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Species diversity and ecosystem response to carbon dioxide fertilization: conclusions from a temperate forest model

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Abstract

This paper explores how the response of a temperate forest ecosystem to climate change might depend on species diversity and community change. In particular, we look at the dynamics of a model of temperate forest growth under doubled CO_2. We combine a detailed, field-calibrated model of forest dynamics (Pacala *et al.* 1993) with greenhouse data on the range of seedling biomass growth response to doubled CO_2 concentrations (Bazzaz *et al.* 1990; Bazzaz & Miao 1993). Because total ecosystem response to climate change depends delicately on many environmental variables other than CO_2, we isolate the effects of community change by comparing runs of the regular model, allowing dynamic community change, with runs of a reduced model that holds species composition static by using a single tree species with average parameters. Simulations that allowed community change instead of holding species composition constant showed a roughly 30% additional increase in total basal area over time scales of 50–150 years. Although the model omits many possible feedbacks and mechanisms associated with climate change, it suggests the large potential effects that species differences and feedbacks can have in ecosystem models and reinforces the possible importance of diversity to ecosystem function (Naeem *et al.* 1994; Tilman & Downing 1994) over time scales within the planning horizon for global change policy.

Keywords: biodiversity, carbon dioxide fertilization, carbon sink, community dynamics, diversity–stability hypothesis, forest models, terrestrial

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Introduction

Many researchers are currently engaged in studying the effects of anthropogenic global climate change on terrestrial ecosystems, and the interaction of climatic and ecosystem processes. The typical paradigm for these studies is to use simplified models of carbon, nitrogen and hydrological cycles in terrestrial ecosystems, coupled to scenarios of global climate change (Potter *et al.* 1993; Schimel *et al.* 1994; Melillo *et al.* 1993). Heterogeneity in vegetation on the large scale is generally incorporated using maps of vegetation types (Potter *et al.* 1993; Melillo *et al.* 1993), and eventually the movement of vegetation types themselves will be estimated from climatic change (Lenihan & Neilson 1993; Smith *et al.* 1992).

But what about successional and evolutionary changes within a given ecosystem? There has been much research into the possible effects of community change (Woodward *et al.* 1991), but little quantitative exploration of its possible effects on ecosystem function. In this paper, we examine the potential size and time scale of shifts in species composition and total above-ground productivity in a temperate forest caused by diversity in species performance, particularly in seedling response to enriched CO_2 atmospheres. We compare the CO_2-induced change in total basal area (roughly proportional to above-ground biomass and hence to above-ground carbon stor-

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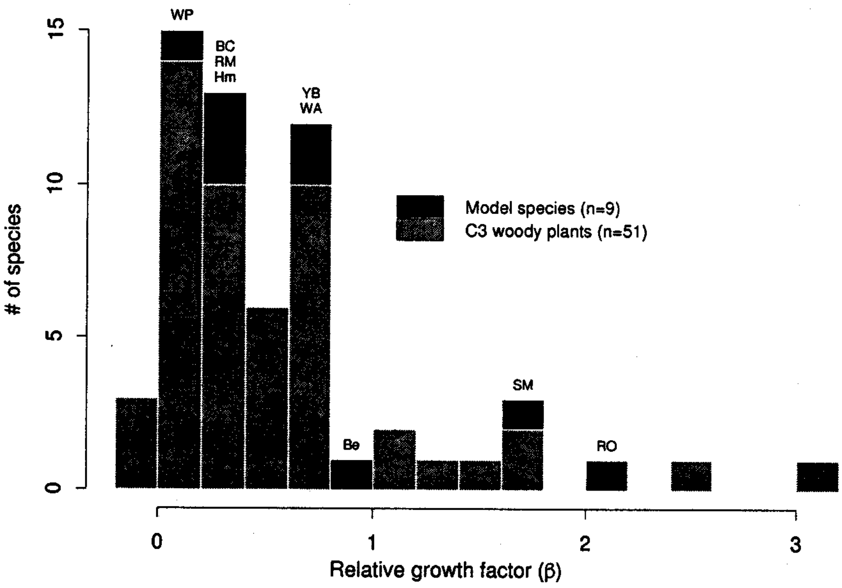

Fig. 1 Histogram of β values for C3 woody plants from Poorter (1993), Bazzaz & Miao (1993), and Bazzaz *et al.* (1990). All values represent the proportional change in total dry biomass of plants grown in enhanced CO_2 (600–720 p.p.m.) relative to plants grown in ambient CO_2 (300–360 p.p.m.). Poorter (1993) is a review of experiments where plants were grown in a variety of greenhouse conditions, using low and high (usually doubled) CO_2 concentrations. Bazzaz *et al.* (1990) grew seedlings in greenhouses at 350 and 700 p.p.m. CO_2, with intermediate N and light conditions; Bazzaz & Miao (1993) grew seedlings in a factorial arrangement of N, light, and CO_2 levels. Species represented in the current model are shown in dark gray and labelled, all others are shown in light gray; note that the β values for SORTIE model species follow the general distribution reasonably well. Model species are black cherry (BC, *Prunus serotina*); white ash (WA, *Fraxinus americanus*); red maple (RM, *Acer rubrum*); white pine (WP, *Pinus strobus*); yellow birch (YB, *Betula alleghaniensis*); beech (Be, *Fagus grandifolia*); hemlock (Hm, *Tsuga canadensis*); sugar maple (SM, *Acer saccharum*); red oak (RO, *Quercus rubra*).

age) in model forests with static species composition to that in forests where the species composition can change dynamically because of differential growth, survivorship, and reproduction. In other words, we compare the response of models with a single average tree species – similar to current global ecosystem models – to models with the full, measured range of early and late-successional species and low and high responders to CO_2 (Fig. 1). Thus, we can form a preliminary idea of the possible size and time scale of community response, and of its effect on ecosystem productivity. All of the uncertainties surrounding the effect of climate change on non-community models apply to our model as well; however, our interest here is in the *difference* between the ecosystem-level conclusions of static-composition and community models. We want to know what qualitative effects biodiversity, which is usually glossed over in large-scale models of global change, could have on the predictions of models (and potentially on real ecosystem function as well).

The observed proportional increase in biomass (β) of C3 woody species grown in enhanced CO_2 atmospheres to those grown in ambient-CO_2 atmospheres ranges from –0.1 to 3.1 (Fig. 1) (Poorter 1993). Ignoring this diversity, most current ecosystem models use a single function for plant response to increased CO_2 concentrations, either multiplying growth by an observed species mean $\beta \approx 0{:}35$ (Kimball 1983) (growth enhancement following a doubling of CO_2), or using a physiologically based submodel (e.g. Melillo *et al.* 1993).

The performance differences among species generated by a doubling of CO_2 are large in comparison with the differences in growth response to light that drive succession and can lead to complete species replacement within a few generations. Thus, although tree generation times are long, we still expect to see environment-driven changes in species composition, and through species composition in productivity, within a time scale of 50 to 150 years.

Methods

Forest model

Our analysis uses an individual-based forest simulator, SORTIE (Pacala *et al.* 1993), incorporating measured species-specific patterns of growth, mortality, reproduction and dispersal. The model is spatial and mechanistic; individual trees compete by depleting resources (light) available to their neighbours.

Initially, the model is seeded with a specified density of individuals of different species with the same initial diameter at breast height (d.b.h.), at random positions on a continuous two-dimensional square; we typically use a 9-ha arena which contains on the order of 1000 adult trees. All of the simulations reported here were started after at least 100 years had passed from this initial randomized configuration, so that more realistic size distributions and spatial configurations of trees could evolve from the initial uniform conditions. The model runs in five-year discrete time steps, which give adequate temporal resolution. The first action in each time step is to calculate the current light regime for every sub-canopy tree by computing the shading effects of its neighbours, using a computational 'fish-eye lens' algorithm that takes into account the annual distribution of solar radiation over different parts of the sky. Tree crowns are considered to be cylinders, with species-specific allometric relationships between d.b.h. and total height, crown height and crown radius. Canopy density is also taken into consideration; when a ray coming from a particular part of the sky intersects any part of a tree crown, its intensity is diminished by a species-specific amount. The simulator calculates total growth of sub-canopy trees in a five-year period as a Michaelis–Menten function of available light (Pacala *et al.* 1993). Mortality rates are calculated in turn as exponentially declining functions of the five-year growth rates (Kobe *et al.* in press). Both the growth and mortality curves are based on species-specific, measured parameters. Other resources such as nitrogen and water are not considered to affect growth because field data showed that under current conditions these factors were swamped by the effect of light availability. This assumption could clearly fail under different climatic conditions, but we stress that we are using the model to examine the possible effects of species diversity on ecosystem response, not to make an accurate prediction of ecosystem response itself. Trees switch to being adults (canopy trees) when their absolute growth rate based on available light exceeds their potential growth based on a constant area increment law of $\beta \approx 45\ cm^2\ y^{-1}$. This changeover typically occurs at a d.b.h. of 10–20 cm, depending on the species-specific growth rate and light environment. For canopy trees, mortality occurs at a small constant rate, growth is computed according to the constant area increment law, and seed dispersal is based on measured species-specific dispersal functions (Ribbens *et al.* 1994) that determine the distribution of seedfall. Fecundity is constant across species (except for beech, which has clonal reproduction at the study site in Connecticut). The level of species-specific detail is much smaller for canopy than for sub-canopy individuals, partly because of the difficulty of calibrating these parameters but largely because of the insensitivity of the model (and by inference the forest dynamics) to the details of individual canopy tree growth and mortality. All model parameters were estimated from an extensive set of field measurements collected in Great Mountain Forest, Connecticut, in the northeastern United States, and the model accurately replicates changes in total basal area and successional changes in species abundance (community-level change) observed over historical time in these forests (Pacala *et al.* 1993).

Calibrating CO_2 responses

The same level of field-calibrated detail is not yet possible for the responses of trees to elevated CO_2. However, recent glasshouse estimates of seedling biomass growth response to CO_2 for each tree species used in the model (Bazzaz *et al.* 1990; Bazzaz & Miao 1993; Bazzaz *et al.* 1993) allow us roughly to calibrate a sub-model for the response of sub-canopy trees to enhanced CO_2.

Figure 1 compares the values derived by Bazzaz *et al.* with a wider survey of C3 woody plant growth responses collected by Poorter (1993). The species found in Great Mountain Forest and used in the SORTIE model have a distribution of growth responses that matches the more general distribution among C3 species reasonably well, although red oak is an outlier. Bazzaz *et al.* used factorial combinations of light, nitrogen, and CO_2 concentrations in some of their experiments; growth responses of seedlings to CO_2 were not significantly lower in the low-N than in the high-N case, suggesting that at least for seedlings of these species N availability does not limit CO_2 fertilization effects. There is no apparent correlation between successional status and CO_2-fertilization; red oak and hemlock, at opposite ends of the successional gradient, both have larger-than-average growth response.

We translated the experimental ratios of total dry biomass for one-year seedlings in CO_2-enhanced and normal conditions (β) into multiplicative factors of the baseline relative diameter growth rate by assuming one year of growth at the field-measured growth rates for each species. We estimated light levels from descriptions of experimental conditions (Bazzaz *et al.* 1990; Bazzaz & Miao 1993) and adjusted growth rates for high-nitrogen conditions by a factor of 5.0 based on the observed growth differences between low- and high-nitrogen treatments; our results do not differ qualitatively for N-fertilization factors in the range 4.0–6.0. In the CO_2-enriched model runs, each seedling's relative growth rate is multiplied by the estimated species-specific fertilization factor.

CO_2 concentrations near the forest floor tend to be higher than the average atmospheric level of 350 p.p.m. during the growing season (Bazzaz & Williams 1991). Although this phenomenon could affect our parametrization slightly, seedlings in Sortie come into existence with a diameter of 0.2 cm, corresponding to a height of ≈ 30 cm; at this height, average CO_2 levels do not reach more than about 400 p.p.m. at any time of year (Bazzaz & Williams 1991), a fairly small change relative to our simulated doubling of CO_2 concentrations.

While these medium-term estimates of seedling response in the greenhouse are necessarily inadequate indicators of the response of forest communities to CO_2 in field conditions, we stress that these data are the best currently available measurements of whole-plant growth responses to CO_2 enrichment.

One of the biggest problems in calibrating the CO_2 response submodel is figuring out how to extend the available seedling data to older (sub-canopy and canopy) trees. Extremely few data are available on long-term effects of CO_2 fertilization on trees (Idso & Kimball 1993), and even less in anything approaching field conditions. The combined effects of differences in physiology (allocation, dark respiration, etc.), acclimation (Oechel *et al.* 1994; Tolley & Strain 1984b ; Tolley & Strain 1984a; Oechel & Strain 1985), and possible nitrogen limitation (Rastetter *et al.* 1992) make predicting the effects of CO_2 on canopy trees from basic physiological considerations nearly impossible. Almost any extrapolation of the results of one-year experiments on seedlings to adult trees (e.g. a 50 – 100% increase in growth rates) leads to nonsensical results. Our first approximation was to apply the observed growth multipliers only to the sub-canopy growth phase; canopy trees grow according to an unmodified CAI law. From an ecosystem perspective, this assumption is conservative because it assumes that acclimation or resource limitation definitely occurs before the canopy stage, and hence sharply limits the total growth enhancement of the forest. To test the sensitivity of the results to even faster acclimation, we also ran simulations where CO_2 enhancement cut off at 1 cm diameter (height 1.5 m), allowing only seedlings and small saplings to benefit from the enhanced growth and decreased mortality associated with higher CO_2 concentrations.

Other factors potentially changing individual growth, survivorship and reproductive parameters such as limited nitrogen or water supply (Rastetter *et al.* 1992; Solomon, 1986; Pastor & Post 1988) or other climatic changes in nitrogen deposition, temperature, or hydrology (Solomon 1986; Pastor & Post 1988), may affect the responses of individuals and communities to increased CO_2 in hard-to-predict ways. We also recognize that the decline in CO_2 enhancement with time occurs at different rates for species from the same ecosystem (Bazzaz *et al.* 1993). As discussed above we are primarily interested not in the absolute ecosystem growth response to CO_2 fertilization, but in the relative effects of species diversity and community change, which may be less affected by changes in multiple environmental factors; it is unlikely that differential responses of species to different environmental factors will cancel out.

Terrestrial forests store carbon in several compartments other than living trees, and a more extensive model would account for the residence times of carbon in plant litter and soil, and possibly for changes in litter and soil dynamics with climate change (Schimel *et al.* 1994; Pastor & Post 1988; Rastetter *et al.* 1991; Rastetter *et al.* 1992). New information also suggests that litter lignin content may increase in CO_2-enriched environments (F. Bazzaz and J. Melillo, unpublished data), making litter and soil carbon more resistant to decomposition and amplifying the effects of CO_2-fertilization.

In any case, our analysis should be viewed as a qualitative exploration of the effects of biodiversity on CO_2 fertilization, rather than as a quantitative forecast. Our main point is to demonstrate that ignoring interspecific differences and community change represents a serious omission that can affect estimates of changes in ecosystem productivity by factors of more than 30%; it remains to determine exactly how, and whether, to incorporate all of the complex changes caused by a shifting growth environment.

Simulation runs

To assess the effects of diversity, we compared the full nine-species model (dynamic species composition) with a single-species reduction of the model analogous to current ecosystem models incorporating a single set of plant response parameters for northern transition–hardwood forests (static species composition). By averaging the growth, mortality, reproduction, and CO_2 response parameters of all species we effectively locked the species composition and successional status of the forest at their initial conditions. To minimize the differences between the static- and dynamic-composition runs, all parameters for the static model were obtained by taking the individual-weighted average parameters of all the trees present at the beginning of the dynamic runs, and taking exactly the same initial spatial distribution of trees (but all belonging to the mean species) as in the dynamic run.

Since differences between the static and dynamic runs are sensitive to starting density and successional status, we explored a factorial combination of initial conditions, corresponding to early and late successional forests that were either left undisturbed or 'clear-cut' just prior to the start of the simulation and a doubling of CO_2. (Although we focus here on a scenario with instantaneous doubling of atmospheric CO_2 concentrations, more realistic CO_2 schedules – a linear increase from 350 to 700 p.p.m. in 50 years, and an increase following the IPCC '750 p.p.m.' scenario (Houghton *et al.* 1990) – produce qualitatively similar results.) In every case, the ultimate starting point was a random distribution of seedlings with equal densities from each species; this model forest was allowed to grow for either 100 (young forest) or 250 years (old forest) in ambient CO_2 (i.e. with unmodified growth rates) before doubling CO_2, and then was either left undisturbed or 'clearcut' (removal of all trees > 5 m in height) to generate the initial conditions for further simulation.

Finally, because the rate of aggradation in the dynamic and static-composition simulations differs even in ambient CO_2 (because successional change and ensuing changes in growth and mortality do not occur in the static simulation), we present all of our simulation results as comparisons between the *ratios* of basal area of the ambient and high-CO_2 runs for static and dynamic species compositions separately.

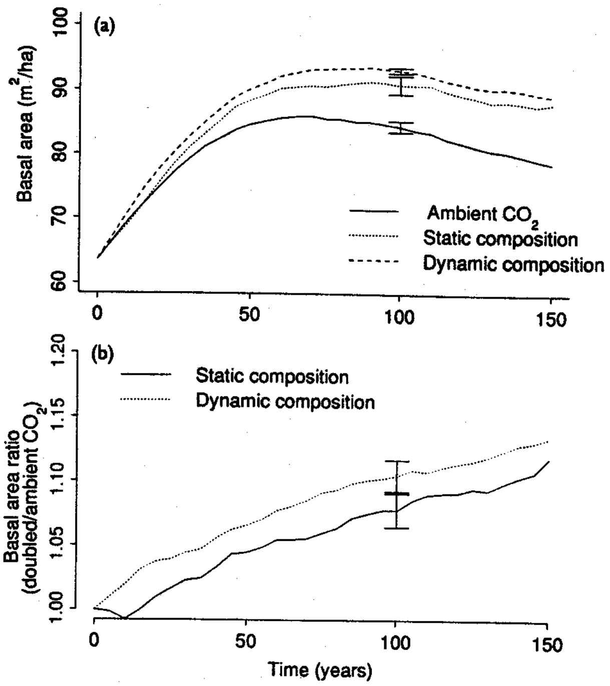

Fig. 2 (a) Total basal areas ($m^2\ ha^{-1}$) for a simulation at ambient CO_2, a simulation with static species composition (a single 'mean' tree species) in doubled CO_2, and a simulation including community dynamics (using the nine species indicated in Fig. 1) in doubled CO_2. The figure shows mean basal areas for 10 replicates of each simulation; error bars show one standard error of the mean. The trajectory of basal area in the static-composition runs (even without enhanced CO_2) differs from the baseline runs, because successional change and resulting changes in growth and mortality rates cannot occur; the mean basal area curve shows $((M'/M) \times A)$ instead, where M' and M are the basal areas in the static-composition high- and ambient-CO_2 basal area and A is the normal ambient-CO_2 basal area. Simulations were run from the same initial conditions, 100 years of (ambient CO_2) simulation after initial seeding with equal numbers of seedlings of all species (compare Fig. 3). (b) Average ratios of basal areas (enhanced CO_2/ambient CO_2), for static- and dynamic-composition simulations, for 10 replicate runs.

Results

Allowing community change generates a large additional enhancement in basal area above the static-composition response, over time scales of 50–150 years (Fig. 2). The first set of simulation runs compares dynamic or static species compositions (parameters derived as discussed above) with ambient or doubled CO_2, starting in a young, undisturbed forest.

Because of the limitation of CO_2 fertilization to subcanopy trees, the total enhancement of basal area accumulation by CO_2 is fairly small, about 5–20%. However, the difference between relative enhancement in the static and dynamic runs is large. We define the 'community-change effect', which summarizes the magnitude of basal area enhancement caused by species composition changes relative to the magnitude in a static-composition run, as $[\Delta(\text{dynamic})-\Delta(\text{static})]\ /\Delta(\text{static})$, where Δ stands for the percentage enhancement in basal area caused by CO_2. The community-change effect is 35% after 100 years ($\Delta(\text{static}) = 6\%$, $\Delta(\text{dynamic}) = 9\%$), and averages about the same level over the period from 50 to 150 years (Fig. 2). *If* CO_2 fertilization turns out to be an important component in regional or global carbon budgets, then the effects of dynamic changes in species composition should be important as well.

To test the generality of this result, additional simulations were run with initial conditions reflecting different management regimes (Fig. 3) and with different size cutoffs for CO_2 fertilization, representing faster acclimation or nutrient limitation. In particular we used as initial conditions young (early successional) and old (late-successional) forests that were either left undisturbed or clear-cut at the beginning of the simulations, and compared 1 cm and 10–20 cm d.b.h. fertilization cutoffs.

Different successional and density conditions lead to significantly different diversity effects (Fig. 3). When young forest is clear-cut, highly enhanced red oak takes over the canopy, generating a large community-change effect; in contrast, old, undisturbed forest shows much less community-change effect. Figure 4 shows relative changes in species composition after 100 years for all four initial conditions, with species sorted either by CO_2 response or by successional status. High CO_2 responders and early successional species do well in enhanced CO_2 conditions, high responders for obvious reasons and

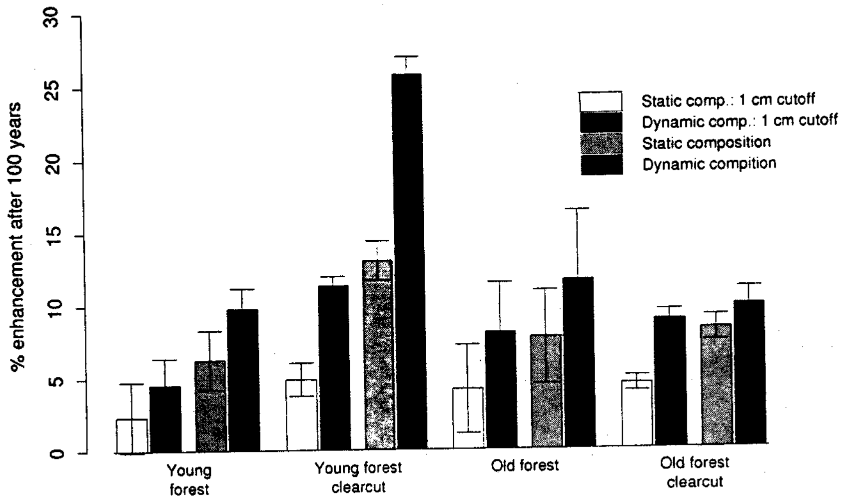

Fig. 3 Results of simulations with different species compositions (static and dynamic), forest age (young/old), disturbance regime (no disturbance/clear-cut), and CO_2-fertilization cutoff (canopy height and 1 cm d.b.h.). Solid bars show the mean percentage enhancement of basal areas (m^2 ha^{-1}) between ambient and doubled-CO_2 conditions, after 100 years of growth; error bars show one standard error of the mean. Five replicates were run for each treatment/diversity combination. Growth and CO_2 parameters for the static- and dynamic-composition simulations were derived as described in Fig. 2.

early successional species because their high understory mortality rates are substantially reduced by increased growth.

Although reducing the size cutoff for CO_2 fertilization (unsurprisingly) lowers the absolute enhancement of basal area for both static and dynamic species compositions, it does not qualitatively change the relative effects of changing species composition. Species compositional changes themselves (not shown) maintain the same patterns but are roughly half the magnitude, with changes ranging from −4 to + 8%.

The mechanism generating increases in basal area is somewhat subtle. Because the model assumes CO_2-fertilization only in non-canopy trees, and because the basal area of the forest is dominated by canopy trees, the only changes in forest composition that affect basal area are those that change stand density, allowing more similar-sized canopy trees to coexist. (Simulations including canopy-tree fertilization would generate far larger changes in total basal area.) Forests with a greater proportion of early successional species show enhanced survival in the understory because of increased growth, higher light levels in the understory because of lighter canopies, and increased dispersal into gaps; all of these changes allow denser stands, with fewer gaps and more surviving canopy trees in a given area of forest. Mid-successional red oak, with its extreme response to CO_2, drives many of the patterns observed in these simulations. These results contradict earlier studies of climate change and forests, which found an increased tempo of succession and increased importance of late-successional species (Solomon 1986), and also contrasts with recent suggestions that competitive takeover by gap-dominant species could turn tropical forests into net carbon sources (Philips & Gentry 1994).

The single species used in the static-composition simulations incorporated average values for both the mortality and growth parameters and the CO_2-response parameters. One way to assess the relative importance of these averages, as well as of initial conditions, is to use an analysis of variance across simulations with replicated factorial combinations of mean and diverse parameters. Treatment of the 'successional' (mortality, growth, and dispersal) parameters, CO_2 parameters, and initial conditions accounted for ≈ 80% of the total variation in basal area enhancement at 100 years (as in Fig. 3). Initial conditions (age and clearcut status) explained 24% of the variation. The surprising result is that diversity in successional parameters explained 32% of the variation in response to CO_2, while the interaction between CO_2-response and successional parameters explained 10%, and all other terms and interactions were smaller than 3%. In other words, the response caused by successional differences (for example in low-light survivorship) was *larger* than the response caused by differences in CO_2 response, which appeared only in an interaction term with the successional parameters.

While the insignificance of differential CO_2 response in this case is somewhat artificial (hemlock, which has the second-lowest β value among the species modelled, is abundant in the initial distribution of species and depresses the overall response of the forest), the general conclusion is that it is not just the explicit plant responses to climate changes that matter, but the interaction between climate change and existing competitive and successional dynamics. For example, in our model the interaction between growth, understory survival and stand density of early successional species is the determinant of productivity increase. In a serpentine grassland, Field *et al.* (1994) have found that enhanced CO_2 atmospheres favour late-season growers by changing the seasonal soil water balance. Similar interactions with the determinants of survival and competitive success in a particular environ-

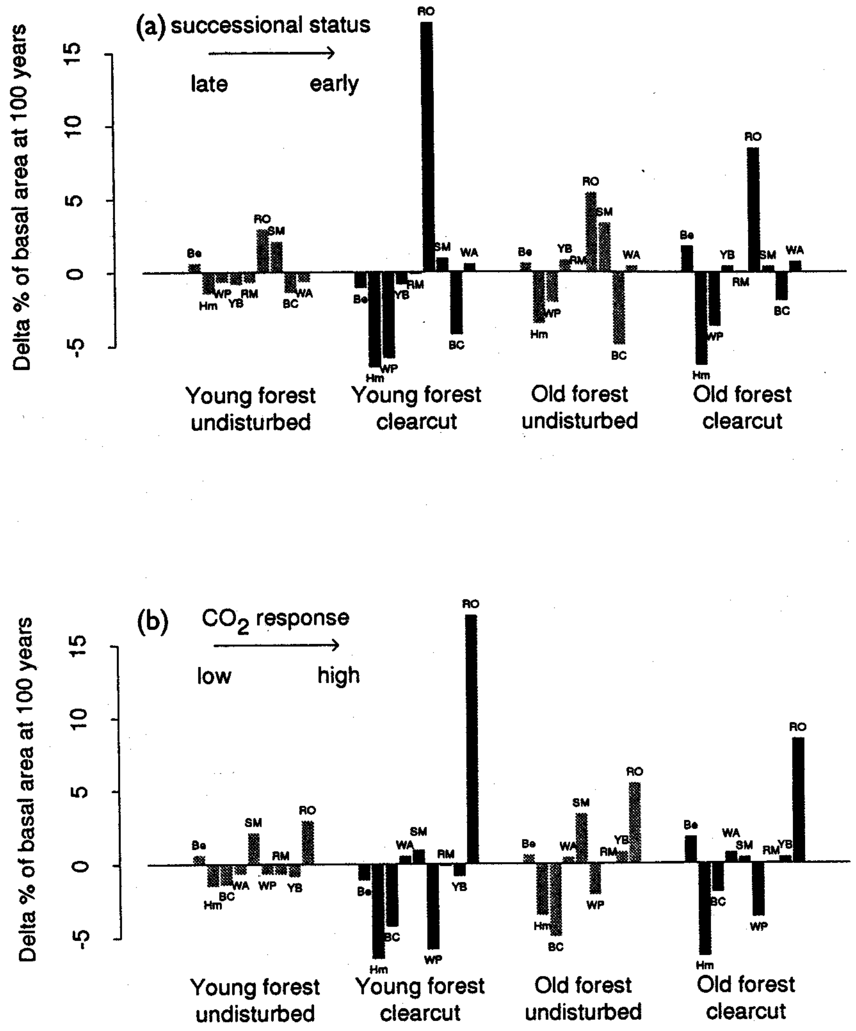

Fig. 4 Relative changes in species composition after 100 years of CO_2 enrichment. Relative change is defined as the change in percentage composition of the forest between the ambient and high-CO_2 simulations. (a) Species sorted by successional status (slope of the exponential relationship between growth and mortality, highest for early successional species). (b) Species sorted by magnitude of response to CO_2.

ment are likely to take place in other terrestrial ecosystems.

We note that, although these simulations always showed a greater basal area for dynamic than for static-composition forests, other, cruder methods for picking the parameters of the mean species present at the start of the static simulation occasionally produced extremely large enhancements in the static-composition case for some initial conditions. We take these effects as a warning that as well as overlooking the consequences of community change, static-composition models can be sensitive to the precise choice of parameters.

Discussion

These simulations predict strong dependence of community-change effects both on forest management regime and on the particular distribution of CO_2 enhancement among species with different successional status (Fig. 1). The realization of a large community change and a large CO_2 response in a particular forest may depend on the presence of a particular species that happens to be well adapted – by chance, since there is no selective pressure in current environments for response to high CO_2 concentrations – both to high CO_2 and to a particular successional environment. If such a suitable species does not exist, species-specific enhancement may be small. However, high-diversity plant communities will be more likely to include a species capable of responding to particular changes in the environment (the diversity–stability hypothesis — Tilman & Downing 1994; Naeem *et al.* 1994).

The simulations show that diversity and the resulting community change under anthropogenic CO_2 forcing can significantly affect forest growth rates. The rapid pace of community change is not surprising when we consider that normal successional dynamics can drive species replacement within one or two generations, and that the differences among CO_2 responses and the magnitude of their effects are large in comparison to the interspecies differences that normally drive succession. Eventually, the changes we describe will be limited by the effect of factors other than CO_2 and light, and by phenotypic and genotypic adaptation to new conditions — the same forces that limit the normal progress of selection and succession.

Including climatic changes other than increasing CO_2 concentrations will produce many unpredictable changes, but may actually strengthen our conclusions. In our simulations, particular species are able to overcome light-limitation on growth in the understory because of CO_2-fertilization. With more independent limitations on growth, and more different environmental stresses, the subset of organisms capable of thriving under new conditions will grow even smaller and the importance of diversity will become proportionally larger. Our results argue for the preservation of biodiversity in purely practical terms, for its possible ability to mitigate the effects of anthropogenic environmental change.

We have shown that the existence of species diversity and community change can amplify the effects of CO_2 fertilization in a forest model by as much as 30% (of an admittedly relatively small absolute effect). These results vary with forest history and management (initial conditions); diversity of species' competitive strategies under current conditions (successional status); and diversity of species response to future changes (seedling growth response to CO_2). Our strongest conclusion is that the existing structure and diversity of communities may have a significant, and not naively predictable, effect on ecosystem-level responses to climate change. It is no accident that our analysis was performed on one of the few terrestrial systems where a field-calibrated mechanistic model of community dynamics was available; the best confirmation of our results would be the construction and validation of such a model in a model system where climate could be varied experimentally to match expected anthropogenic changes.

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