GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Will the CO$_2$ fertilization effect in forests be offset by reduced tree longevity?

Harald Bugmann · Christof Bigler

Abstract Experimental studies suggest that tree growth is stimulated in a greenhouse atmosphere, leading to faster carbon accumulation (i.e., a higher rate of gap filling). However, higher growth may be coupled with reduced longevity, thus leading to faster carbon release (i.e., a higher rate of gap creation). The net effect of these two counteracting processes is not known. We quantify this net effect on aboveground carbon stocks using a novel combination of data sets and modeling. Data on maximum growth rate and maximum longevity of 141 temperate tree species are used to derive a relationship between growth stimulation and changes in longevity. We employ this relationship to modify the respective parameter values of tree species in a forest succession model and study aboveground biomass in a factorial design of growth stimulation × reduced maximum longevity at multiple sites along a climate gradient from the cold to the dry treeline. The results show that (1) any growth stimulation at the tree level leads to a disproportionately small increase of stand biomass due to negative feedback effects, even in the absence of reduced longevity; (2) a reduction of tree longevity tends to offset the growth-related biomass increase; at the most likely value of reduced longevity, the net effect is very close to zero in most multi- and single-

species simulations; and (3) when averaging the response across all sites to mimic a "landscape-level" response, the net effect is close to zero. Thus, it is important to consider ecophysiological responses with their linkage to demographic processes in forest trees if one wishes to avoid erroneous inference at the ecosystem level. We conclude that any CO$_2$ fertilization effect is quite likely to be offset by an associated reduction in the longevity of forest trees, thus strongly reducing the carbon mitigation potential of temperate forests.

Keywords Carbon storage · Climate change mitigation · Growth stimulation · Succession model · ForClim

Communicated by Christian Wirth.

H. Bugmann (✉)
Laboratory of Tree-Ring Research, University of Arizona,
Tucson, AZ 85721, USA
e-mail: harald.bugmann@env.ethz.ch

H. Bugmann · C. Bigler
Forest Ecology, Department of Environmental Sciences,
Institute of Terrestrial Ecosystems, ETH Zurich, 8092 Zurich,
Switzerland

Introduction

The impact of enhanced atmospheric CO$_2$ fertilization on the carbon storage of the biosphere is of the utmost importance because of a possible negative feedback to the global climate (Friedlingstein et al. 2006). However, due to experimental constraints, it is difficult to ascertain this effect in the long term and to disentangle its various components (cf. Körner 2006). This is particularly true for the case of forests, which harbor a disproportionately large fraction of the carbon of the terrestrial biosphere (cf. Norby et al. 1999). At sufficiently large spatial scales, ecosystems are in dynamic equilibrium with their environment; the spatial scale at which this occurs depends largely on the disturbance regime (Shugart 1998). Aboveground biomass at such large scales (referred to as the "landscape scale" below) depends critically on two counteracting processes, namely the rate of gap filling vs. the rate of gap creation (cf. Körner 2004).

In a large number of experiments, CO$_2$ fertilization has been found to increase the rate of gap filling by enhancing

biomass accumulation in young stands (e.g., Norby et al. 1999). Although the fertilization effect may last for an extended time (cf. Norby et al. 2005; Moore et al. 2006), there is increasing agreement that CO_2 effects are smaller at later stages of stand development, i.e., when canopy size and leaf area index have reached steady-state values (cf. review by Körner 2006). In natural forests, CO_2 fertilization rates with regard to biomass increment are likely to vary between a few and perhaps up to 30 or even 40%, with a strong attenuation over time such that peak values are typically maintained for a few years only.

Regarding gap creation, much effort has been focused recently on indirect CO_2 effects via lianas that grow in deep shade and are likely to become more vigorous in a high-CO_2 atmosphere, both in tropical (Philips and Gentry 1994; Granados and Körner 2002; Wright et al. 2004) and temperate forests (Zotz et al. 2006), thus potentially enhancing tree mortality. While increased liana vigor is documented well, the link to increased gap creation rates is still under debate (cf. Philips et al. 2004).

There is a possible direct link between CO_2-enhanced growth rates and plant longevity, however. It is known from agricultural CO_2 fertilization studies that plant longevity tends to decrease under high-CO_2 conditions, i.e., crop maturation is accomplished earlier such that plants senesce and die prematurely compared to control conditions (e.g., Kimball et al. 1995). However, these results cannot be extrapolated readily to forest trees. Backman (1943) published a mathematical treatise on growth rates and longevity of forest trees that provided the theoretical underpinning for the widely observed phenomenon that early successional tree species, which feature high maximum growth rates, are typically short-lived, whereas slow-growing, late-successional species tend to reach high ages (cf. Kimmins 2004; Loehle 1988; Waring 1987; Botkin et al. 1972).

In an intra-specific context, Backman's (1943) arguments apply as well: although fast-growing tree individuals benefit from a higher competitive ability, they are subject to trade-offs with, for example, reduced investment in defenses and a lower mechanical strength of the wood (cf. Arendt 1997; Schulman 1954; Jenkins and Pallardy 1995), thus reducing their life expectancy. For obvious reasons, no direct experimental measurements of tree longevity under elevated CO_2 are available. It is possible that trees would use the extra carbon that becomes available via CO_2 fertilization not only for enhancing growth rates, but also for enhanced investment in defenses, such that their longevity would not decrease. Gayler et al. (2008) suggested that in nutrient-limited environments (such as in most terrestrial ecosystems), investment of carbon into defense is not favored, such that most of the extra carbon would be used for growth. Several CO_2 enhancement experiments

confirmed this expectation for both deciduous (e.g., Luo et al. 2008) and coniferous (e.g., Litvak et al. 2002) trees, whereas Lavola and Julkunen-Tiitto (1994) found a slightly increased investment in defenses. Thus, it appears reasonable to assume that enhanced carbon supply via CO_2 fertilization would be invested mostly into enhanced growth rather than defense.

In addition, there is circumstantial evidence for a speeding up of tree life cycles under enhanced carbon supply, e.g., earlier cone production found in the Duke FACE experiment (Ladeau and Clark 2006). Also, there is recent empirical evidence from several species of the Colorado Rocky Mountains and the Swiss Alps that high growth rates early in tree life are associated with lower individual longevity (Bigler and Veblen 2009). However, data for the full range of species dominating forests in any particular area are lacking, and we are thus missing a critical piece of the puzzle for determining the overall effect of CO_2 fertilization on aboveground carbon storage in forests.

Here, we use information on the interspecific growth–longevity relationship across a broad range of tree species from temperate and boreal forests on three continents to derive scenarios of the intraspecific growth–mortality relationship. In combination with literature-based scenario data for the likely range of the CO_2 fertilization effect on biomass increment, these growth–longevity relationships are used to simulate changes in landscape-scale biomass storage using a forest succession model.

Key questions in this context are:

1. Is it possible to derive a generalized relationship between growth stimulation and the reduction of longevity, or are these patterns region-specific?
2. How large is the effect of reduced longevity under enhanced atmospheric CO_2 fertilization relative to the growth stimulation? Would forests feature more or less aboveground biomass compared to ambient atmospheric conditions?
3. Do multispecies forests differ in their behavior from single-species forests?

Materials and methods

Data on maximum growth rate and longevity

In forest succession models that are based on the gap dynamics paradigm (Botkin et al. 1972; Shugart 1984), the life history strategies of tree species are captured via sets of parameters that are either species specific (e.g., longevity or maximum diameter increment rate) or relate to functional groups (e.g., shade tolerance). Over the past

Table 1 Sources of species-specific data for 141 tree species of the temperate zone

Region	Species number	Maximum growth rate	Maximum longevity	Reference
Europe	30	F. Kienast	H. Bugmann	Bugmann (1996)
Eastern N America	72	H. Bugmann	A. Solomon	Bugmann and Solomon (1995)
Pacific Northwest of US[a]	20	A. Solomon	H. Bugmann	Bugmann and Solomon (2000)
Northeastern China	19	X. Yan	X. Yan	Shao et al. (2001)

[a] This dataset currently contains the major tree species of the states of Oregon and Washington only

15 years, we have compiled such data for 141 tree species of temperate forests in central Europe, North America, and northeastern China (cf. Table 1) based on collaborations with scientists from the respective regions.

This compilation was used to explore the relationship between the maximum species-specific growth rate parameter (commonly denoted G, cf. Botkin et al. 1972; Bugmann 2001a) and the maximum species-specific longevity parameter (commonly denoted A_{max}). We did this on a per-region basis for the species of that region using regression analysis in the open source statistics software R 2.8.0 (R Development Core Team 2008).

Forest model

To derive the implications of species-specific changes in growth rates and maximum longevities for stand-scale biomass levels, the forest succession model ForClim v.2.9.1 (Bugmann and Solomon 2000) was used. ForClim was developed for simulations over a wide range of environmental conditions without the need for any "parameter tuning." The model is based on a minimum number of ecological assumptions, among others to reduce parameter requirements (cf. Bugmann 1996).

Following the standard approach of gap models (Botkin et al. 1972), ForClim simulates the establishment, growth, and mortality of trees on multiple forest patches (size ca. 1/12 ha per patch) to derive stand properties at a spatial extent of ca. 15–20 ha by averaging the properties simulated at the patch scale (cf. Bormann and Likens 1979; Shugart 1984; Bugmann 2001a).

Trees are established with a diameter at breast height of 1.27 cm as a function of species-specific responses to winter temperature, light availability at the forest floor, growing degree-days and browsing pressure (Bugmann 1994).

Growth (i.e., stem diameter increment at breast height) is modeled using an empirical growth equation (cf. Moore 1989). In a similar manner to tree establishment, growth is regulated by growing degree-days and light availability, and additionally by soil moisture and nitrogen status. Most of these factors depend on the abiotic environment, which is represented by the mean monthly temperatures and the monthly precipitation sums, as well as soil water holding capacity and nitrogen availability. Trees grow as a function of species-specific constraints such as maximum growth rate (G) and maximum tree height. From diameter at breast height, the sizes of other compartments (e.g., foliage or roots) as well as total aboveground biomass are estimated using allometric equations (Bugmann 1994). Hence, a stimulation of diameter growth by increased atmospheric CO_2 concentration is equivalent to a stimulation of biomass increase in this type of model. An enhancement of growth at the individual tree level leads to a higher leaf area, which increases shading, thus providing a negative feedback that determines overall stand density, biomass and leaf area at the stand level. There is no a priori constraint on either stand density, biomass or leaf area that the model could achieve, but this is an emergent property of the simulated population dynamics.

Tree mortality has a longevity-related and a growth-related component. The longevity-related component depends on maximum longevity (A_{max}) as prescribed by a species-specific parameter. A negative exponential survivorship curve is assumed (cf. Harcombe 1987), i.e., the longevity-related mortality probability is constant across tree life. Hence, reduced longevity (as expected under enhanced CO_2 concentrations) increases this annual mortality probability. The growth-related mortality component is an integral proxy for stress conditions (Bigler and Bugmann 2003). Specifically, series of years with low diameter increments (induced by unfavorable abiotic conditions or competition) lead to an enhanced mortality probability. Hence, increased growth rates (as expected under enhanced CO_2 concentrations) reduce this annual mortality probability.

A comprehensive description of the concept, the design and the details of the ForClim model can be found in Bugmann (1996, v.2.4), Bugmann and Cramer (1998, v.2.6) and Bugmann and Solomon (2000, v.2.9.1).

ForClim has evolved from a simulator of forests in the Swiss Alps to a general model that is applicable to temperate forests of central Europe (Bugmann and Cramer 1998), eastern North America (Bugmann and Solomon 1995), the Pacific Northwest of the US (Bugmann and Solomon 2000), northeastern China (Shao et al. 2001) and

the Colorado Front Range of the Rocky Mountains (Bugmann 2001b). ForClim is not based on a hybrid approach between physiology-based modules for plant growth (which would feature a "mechanistic" treatment of photosynthesis and respiration) and a more traditional approach for handling tree demography (e.g., Friend et al. 1997; Lexer et al. 2001). This, however, does not limit its applicability under changing environmental conditions (cf. Reynolds et al. 2001). As a matter of fact, to our knowledge ForClim is the only forest succession model that has been demonstrated to be applicable "out of the box" (i.e., without any re-parameterization) across widely different climates while still keeping a species resolution.

Simulation experiments

A factorial design was employed to study the response of forest biomass to changes in the maximum growth rate parameter and maximum tree longevity. Based on a literature survey regarding the stimulation of tree biomass increment by enhanced CO_2 (typically, a doubling of pre-industrial conditions, i.e., 560 ppm), three levels of growth increase (+10, +20, and +30%) were selected. These changes were combined with five levels of maximum longevity (see the "Results" section), thus yielding 15 simulation experiments per site. Six sites along a large climatic gradient from the upper (cold-wet) to the lower (warm-dry) treeline in central Europe were used, giving a total of 90 simulation experiments. Simulations were always run under current climatic conditions (cf. Table 2), with modified G and A_{max} parameters being held constant during any individual simulation experiment.

Our analyses focused on the equilibrium species composition of the model, which was calculated using the approach described by Bugmann (1997) by sampling from the stochastic simulation results over a sufficiently long period in intervals that minimize the autocorrelation of the samples. Although transient dynamics under rising CO_2 levels could be simulated easily by the model, we decided to focus on the equilibrium (steady-state) response here because we deemed

transient simulations to be too speculative, and because we primarily wished to evaluate the overall sensitivity of forest stands to changes in process rates rather than to make precise "predictions" of their behavior over the coming decades (cf. Bugmann 2003). Thus, we compared forest properties under standard CO_2 concentrations (ca. 350 ppm) with a range of enhanced CO_2 situations.

To quantify the differences between the control run (default G and A_{max} values) and the other simulation experiments, relative changes in total aboveground biomass were calculated and displayed as contour plots using the R software. Biodiversity effects (i.e., changes in tree species composition) as a consequence of the changes in G and A_{max} were evaluated statistically using the percentage similarity coefficient described by Bugmann (1997).

Simulations were run in two different modes: first by allowing the establishment of all 30 central European tree species included in the model (multispecies simulations; cf. Table 1), to mimic "natural" forest dynamics; and second by allowing the establishment of the most dominant timber species only (single-species simulations; Table 2), to mimic the response patterns in commercial forests.

Results

Relationship between maximum growth rate and maximum longevity

Regression analysis showed that log-linear models (i.e., exponential equations) between maximum growth rate and maximum longevity provided a good fit to the data (Table 3, Fig. 1). All regression coefficients were significant. It is remarkable that the two data sets with the largest sample sizes, Europe and eastern North America (together $n = 102$), yielded exactly the same slope parameter (Table 3), whereas the other two data sets (Pacific Northwest and northeastern China) led to somewhat larger and smaller slope parameters, respectively. The amount of variation explained by the regressions varied considerably,

Table 2 Data characterizing the test sites used for the simulation studies

Site	Lat. (°N)	Long. (°E)	Elev. (m)	T (°C)	P (mm)	Observation period	WHC (cm)	Major species (used for single-species simulation)
Bever	46.6	9.9	1,712	1.5	841	1.1901–12.1982	10	*Pinus cembra*
Davos	46.8	9.8	1,590	3.0	1007	1.1901–12.1989	10	*Picea abies*
Adelboden	46.5	7.6	1,325	5.5	1351	1.1966–12.1989	15	*Abies alba*
Bern	46.9	7.4	570	8.4	1006	1.1901–12.1989	20	*Fagus sylvatica*
Basel	47.5	7.6	317	9.2	784	1.1901–12.1989	15	*Quercus petraea, Q. robur*
Sion	46.2	8.6	542	9.7	597	1.1901–12.1977	15	*Pinus sylvestris*

lat latitude; *long* longitude; *elev* elevation above sea level; *T* long-term annual average temperature; *P* long-term annual average precipitation sum; *WHC* water-holding capacity of the soil (difference between field capacity and permanent wilting point)

Table 3 Results of the regression analysis of the form $\ln(A_{max}) = -a \cdot G + b + \varepsilon$, where A_{max} is the maximum longevity and G is the maximum growth rate

Region	n	a	b	r^2
Europe	30	0.0048**	6.840***	0.25
Eastern North America	72	0.0048***	6.214***	0.70
Pacific Northwest	20	0.0031*	7.374***	0.22
Northeastern China	19	0.0061**	6.816***	0.45

n number of species

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

being by far the highest for the largest data set (eastern North America), followed by northeastern China.

Taking into account the results of Table 3, we varied the growth–longevity relationship in the simulations according to the following formula:

$$A_{max,modif} = A_{max,default} \cdot e^{(-a \cdot f \cdot G_{default})} \qquad (1)$$

where $A_{max,\ modif}$ denotes the modified longevity and $A_{max,\ default}$ the standard value of longevity; a is the slope of the relationship; f is the magnitude of the CO_2 fertilization effect, $f = \{0.1, 0.2, 0.3\}$ corresponding to +10, +20, and +30% growth increases; and $G_{default}$ is the standard value of the G parameter. All values of the G and A_{max} parameters are species specific. The value of the slope parameter a in Eq. (1) was set to $a = \{0.003, 0.004, 0.005, 0.006\}$ to bracket the range of slope parameters found in the regression analysis (Table 3) and to take into account that there is some uncertainty in applying these interspecific relationships in an intraspecific context (see the

"Discussion" section). In addition, the effect of the growth stimulation was investigated in isolation by setting the slope parameter a to zero, thus keeping A_{max} at the default value while only varying G.

To illustrate the resulting changes in species properties for the six major European tree species of Table 2, their maximum longevities under the three growth stimulation scenarios are summarized in Table 4. Changes in maximum longevity amounting to more than 100 years and even up to 211 years (for *Quercus petraea*) would be expected; based on these data alone, one would predict that the single-species simulations for the sites Davos (where *Picea abies* dominates) and particularly Bern (dominance by *Fagus sylvatica*) and Basel (dominance by *F. sylvatica* and *Quercus petraea*) should experience the strongest effect of reduced longevity in terms of offsetting the growth stimulation.

Simulation results for mixed stands

Growth stimulation without any longevity effect

The growth stimulation in isolation led to increases in simulated aboveground tree biomass at most sites (cf. biomass values under a zero slope of the growth-age relationship in each panel of Fig. 2). Under a 10% stimulation of growth, the increase in simulated biomass was generally small (2.6–7.1%), with a maximum at Sion amounting to 8.8%; under a 20% stimulation, the corresponding values were 5.4–10.4%, again at Sion showing the highest stimulation (12.3%); and under the strongest growth stimulation, they ranged between 7.3 and 16.9% at five sites, whereas an even stronger increase in biomass was reached at the site Sion (Fig. 2).

Fig. 1 Relationships between the growth rate parameter G and log-transformed maximum longevity (A_{max}) for 141 species of four biogeographical regions. The detailed results of the regressions are given in Table 3
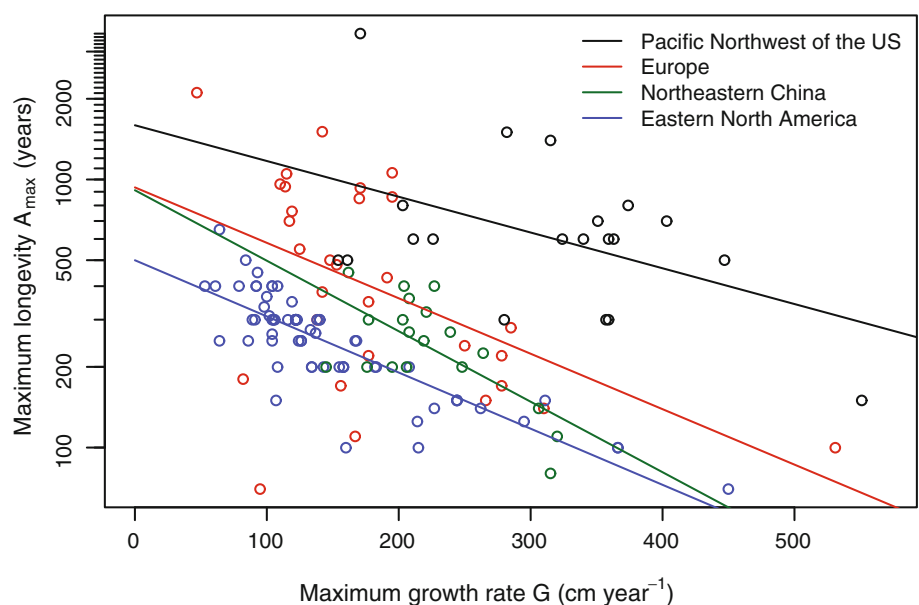
Table 4 Examples of the changes in maximum longevity of six major European tree species according to the results of the regression analysis (Table 3), using Eq. (1) and the slope parameter $a = 0.0048$

Species	$G_{default}$	$A_{max,}$ default	$A_{max,modif}$ for a change of G by…					
			+10%		+20%		+30%	
Pinus cembra	115	1,050	994	−5%	940	−10%	890	−15%
Picea abies	171	930	857	−8%	789	−15%	727	−22%
Abies alba	117	700	662	−5%	626	−11%	591	−16%
Fagus sylvatica	191	430	392	−9%	358	−17%	327	−24%
Quercus petraea	195	860	783	−9%	713	−17%	649	−24%
Pinus sylvestris	119	760	718	−6%	678	−11%	640	−16%

For an explanation of the units (cm/year) and range of values of the G parameter, see Moore (1989); the values of A_{max} are given in years

Growth stimulation including a longevity effect

As expected, the reduction in tree longevity counteracted the growth stimulation, thus leading to a reduction in simulated total biomass compared to the "growth stimulation only" scenario (Fig. 2). Relative to the conditions of the control scenario (defined as no growth stimulation and no longevity effect), simulated biomass was consistently higher—at least for the range of parameters investigated here—at the warm-dry site Sion (close to the dry treeline), and to a very small extent also at the cold-wet site Bever (close to the cold treeline). At the other four sites, however, simulated biomass approached control conditions as the slope of the growth–longevity relationship became steeper, with a net effect of zero at parameter values of around 0.004. At still steeper slopes, the simulated biomass was even 3–8% lower than under the control scenario, i.e., longevity effects outweighed growth stimulation effects at these four sites.

Biodiversity effects

Statistically significant ($p < 0.05$; cf. Bugmann 1997) changes in tree species composition were found only at the site Adelboden for growth stimulations of 20 and 30% in the absence of reduced longevity. In this case, the slow-growing *Abies alba* gained considerably in biomass at the expense of *Fagus sylvatica* and *Picea abies*. The generally low responsiveness of species composition in the simulations is not surprising, because the growth stimulation was applied uniformly across all species, i.e., possible species-specific fertilization effects were not taken into account.

Average response across sites

Since any real landscape, particularly in a complex topography, is composed of ecosystems of strongly varying composition, we also calculated the net effect of growth

stimulation and reduced longevity as an average over the six study sites. This should not be taken as a true landscape-scale biomass signal, but it serves to illustrate the point that over all of the sites studied here, the longevity reduction effect equals the growth stimulation effect at a slope parameter of about 0.004 (with opposite signs of the two effects, of course), and there is a net zero effect at still stronger reductions of longevity because sites with strongly negative signals (Davos, Adelboden) cancel out the single site with a pronounced positive signal (Sion).

Simulation results for single-species stands

In the absence of interspecific competition, highly similar results to the mixed-stand simulations were obtained (Fig. 3). As a rule, the biomass responses were quantitatively even somewhat more pronounced than in the mixed-species cases, particularly with respect to the reductions of biomass relative to control conditions at higher slopes of longevity reduction (slopes larger than 0.004, Fig. 3).

Discussion

Relationship between maximum growth rate and maximum longevity

To our knowledge, this study is the first to quantitatively evaluate the impacts of a possible reduced longevity under CO_2 fertilization on aboveground carbon storage in forests. Three lines of reasoning support our decision to use interspecific data on the relationship between maximum growth rate and maximum longevity to model the intraspecific relationship. First, the power of our approach is that data from 141 species from three continents could be exploited, and they show a consistent pattern with similar slopes of the growth–longevity relationship (Table 2). Second, in an environment of limited resources, tree life history strategies evolved as a consequence of ecological trade-offs, e.g., between investment in defenses versus investment in growth (cf. Loehle 1988; Bigler and Veblen 2009). Thus, every member of a given species is constantly facing the decision of how to invest the available resources, thus leading to similar trade-offs across members within a species to those between different species (Backman 1943). Third, the only study that has quantitatively addressed the relationship between growth and maximum longevity of temperate trees using empirical data (Bigler and Veblen 2009) resulted in highly compatible findings, as explained below.

Bigler and Veblen (2009) used average annual ring width to an age of 50 (in units of mm/year) as the variable to predict maximum individual longevity of the members of three conifer species. They found a highly significant

Fig. 2 Simulated percentage changes in total aboveground biomass of multispecies forests at six sites in response to increasing growth rates due to CO_2 fertilization as combined with changes in the slope a of the growth–age relationship (Table 3)
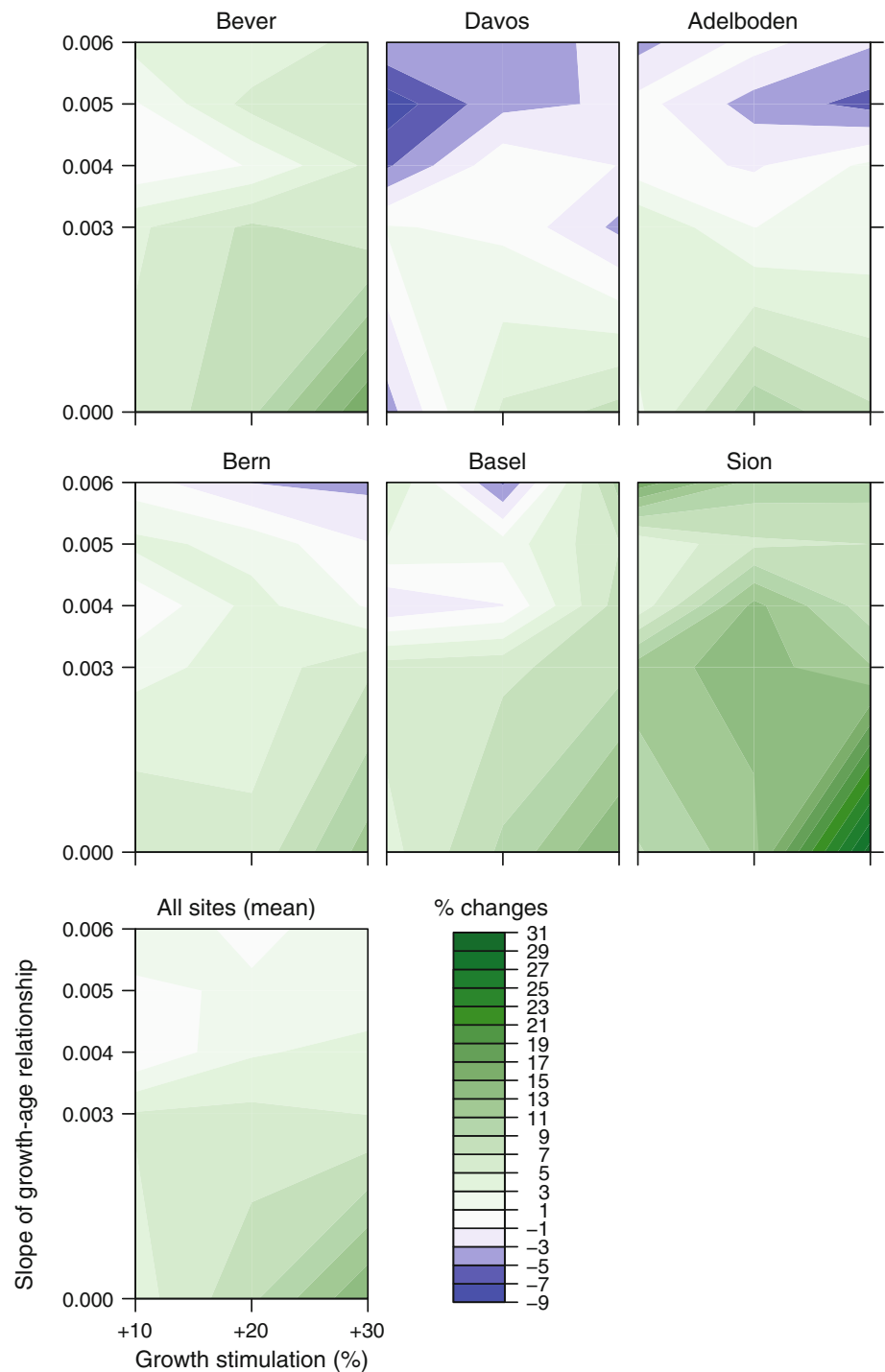
negative exponential relationship with slope parameters ranging between 0.35 and 0.64. Because the slope parameter changes linearly with the scaling of the predictor variable, their results are not directly comparable to those of Table 3. However, a scaling factor can be approximated as follows: the values of G used in the present study typically range between 100 and 300 cm/year (Bugmann 1994; Table 5a; note that G is a compound parameter that cannot be interpreted directly as either height or diameter increment; cf. Moore 1989), whereas during the first 50 years of tree life in the mountain forests studied by Bigler and Veblen (2009), average ring widths typically ranged between 0.5 and 3 mm/year (Table 5b). A comparison of the frequency distributions of the predictor variables of Bigler and Veblen's data with those of the present study (Table 5c) suggests that the slope coefficients

Fig. 3 Same as Fig. 2, but for the single-species simulations (see text)
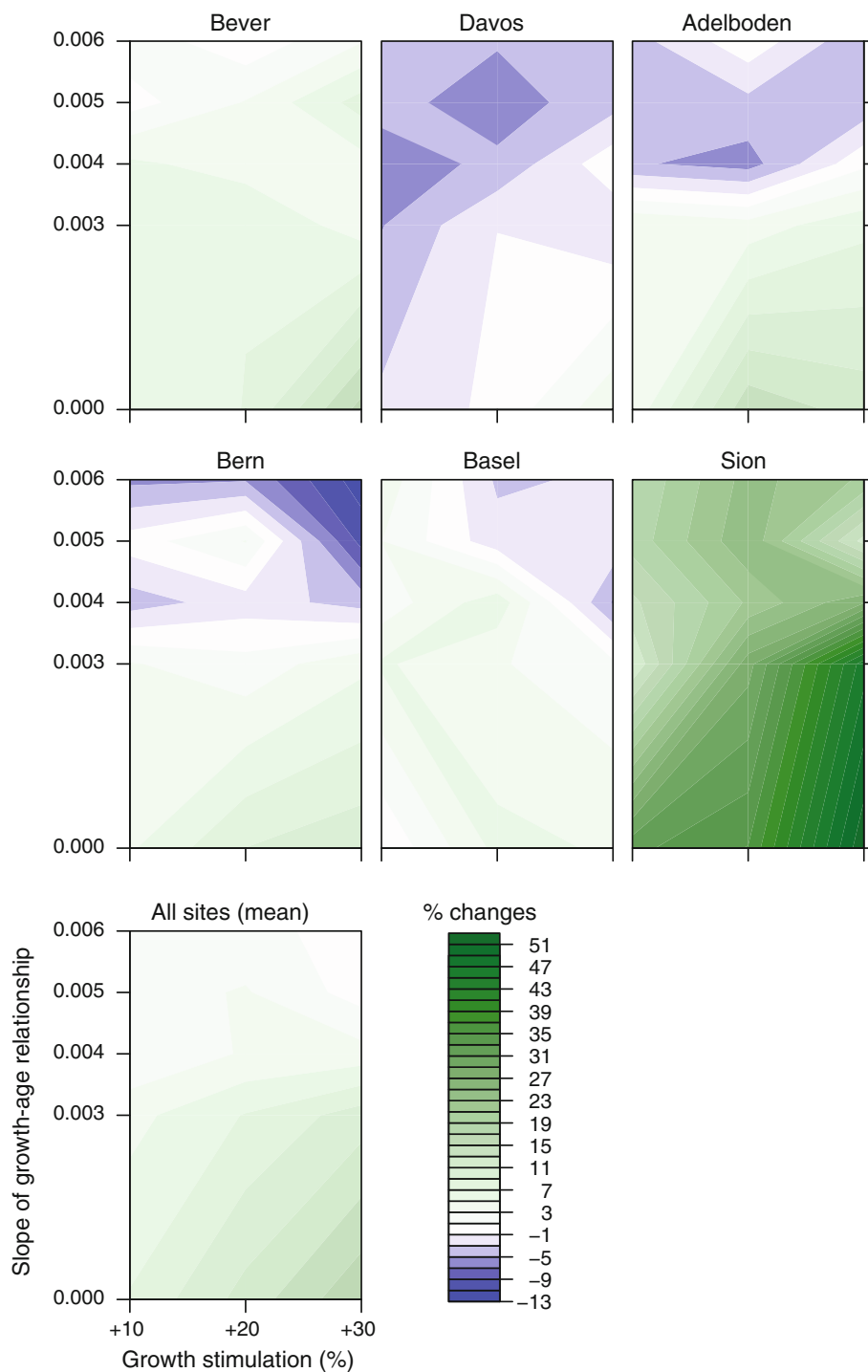
should differ by about two orders of magnitude (a factor of 100) between the two studies; that is, the two analyses match very well not only qualitatively, but even quantitatively.

Therefore, we conclude that the approach used here is consistent not only with theoretical reasoning (Backman 1943; Schulman 1954), but also with the available empirical data (Bigler and Veblen 2009). Clearly, a key priority

for further research is to provide empirical data on the growth–mortality relationship for a broad suite of tree species. The present paucity of data reflects the fact that tree mortality and the underlying ecological processes continue to be an under-researched topic in forest ecology (cf. Wyckoff and Clark 2002).

Mortality investigations of forest trees based on tree-ring data or forest inventories are labor intensive (cf.

Table 5 Derivation of a scaling factor by comparing the frequency distributions of the G parameters (cf. Table 1, predictor variable of the present study) with the frequency distribution of the predictor variable used by Bigler and Veblen (2009)

(a)	G_{EUR}	G_{ENA}	G_{PNW}	G_{NEC}
Minimum	47	53	154	145
Lower quartile	120.5	104	222.2	199
Median	161.5	122	332	208
Mean	181.5	147.5	311.6	223.3
Upper quartile	195	158.5	360	243.5
Maximum	531	450	551	320

(b)	Abies lasiocarpa	Picea engelmannii	Picea abies	
Minimum	0.15	0.21	0.91	
Lower quartile	0.60	1.18	1.43	
Median	0.87	1.47	1.63	
Mean	0.91	1.43	1.97	
Upper quartile	1.14	1.80	2.65	
Maximum	2.06	2.78	3.44	

(c)	Abies lasiocarpa	Picea engelmannii	Picea abies	Average across species
Based on median	0.00713	0.01205	0.01009	0.00976
Based on mean	0.00617	0.00969	0.01085	0.00891

(a) Frequency distribution of the G parameter values (cm/year; for units and values cf. Moore (1989); (b) frequency distribution of average annual ring width to age 50 (mm/year; Bigler and Veblen (2009); (c) scaling factors for the slopes of the regression by Bigler and Veblen (2009) based on the ratio of mean and median values, respectively, from (b) and (a), using G_{ENA} values for the North American species *Abies lasiocarpa* and *Picea engelmannii*, and G_{EUR} values for the European species *Picea abies*

EUR Europe; *ENA* Eastern North America, *PNW* Pacific northwest of the US, *NEC* Northeastern China

The scaled slopes are in the range [0.0026–0.007] (cf. Table 3)

Laurance et al. 2004; Bigler and Veblen 2009). Long-term data from forest inventories in forest reserves (e.g., Wunder et al. 2008) or from national forest inventories (e.g., Purves et al. 2007) may be able to provide high-quality insights in the future.

Implications for simulated aboveground biomass under CO_2 fertilization

The results obtained from both mixed-species as well as single-species simulation experiments at six sites along an extended climatic gradient in central Europe led to the following conclusions.

First, a given growth stimulation at the tree level (here, up to a 30% increase in growth rate) leads to a disproportionately small increase in total stand biomass. This is due to negative feedback effects in the model, particularly increased competition for light in the long term, even in the absence of any reduced longevity. Besides confirming early findings (e.g., Shugart and Emanuel 1985), these results are in agreement with the picture emerging from longer-term CO_2 fertilization experiments, particularly those in closed-canopy stands, where an attenuation of the initial stimulation was observed after a few years (e.g., Oren et al.

2001; Schäfer et al. 2003; Norby et al. 2004; Körner et al. 2005). Hence, the present study serves as another example that strong effects at the individual plant level are often greatly attenuated (buffered) at higher levels of organization.

Second, the growth stimulation is highly likely to be associated with a reduction in tree longevity (Backman 1943) as an ecological trade-off (cf. Arendt 1997). This counteracting effect tends to offset the moderate increase in standing biomass that is simulated as a consequence of the growth stimulation, thus effectively speeding up forest dynamics without increasing carbon storage (cf. Körner 2009). In the present study, a positive balance between the two effects (i.e., higher standing biomass) was restricted mostly to sites close to the cold and dry treeline (Bever, Sion). It is noteworthy that these are relatively open stands as a consequence of strong climatic constraints (mainly low growing season temperature and low water availability, respectively), so that canopy expansion in response to CO_2 fertilization appears to still be possible. This is in agreement with Körner's (2006) hypothesis that expanding systems (or those that have at least the potential to expand) are likely to be most reactive to CO_2 fertilization (cf. Handa et al. 2005 for a cold treeline example). Still, it

needs to be acknowledged that even if elevated CO_2 does not enhance aboveground biomass, total net C fixation may remain enhanced, and could provide a mechanism for adding C to the soil, a factor we could and did not study in the approach presented here.

Third, if we assume that those two analyses that yielded the same slope of the growth–longevity relationship (and which cover 102 out of 141 species) represent the most likely relationship (i.e., with a slope of around 0.005, Table 3), the net effect of the two processes (growth stimulation vs. reduced longevity) is very close to zero in most multispecies simulations. Overall, our simulation results are also supported by evidence emerging from detailed studies of South American tropical forests showing that ecosystems featuring high net primary productivity (high growth rates) tend to be characterized by low carbon stocks (Malhi et al. 2006), which must be due to a lower longevity of the trees (cf. also Vieira et al. 2005).

Fourth, the single-species and multispecies simulations showed a highly similar response pattern across the environmental gradient, and thus they do not conform to the expectation that in single-species stands, the species with intrinsically high growth rates (*Pinus* in Sion, *Picea* in Davos, *Fagus* in Bern) should experience the strongest negative biomass signal due to strongly reduced longevities (Table 4). The simulation results arise from a multitude of interactions among highly nonlinear processes in the forest succession model, as follows. On the one hand, the growth stimulation influences competition, which leads to a negative feedback on growth (increased shading) of some trees; however, as soon as a tree overtops its neighbors, the feedback is positive. In addition, there is a positive feedback on mortality (higher growth rate reduces mortality risk in the short term, cf. Bigler and Bugmann 2003). On the other hand, reduced longevity has a direct impact on mortality (increased mortality rates). The joint effect of all these processes and their interaction with other species properties cannot be anticipated quantitatively without the help of a succession model (or a very long experiment with forest trees). This is another example showing that simple extrapolations from species properties often fail: linear upscaling to the ecosystem level from autecological information for a single species must be viewed with great caution.

Lastly, when averaging the response across all sites to mimic a "landscape-level" response, the net effect of growth stimulation and reduced longevity is very close to zero at the most probable values of reduced longevity, irrespective of the exact amount of growth stimulation. This is in sharp contrast with the results of most current dynamic global vegetation models (DGVMs, cf. Cramer et al. 2001; Friedlingstein et al. 2006; Prentice et al. 2007), which project a high potential of the biosphere to absorb atmospheric carbon due to the direct CO_2 fertilization effect for a good portion of the twenty-first century. None of these models, however, includes an effect of CO_2 on plant longevity. The present study suggests that it would be desirable to upgrade DGVMs with better descriptions of tree demography, including longevity effects of CO_2. We view this as quite relevant, particularly because DGVMs are increasingly implemented as an element of coupled atmosphere–ocean biosphere general circulation models to simulate the behavior of the entire Earth system (Friedlingstein et al. 2006). In their current state, DGVMs are likely to misrepresent biosphere dynamics in this important regard.

The use of a "nonmechanistic" forest model may entail certain limitations to our study and thus the above interpretations. For example, increased water-use efficiency, which is probably the most undisputed effect of CO_2 fertilization, at least for deciduous trees (cf. Körner et al. 2007), was not simulated here, thus potentially leading to exaggerated simulated stress levels at dry sites (here, mostly Sion). Also, the model is based on fixed allometric relationships, whereas it is known that allometries are likely to change in a high-CO_2 world, thus possibly leading to deviations from the simulation results obtained here. Still, it should be kept in mind that our results are not intended to be predictions of the future state and fate of forests. Rather, they serve as a sensitivity study, and thus provide a first quantification of a potentially very important, but to date largely ignored, ecological trade-off that plays out in the long term only. In the absence of "hard" data regarding the impacts of high CO_2 concentrations on the longevity of forest trees, we need to rely on scenario analyses using simulation models. Detailed follow-up studies based on different models would be highly welcome.

Overall, the present study shows that it is indispensable to consider ecophysiological responses (such as CO_2 fertilization effects on plant growth) in conjunction with their linkage to demographic processes in forest trees (such as mortality rates) if one wishes to avoid erroneous inference at the ecosystem level. Considerable hope is sometimes placed in the ability of the global forest to mitigate anthropogenic CO_2 emissions because of CO_2 fertilization (e.g., Malhi et al. 2002; Kimball et al. 2007). We conclude that any CO_2 fertilization effect is quite likely to be offset by an associated reduction in the longevity of forest trees, thus strongly reducing the carbon mitigation potential of temperate forests.

References

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72:149–177

Backman G (1943) Wachstum und organische Zeit. Verlag Johann Ambrosius Barth, Lepizig

Bigler C, Bugmann H (2003) Growth-dependent tree mortality models based on tree rings. Can J For Res 33:210–221

Bigler C, Veblen TT (2009) Increased early growth rates decrease longevities of conifers in subalpine forests. Oikos 118:1130–1138

Bormann DB, Likens GE (1979) Pattern and process in a forested ecosystem. Springer, New York

Botkin DB, Janak JF, Wallis JR (1972) Some ecological consequences of a computer model of forest growth. J Ecol 60:849–872

Bugmann H (1994) On the ecology of mountainous forests in a changing climate: a simulation study (PhD thesis, no. 10,638). Swiss Federal Institute of Technology, Zurich

Bugmann H (1996) A simplified forest model to study species composition along climate gradients. Ecology 77:2055–2074

Bugmann H (1997) An efficient method for estimating the steady-state species composition of forest gap models. Can J For Res 27:551–556

Bugmann H (2001a) A review of forest gap models. Clim Change 51:259–305

Bugmann H (2001b) A comparative analysis of forest dynamics in the Swiss Alps and the Colorado Front Range. For Ecol Manag 145:43–55

Bugmann H (2003) Predicting the ecosystem effects of climate change. In: Canham CD, Lauenroth WK, Cole JS (eds) Models in ecosystem science. Princeton University Press, Princeton, pp 385–409

Bugmann H, Cramer W (1998) Improving the behaviour of forest gap models along drought gradients. For Ecol Manag 103:247–263

Bugmann H, Solomon AM (1995) The use of a European forest model in North America: a study of ecosystem response to climate gradients. J Biogeogr 22:477–484

Bugmann H, Solomon AM (2000) Explaining forest composition and biomass across multiple biogeographical regions. Ecol Appl 10:95–114

Cramer W et al (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Glob Change Biol. 7:357–373

Friedlingstein P et al (2006) Climate–carbon cycle feedback analysis: results from the C4MIP model intercomparison. J Clim 19:3337–3353

Friend AD, Stevens AK, Knox RG, Cannell MGR (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecological Modelling 95:249–287

Gayler S, Grams TEE, Heller W, Treutter D, Priesack E (2008) A dynamical model of environmental effects on allocation to carbon-based secondary compounds in juvenile trees. Ann Bot 101:1089–1098

Granados J, Körner C (2002) In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. Global Change Biol 8:1109–1117

Handa IT, Körner C, Hättenschwiler S (2005) A test of the treeline carbon limitation hypothesis by in situ CO_2 enrichment and defoliation. Ecology 86:1288–1300

Harcombe PA (1987) Tree life tables. Bioscience 37:557–568

Jenkins MA, Pallardy SG (1995) The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Can J For Res 25:1119–1127

Kimball BA, Pinter PJ, Garcia RL, LaMorte RL, Wall GW, Hunsaker DJ, Wechsung G, Wechsung F, Kartschall Th (1995) Productivity and water use of wheat under free-air CO_2 enrichment. Glob Change Biol 1:429–442

Kimball BA, Idso SB, Johnson S, Rillig MC (2007) Seventeen years of carbon dioxide enrichment of sour orange trees: final results. Glob Change Biol 13:2171–2183

Kimmins JP (2004) Forest ecology. Prentice-Hall, Upper Saddle River

Körner C (2004) Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. Phil Trans R Soc Lond B 359:493–498

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. New Phytol 172:393–411

Körner C (2009) Responses of humid tropical trees to rising CO_2. Annu Rev Ecol Evol Syst 40:61–79

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362

Körner C, Morgan JA, Norby R (2007) CO_2 fertilisation: when, where, how much? In: Canadell JG, Pataki D, Pitelka LF (eds) Terrestrial ecosystems in a changing world. Springer, Berlin, pp 9–21

Ladeau SL, Clark JS (2006) Elevated CO_2 and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. Glob Change Biol 12:822–833

Laurance WF, Nascimento HEM, Laurance SG, Condit R, D'Angelo S, Andrade A (2004) Inferred longevity of Amazonian rainforest trees based on a long-term demographic study. For Ecol Manag 190:131–143

Lavola A, Julkunen-Tiitto R (1994) The effect of elevated carbon dioxide and fertilization on primary and secondary metabolites in birch *Betula pendula* (Roth). Oecologia 99:315–321

Lexer MJ, Hönninger K (2001) A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For Ecol Manag 144:43–65

Litvak ME, Constable JVH, Monson RK (2002) Supply and demand processes as controls over needle monoterpene synthesis and concentration in Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco]. Oecologia 132:382–391

Loehle C (1988) Tree life history strategies: the role of defenses. Can J For Res 18:209–222

Luo ZB, Calfapietra C, Scarascia-Mugnozza G, Liberloo M, Polle A (2008) Carbon-based secondary metabolites and internal nitrogen pools in *Populus nigra* under free air CO_2 enrichment (FACE) and nitrogen fertilization. Plant Soil 304:45–57

Malhi Y, Meir P, Brown S (2002) Forests, carbon and global climate. Phil Trans R Soc Lond B 360:1567–1591

Moore AD (1989) On the maximum growth equation used in forest gap simulation models. Ecological Modelling 45:63–67

Moore DJP, Aref S, Ho RM, Pippen JS, Hamilton JG, DeLucia EH (2006) Annual basal area increment and growth duration of *Pinus taeda* in response to eight years of free-air carbon dioxide enrichment. Glob Change Biol 12:1367–1377

Norby RJ, Wullschleger SD, Gunderson CA, Johnson DW, Ceulemans R (1999) Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ 22:683–714

Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neill EG (2004) Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. Proc Natl Acad Sci USA 101:9689–9693

Norby RJ et al (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Natl Acad Sci USA 102:18052–18056

Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schäfer KVR, McCarthy H, Hendrey G, McNulty SG, Katul GG (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472

Philips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. Science 263:954–957

Philips OL et al (2004) Pattern and process in Amazon tree turnover, 1976–2001. Phil Trans R Soc Lond B 359:381–407

Prentice IC, Cramer W, Harrison SP, Hickler T, Lucht W, Sitch S, Smith B, Sykes MT (2007) Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell JG, Pataki D, Pitelka LF (eds) Terrestrial ecosystems in a changing world. Springer, Berlin, pp 175–192

Purves DW, Lichstein JW, Pacala SW (2007) Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PLoS ONE 2(9):e870

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Reynolds JF, Bugmann H, Pitelka LF (2001) How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. Clim Change 51:541–557

Schäfer KVR, Oren R, Ellsworth DS, Lai CT, Herrick JD, Finzi AC, Richter DD, Katul GG (2003) Exposure to an enriched CO_2 atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. Glob Change Biol 9:1378–1400

Schulman E (1954) Longevity under adversity in conifers. Science 119:396–399

Shao G, Bugmann H, Yan X (2001) A comparative analysis of the structure and behavior of three forest gap models at sites in northeastern China. Clim Change 51:389–413

Shugart HH (1984) A theory of forest dynamics: the ecological implications of forest succession models. Springer, New York

Shugart HH (1998) Terrestrial ecosystems in a changing environment. Cambridge University Press, Cambridge

Shugart HH, Emanuel WR (1985) Carbon dioxide increase: the implications at the ecosystem level. Plant Cell Environ 8:381–386

Vieira S, Trumbore S, Camargo PB, Selhorst D, Chambers JQ, Higuchi N, Martinelli LA (2005) Slow growth rates of Amazonian trees: consequences for carbon cycling. Proc Natl Acad Sci USA 102:18502–18507

Waring RH (1987) Characteristics of trees predisposed to die. Bioscience 37:569–573

Wright SJ, Calderon O, Hernandez A, Paton S (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484–489

Wunder J, Brzeziecki B, Żybura H, Reineking B, Bigler C, Bugmann H (2008) Growth–mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. Oikos 117:815–828

Wyckoff PH, Clark JS (2002) The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. J Ecol 90:604–615

Zotz G, Cueni N, Körner C (2006) In situ growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO_2. Funct Ecol 20:763–769