte Brè 16: Locarno 17: St. Gotthard 18: Grimsel

Fig. 1. Climatological range of the forest simulations presented in this paper. The meteorological stations used to derive the climatic scenarios are represented with black dots. The position of each dot indicates mean annual temperature and annual precipitation of the corresponding station. The naturally dominating tree species as hypothesized by Ellenberg (1982) are exhibited for each temperature/precipitation combination. Key to the species mnemonics: PCAB (*Piceaabies*); ABAL (*Abiesalba*); PISY (*Pinus sylvestris*); PICM (*Pinus cembra*); FGSY (*Fagussylvatica*); QCRB (*Quercusrobur*); QCPT (*Quercuspetraea*); QCPB (*Quercuspubescens*); QCIL (*Quercus ilex*); CSSA (*Castaneasativa*).

The pioneer stage (0–150 yrs) is characterized by a high percentage of *Populus tremula* and *Betula pendula* with an increasing importance of *Picea abies*. At a stand age of ca. 250 yrs the canopy of the average forest plot is almost entirely dominated by *Picea abies* with an understory of *Abies alba*. The *Picea* canopy starts to break up at a stand age of 400 yrs and *Abies alba* and *Acer* begin to outgrow *Picea abies*.

Under warming and increased CO₂ concentrations model output differs significantly from the control at a stand age of > 485 yrs (t-test for independent samples). At the 95% significance level the first species to show significantly positive biomass changes is *Fagus sylvatica* (starting at yr 485), followed quickly by *Acerplatanoides* (starting at yr 490), *Carpinus betulus* (starting at yr 510), *Tilia*

platyphyllos (starting at yr 520), and *Ulmus glabra* (starting at yr 550). Biomass of *Picea abies* is drastically reduced after 545 yrs and the species is finally eliminated at 560 yrs due to the competitive advantage of deciduous species under increasing degree day sums. *Abies alba* tolerates the invasion of deciduous trees and even increases its biomass. The last species to show significant biomass increases under CO₂-induced climate change is *Castanea sativa* (starting at yr 725). However the climate and CO₂-induced gain in biomass cannot be sustained, and at a stand age of 940 yrs biomass of the CO₂ scenario is no longer statistically different from the control. The same phenomenon can be reported for *Ulmus glabra* and *Abies alba*. Growth gains due to elevated temperature and CO₂ concentrations cease at a stand age of 895 yrs (*Ulmus glabra*) and

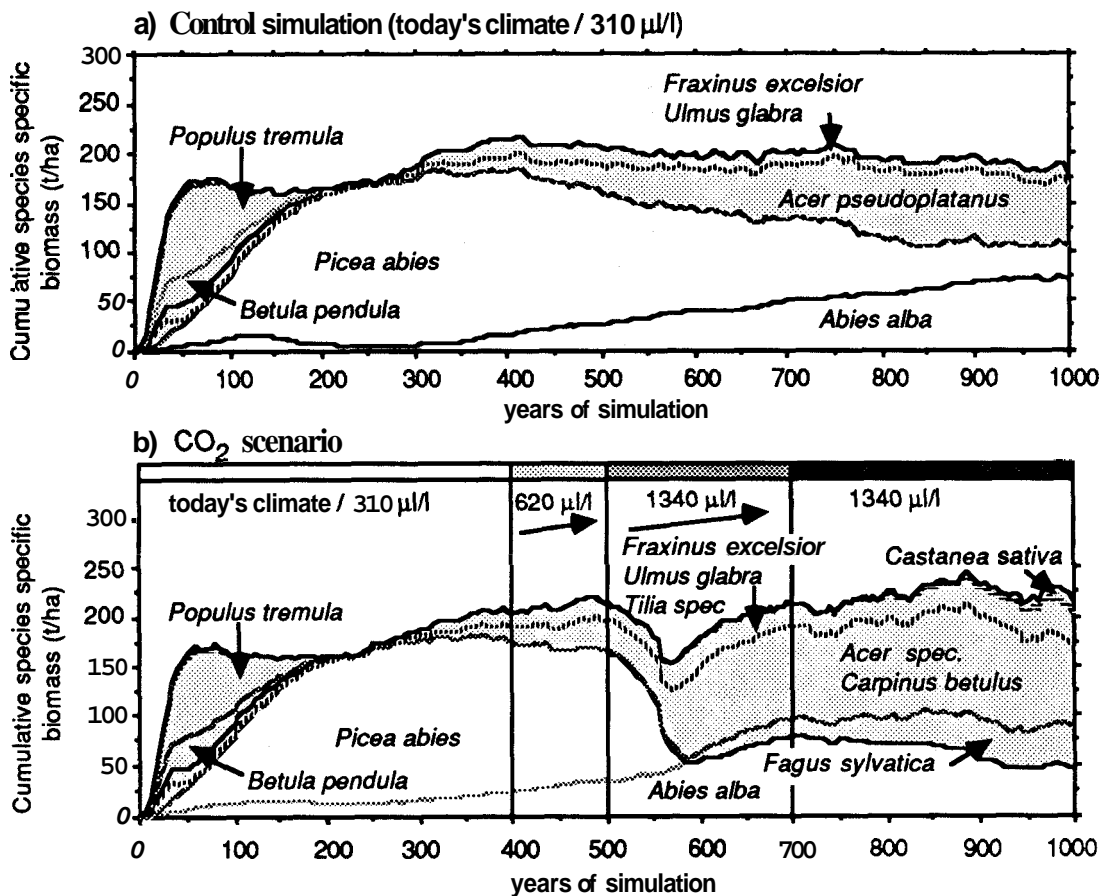


Fig. 2. Averaged simulated responses of 50 high montane forest plots to elevated CO₂ concentrations and climatic change (climatic station Airolo, 1149 m). The lower graph (Fig. 2b) represents biomass estimates for the most important species for the CO₂ scenario whereas the upper graph (Fig. 2a) exhibits simulated data for the control run with today's conditions. Available soil water content is 100mm and the Ellenberg indicator index for soil moisture is 6 (relatively moist). Each species biomass in any particular year is represented by the vertical distance between two neighbouring curves. Biomass was calculated yearly and recorded in 5-yr intervals.

755 yrs (*Abies alba*), respectively. Total biomass of this site is significantly higher starting at a stand age of 770 yrs.

The simulation of a colline forest on xeric soils under control conditions (Fig. 3a) generates a *Pinus sylvestris* – *Quercus pubescens* forest, consistent with field studies of Burnand (1976), Schmid (1949), and Stein (1978). The ecological importance of *Quercus pubescens*, however is underestimated by the model if biomass alone is considered. Owing to the fact that the modeled species has a low maximum height, it is restricted to the understory. Thus, the simulated biomass might be low despite the important ecological role of this species. The height distribution through time confirms that *Quercus*

pubescens is the most important species in the understory. Under the CO₂ scenario (Fig. 3b) significant changes in biomass start as early as 40 years after carbon dioxide levels are assumed to rise. This is equivalent to a 1.5°C warming or to a CO₂ level of 440 $\mu\text{l/l}$. The dieback of *Pinus sylvestris* is followed by a short dominance of *Quercus petraea*. Starting at a stand age of 560 yrs (warming ca. 4.5°C) *Quercus petraea* is consistently losing importance until a complete destruction of the forest community takes place and a steppe-like vegetation dominates the stands around 700 yrs. These changes are mainly caused by increasing water stress due to CO₂-induced higher temperatures. Moisture stress first reduces the potential growth

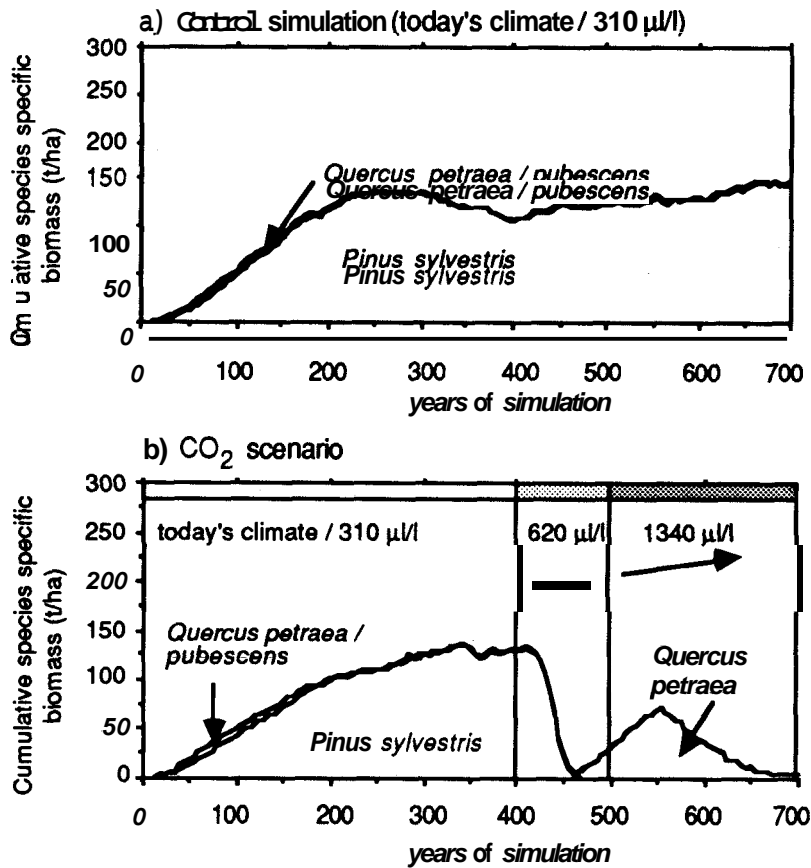


Fig. 3. Averaged simulated responses of 50 colline forest plots to elevated CO₂ concentrations and climate change (climatic station Sion, 542 m). The lower graph (Fig. 3b) represents biomass estimates for the most important species for the CO₂ scenario whereas the upper graph (Fig. 3a) exhibits simulated data for the control run with today's conditions. Available soil water content is 140 mm and the Ellenberg indicator index for soil moisture is 3 (xeric). Each species biomass in any particular year is represented by the vertical distance between two neighbouring curves. Biomass was calculated yearly and recorded in 5-yr intervals.

rate of *Pinus sylvestris* and confers competitive advantages to smaller and slower growing *Quercus* species. The successional replacement is rather abrupt and characterized by a striking biomass depression between the pine and the oak period. It is obvious that the quick dieback of mature *Pinus sylvestris* trees could not be compensated for by the ingrowth of *Quercus*.

The simulation represented in Fig. 4 explores responses that may occur on a site above today's upper timberline in an area with high precipitation. It is clear from fossil tree samples that the upper timberline in this region was once located significantly higher and may have reached an altitude of 2060 m at least in the postglacial period (Renner

1982). Climatic changes as well as disturbances by humans have lowered the tree line considerably. It is a question of speculation whether this process is reversible and which time lag might occur due to today's soil degradation. The run presented in Fig. 4 assumes ingrowth of trees as soon as the number of degree days is above the critical value for a species. No forest is simulated during the first 400 yrs with today's climatic conditions. Twenty years after temperatures are assumed to rise *Pinus cembra* and *Alnus viridis* colonize the plot and build an open-canopy forest with a relatively low leaf area index (< 5). As warming continues *Pinus cembra* reaches its optimum growth and then is soon outcompeted by *Picea abies* which is able to invade the plot. The

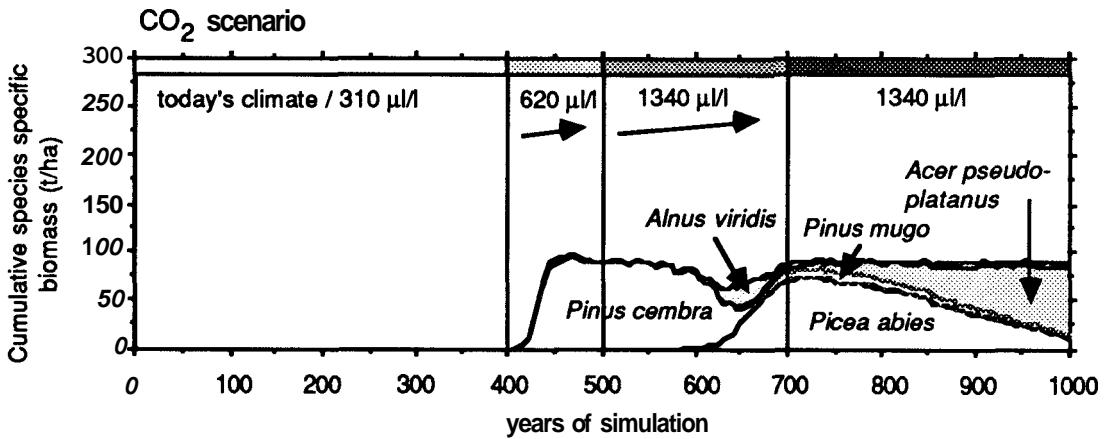


Fig. 4. Averaged simulated responses of 50 plots in the present alpine vegetation belt to elevated CO_2 concentrations and climate change (climatic station St. Gotthard, 2090 m). The graph represents biomass estimates for the most important species for the CO_2 scenario. The control run with today's conditions exhibits no forest growth. Available soil water content is 100mm and the Ellenberg indicator index for soil moisture is 6 (relatively moist). Each species biomass in any particular year is represented by the vertical distance between two neighbouring curves. Biomass was calculated yearly and recorded in 5-yr intervals.

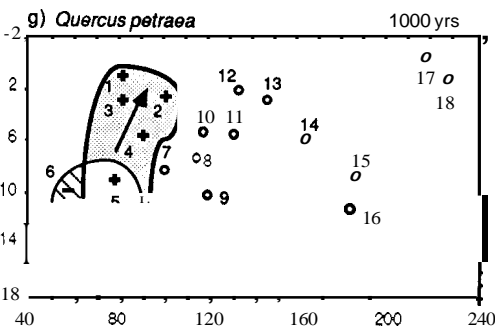
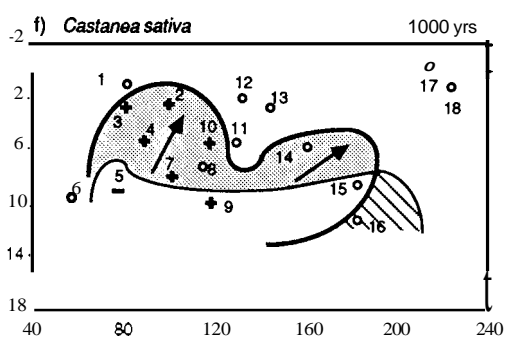
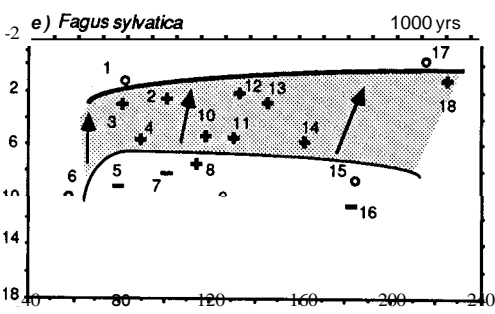
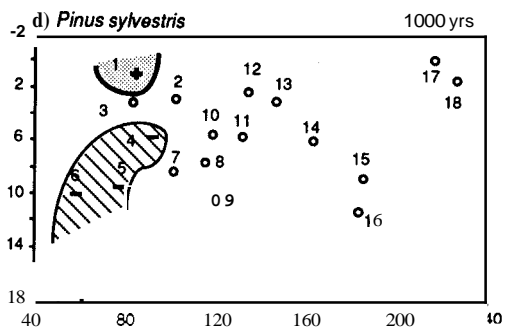
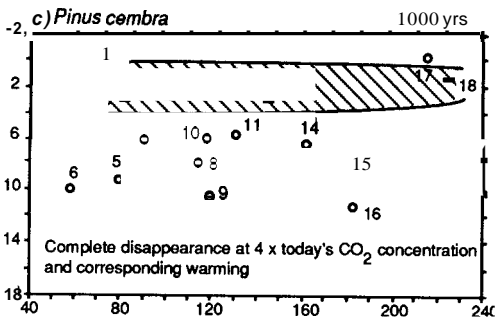
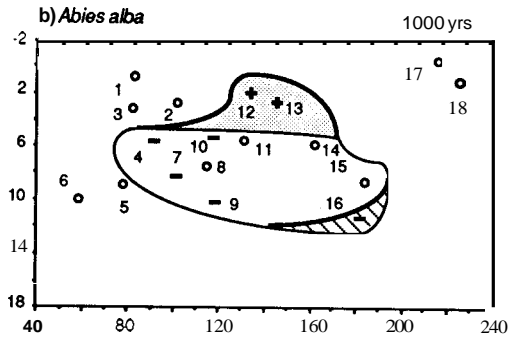
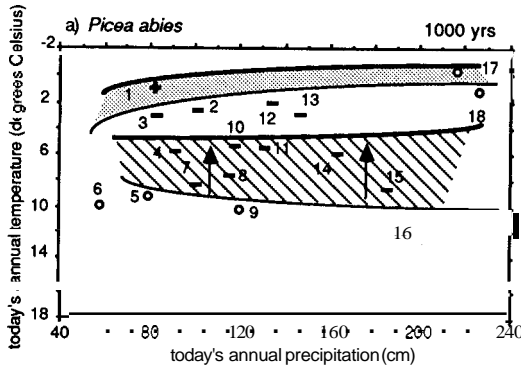
gaps caused by the dieback of *Pinus cembra* are immediately colonized by *Alnus viridis*, a typical pioneer species. The *Picea abies* communities, however, are transformed into maple-dominated stands as climate stabilizes at the CO_2 level of 1340 $\mu\text{l/l}$.

On the species level the most obvious changes in community patterns are caused by invasion of relatively fast growing warm-temperate species on montane, high montane and subalpine sites. This in turn alters the competitive interactions among the individuals that are well adapted to today's cold climate regime and causes certain species to be out-competed. The resulting migration pattern is best illustrated in Fig. 5. *Picea abies* biomass drastically decreases on all montane, high montane and subalpine stations (Fig. 5a). Sites with an annual temperature of more than 5°C (today's conditions) completely lose this species. This translates into an elevational shift of the lower distribution limit of 300 to 1000m depending on the amount of precipitation. The upper limit of the *Picea abies* distribution extends into today's alpine and even into the subnival belt. Here *Picea abies* is able to maintain

an important role as a tree line species even at a warming that corresponds to a $4\times$ today's CO_2 concentration.

The limit of distribution for *Abies alba* (Fig. 5b) does not experience the same drastic shifts as simulated for *Picea abies*. In the montane and high montane regions biomass is consistently reduced but in contrast to *Picea abies*, simulated *Abies alba* still continues growth. On subalpine stations (*i.e.*, Andermatt and Arosa) the CO_2 -induced temperature increase is sufficient to allow *Abies alba* to invade the plots successfully. It seems that *Abies alba* is able to coexist with *Fagus sylvatica* and other invading species which is consistent with observations under today's conditions (Moor, 1952). *Pinus cembra*, a high elevation tree, disappears from the stands considered (Fig. 5c). The dieback occurs as soon as the sum of degree days reaches the limit of 800°C . Below this limit *Pinus cembra* is able to dominate the stand. Another conifer tree whose range is drastically diminished is *Pinus sylvestris* (Fig. 5d). On all xeric sites in the colline, submontane and montane belt its biomass is significantly reduced due to high water stress.

Fig. 5. Simulated limits of distribution for selected species under the CO_2 scenario and the control run. The curves were derived by recording presence or absence of a given species at the site simulated. The reference year is 1000. All sites with significant biomass differences between CO_2 - and control run are set off graphically (t-test, 95% significance level).



Ecological range of species participating in the model:

- Range under increased temperature (CO₂ concentration 1340 μl/l and stabilized climate)
- Range of control simulation (today's climate 1310 μl/l)
- ▨ Increased range under warming
- ▩ Reduced range under warming

Identification of simulated sites:

- | | | |
|-------------|----------------|------------------|
| 1: Bever | 7: Bern | 13: Anderman |
| 2: Davos | 8: Langenbruck | 14: Airolo |
| 3: Saas-Fee | 9: Montreux | 15: Monte Brè |
| 4: Montana | 10: Chaumont | 16: Locarno |
| 5: Basel | 11: Engelberg | 17: St. Gotthard |
| 6: Sion | 12: Arosa | 18: Grimsel |

- + Biomass of CO₂ scenario significantly higher than control simulation
- o Biomass of CO₂ scenario not significantly different from control simulation
- Biomass of CO₂ scenario significantly lower than control simulation

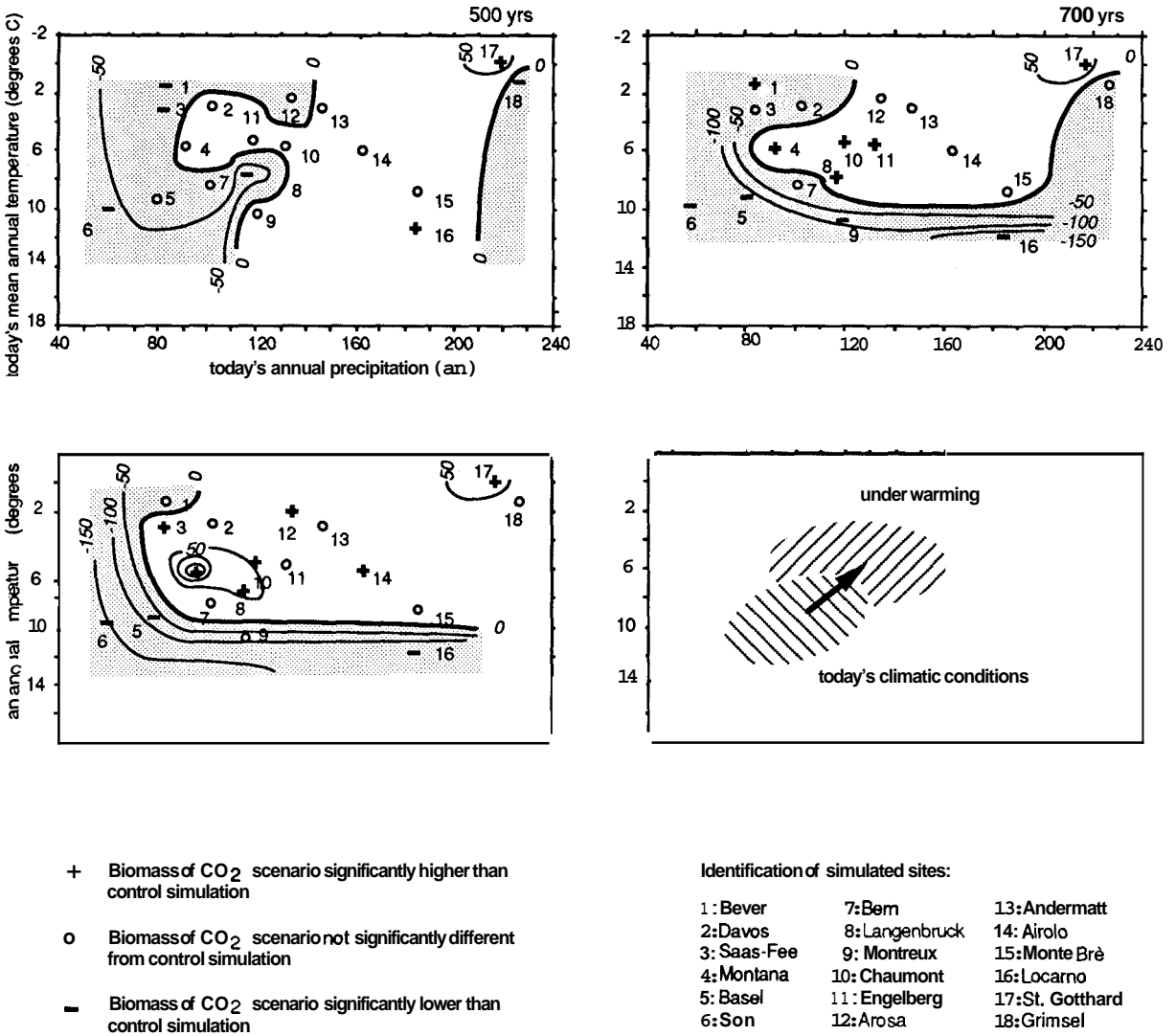


Fig. 6. Responses of total standing biomass to CO₂-induced climate change. The isolines indicate biomass gains or losses for 3 different years of the simulation (500 yrs = 620 μl/l; 700 yrs = 1340 μl/l, 1000 yrs = 1340 μl/l and climate stabilized since 300 yrs). Significant biomass differences between the CO₂ scenario and the control are set off graphically.

Almost all deciduous species are able to expand their ecological range into today's montane, high montane and subalpine zone. This can be illustrated with the geographical limit of *Fagus sylvatica* which is extended into the subalpine belt (Fig. 5e). The pattern of *Fagus sylvatica* is equivalent to *Tilia plutyphyllus*, *Carpinus betulus*, *Acer platanoides*, and *Fraxinus excelsior*. *Castanea sativa* on the other hand has a completely different migration pattern in that the upper limit of distribution does not expand into today's cool, moist regions (Fig.

5f). Finally *Quercus petraea* and *Tilia cordata* (Fig. 5g) expand to sites of today's high montane and subalpine belt with xeric soil moisture conditions.

Impacts of CO₂-induced climate change on the whole stand level

If we consider forests to be pools of fixed carbon, the simulated changes of biomass under the CO₂ scenario may indicate potential carbon sinks or

sources. Averaged over all stations simulated the biomass loss for a temperature rise of approximately 3°C (500 yrs or 2x today's CO₂ concentration) is 4 t/ha whereas the loss for a CO₂-induced climate change of approximately +7°C (700 yrs or 4x today's CO₂ concentration) is 13 t/ha. After climatic stabilization (1000 yrs) the overall biomass decrease reduces to 9 t/ha. Compared with today's total standing biomass that ranges between 100 and 180 t/ha depending on the site considered, these losses are fairly small and on the average not significant. However, carbon sinks and losses are not evenly distributed over the whole spectrum of sites as illustrated in Fig. 6. The graph shows the individual changes in the carbon pool for all sites considered. Three years of the simulation have been selected *i.e.*, yrs 500, 700 and 1000. With the climatic change of a CO₂ doubling (500 yrs) the subalpine station Grimsel (No. 18) as well as xeric and intermediate sites at low and high altitudes experience significant biomass losses. All other stations show positive changes between the CO₂ scenario and the control run, although only two differences are significant at the 95% significance level. The described pattern gets more pronounced at 700 yrs with increased warming. Carbon losses are increasing with values up to 180 t/ha. Carbon gains are still of the same magnitude as calculated for a stand age of 500 yrs but the number of statistically significant changes is increasing. At a stand age of 1000 yrs with stabilized climate, all stations with an annual average temperature > 10°C (today's values) and an annual precipitation rate > 80 cm are carbon sinks. The remaining locations experience biomass losses up to 150 t/ha. It seems that today's economically most productive forestry zones are moved into higher and wetter zones due to increased evapotranspiration rates and subsequent drought periods. On today's most productive sites (Basel, Bern, Langenbruck, Montreux, Chaumont, Monte Brè, Locarno) a loss of 50 t/ha is reported for a 4x today's CO₂ concentration. With stabilized climate conditions at the 4x CO₂ level these forest communities seem to adapt to the new conditions with biomass losses of only 10 t/ha compared with the control scenario. The new most productive zones increase their biomass by 6 t/ha with

doubling CO₂, by 15 t/ha with quadrupling CO₂ and by 50 t/ha with stabilized high temperatures. These 50 t/ha translate into a 30% increase of the total standing biomass on these sites.

Discussion and conclusions

The simulation experiment revealed a set of possible responses of forest communities to elevated CO₂ concentrations. It's clear that the results do not represent reality but merely a model behaviour that is a simplified representation of real processes. Several limitations of the model have to be considered before drawing any conclusions. Effects of temperature and precipitation on plant growth seem to be modeled adequately. Problems might occur on very dry, steppe-like soils, under flooded conditions, and for the Krummholz belt (Holtmeier 1980). Here it might be questionable to use input parameters for tree physiology and physiognomy that were derived mainly on intermediate sites in the submontane belt. Incorporation of site specific growth data would indeed improve the model estimates. However, in order to keep the model as simple as possible, and to avoid an excessive number of 'a priori decisions' no site specific input data have been used. This may lead to an overestimation of biomass and leaf area index on extreme sites but is compensated for by clearer data handling and data interpretation.

The model assumes that the growth responses obtained from short term seedling experiments (direct effects of increasing CO₂ on the photosynthetic rate) are applicable to adult trees and can be sustained in the long term. This assumption remains highly questionable as shown by Kienast and Luxmoore (1988) and Ozenda and Borel (1990). However, in the absence of experimental data and to define an upper limit of response, the assumptions are justified but are no more than crucial estimates of reality. Since the model only distinguishes between soils of different water storage capacity, it is unable to project any responses that are related to soil properties such as acidity or nitrogen supply. As shown by Conroy *et al.* (1986) and Luxmoore *et al.* (1986) nutrient availability might significantly

alter the receptiveness of species to elevated CO₂ concentrations. Another factor that has not been modeled in the present simulations is the influence of pollutants like NO_x, SO_x, and ozone. It can be assumed that the incorporation of potentially damaging agents might lead to a more rapid die-back of sensitive species (Dale and Gardner 1987; McLaughlin and Braker 1985).

The model discussed in this paper assumes immediate recruitment of tree individuals on a plot as soon as the climatic conditions allow photosynthesis of the corresponding species. This simple assumption does not take into account time lags that might occur as a result of soil degradation, unfavorable seedbed conditions, lack of seeds, or slow migration rates. Hence, it is very likely that in reality it takes much longer for plants to get established than simulated by the model. If the simulated altitudinal migration patterns are analyzed for migration rates we find values between 3 and 10 altitudinal meters/yr for *Fagus sylvatica*. Although seeds would not have to travel far horizontally the altitudinal shift is faster than ever experienced during the Holocene.

In the present model, natural ecosystems are subjected to CO₂-induced warming although undisturbed ecosystems can hardly be found in Central Europe. However, since type and frequency of historic management influences are extremely difficult to simulate we decided to ignore any influences of forest management. It is suggested by several authors (Fliihler 1981, Solomon 1986) that natural forest ecosystems are more likely to exhibit responses to human induced changes than are strongly manipulated plantations. Thus, the present simulations might reveal a sensitivity that will never be accomplished by strongly sculptured forest ecosystems. On the other hand we might see increased adaptation of forestry techniques to new climatic conditions and thus an accelerated speed of species migration.

Even under the interpretation limits described above the present modeling experiment is a useful tool to identify forest communities and tree species of the Alpine region that are most sensitive to a CO₂-induced climate change. In conclusion the following inferences can be drawn:

1. The migration patterns that were derived from the 36 model runs suggest invasion of deciduous trees into today's montane and subalpine belt. A major consequence of this shift is the reduction of the altitudinal range of spruce. The elevational shift however does not affect entire plant communities. Instead each species has its own migration pattern which results in new, unknown transition communities. The latter will, if ever, transform into equilibrium communities. As suggested by Ozenda and Borel (1990) species with a broad ecological range and high capacity of regeneration (*i.e.*, *Fagus*) are most successful migrators that outcompete highly specialized individuals (*i.e.*, *Pinus cembra*). The latter often die out due to a lack of suitable habitat niches.

2. Under increased warming and favorable seedbed conditions areas in today's alpine belt will be colonized by conifers. This in turn would enlarge the Krummholz belt and add a maximum of 10% to the actual forested area of Switzerland. This gain will partially be compensated for by the expected loss of forested area on xeric sites due to steppification. According to the model output and information on the actual and potential distribution of xeric forests in intra alpine valleys (Burnand, 1976) we estimate that with a CO₂-induced warming of 3.5" to 6°C (annual mean) a maximum of **7.5%** of the actual forested area in intra alpine dry valleys is subject to a steppification. This result does not take into account invasion and replacement of today's xeric forests by drought tolerant mediterranean species.

3. The model experiment suggests that some of these changes occur as early as 40 yrs after climate is expected to change. This translates into a critical increase of the mean annual temperature of 1.5°C compared with today's average. This value is of the same magnitude as reported for the little ice age cooling (Grove 1988).

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