

Transient response of forests to CO₂-induced climate change: simulation modeling experiments in eastern North America *

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Summary. The temporal response of forests to CO₂-induced climate changes was examined for eastern North America. A forest stand simulation model was used with the assumption that climate will change at a constant rate as atmospheric CO₂ doubles, and then as CO₂ doubles again. Before being used to project future vegetation trends, the simulation model FORENA was verified by its ability to reproduce long, temporal sequences of plant community change recorded by fossil pollen and by its ability to reproduce today's vegetation. The simulated effects of changing monthly temperature and precipitation included a distinctive dieback of extant trees at most locations, with only partial recovery of biomass in areas of today's temperate deciduous forest. In the southern portion of today's deciduous-coniferous transition forests the simulated dieback was indistinct and recovery by deciduous tree species was rapid. In more northerly transition areas, the dieback not only was clearly expressed, but occurred twice, when new dominant species replaced extant conifers, then were themselves replaced, as climate change continued. Boreal conifers also underwent diebacks and were replaced by deciduous hardwoods more slowly in the north than in the south. Transient responses in species composition and carbon storage continued as much as 300 years after simulated climate changes ceased.

The increasing global concentration of atmospheric CO₂ is undisputed (Keeling et al. 1984; Trabalka 1985). In contrast, controversy and concern are being generated by potential effects of a rapid change in atmospheric CO₂ concentrations. Because CO₂ is a "greenhouse gas", the lower atmosphere is expected to warm, although the magnitude of warming is questionable. General circulation models (GCMs) of the atmosphere suggest the globe would warm 2–4° C with a CO₂ doubling (Manabe and Stouffer 1980). The model results also indicate greater warming at the poles than at the equator (Manabe and Wetherald 1980; Mitchell 1983), and greater warming during winter months than summer months (Manabe et al. 1981).

Calculations of subsequent ecosystem response to the temperature shifts, induced by increasing CO₂ (e.g., Emanuel et al. 1985), indicate that profound changes in plant and biome geography would occur. Biotic responses to cli-

mate associated with a CO₂ doubling (Manabe and Stouffer 1980) included reduction of the earth's forest area, expansion of tropical forests at low latitudes, and loss of boreal forests at high latitudes.

Direct "fertilization" effects of CO₂ have been detected in glasshouse experiments with tree seedlings and branches (e.g., articles in Lemon 1983). Growth is more rapid, leaves and roots are larger, and use of water is more efficient when CO₂ is enhanced (Kramer and Sionit 1985). Too little is presently known to project whether the same results will occur in mature trees growing in nutrient-limited unmanaged stands. Model simulations using the little knowledge available of direct CO₂ effects indicated that growth enhancement of whole forests may be much less than expected from growth enhancement of the individual species (Botkin et al. 1973; Shugart et al. 1984).

The GCM projections of climate change, the calculations of vegetation response to CO₂-induced climate change, and the glasshouse experiments and model simulations of carbon fertilization effects all have assumed stable configurations of vegetation and climate at selected higher CO₂ concentrations. Yet, neither a long-lasting, stable concentration of atmospheric CO₂ nor a stable climate that results, is likely to ever exist. Instead, such future conditions will merely be ephemeral points along a continuum of change. Response to this continuous environmental change, including lags induced by the nature of the responding systems, will differ from responses to stable conditions. For example, Schneider and Thompson (1981) suggest that a transient response of climate to changing atmospheric CO₂ will originate with slowly changing ocean temperatures, and will include several decades. Although temperature increases will eventually be greater in winter than in summer, the initial warming will be immediate in summer but lagged up to several decades in winter because oceans control winter atmospheric temperatures. Indeed, Hansen et al. (1985) recently demonstrated that most of the warming in response to CO₂ increases since 1850 may not yet have occurred.

The transients in vegetation response to future changes in climate have not been calculated. Trees in particular are likely to induce complex ecosystem transients because (1) trees are long-lived, (2) trees of differing maximum potential age can occupy the same stands and forests, and (3) tree species determine rates of slowly-changing forest nutrient cycling. The transient response of forests is an important uncertainty in the global CO₂ issue. Forests cover 35–40% of the earth's land surface (Olson 1975), produce 65% of

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the annual carbon fixation of the globe (Whittaker and Likens 1973), and store over 80% of the world's organic carbon (Olson et al. 1983). Forest carbon dynamics can therefore effect the carbon balance of the globe (Houghton et al. 1983; Solomon et al. 1985).

How can the transient response of forests to climate change be projected? The only accurate way is to await development of the changes, an approach which may be unacceptable for those interested in any mitigation strategies whatsoever. Assuming that some level of error is acceptable in order to project effects *a priori*, then models can be substituted for reality. Although empirical regression models may be easily produced and utilized, the interdependencies and nonlinearities in the forcing and response systems indicate that results from carefully-structured, explanatory simulation models will be most informative.

Such models should first be used to describe the change in climate with time. No accepted models presently exist to project the transient changes, although initial test runs with an annually-changing static GCM are in progress (J. Hansen, personal communication). In the absence of such projections, assumptions on the nature of the climate transient must be made and used to connect results from several static GCM simulations. Forest transient response, on the other hand, may be calculated with available forest stand simulation models (Botkin et al. 1972; Shugart and West 1977), modified to include ecological processes operating over large, subcontinental regions (Solomon et al. 1984, and below).

Assume that only minor errors of fact and concept characterize both the stand simulators and the climate models which constrain the stand simulators. Although this is the best that can be expected, the errors become amplified through the systems of models, generating flaws that are large enough to preclude direct application of the model output to the real world. On the other hand, the results of carefully planned simulations focus attention on likely future outcomes and on the unavailable but crucial data and concepts required for acceptable projections of the future changes. This latter application is the objective of the work described below.

Methods

Forest stand simulation model

The initial models by Botkin et al. (1972; JABOWA) are the basis for versions by Shugart and West (1977, 1979; FORET), from which the model described here (FORENA, *FORests of Eastern North America*) was developed. Shugart (1984) describes the models in detail. Briefly, the models are mixed-species and mixed-age stochastic stand simulators, implemented in FORTRAN, and designed to mimic processes controlling tree establishment, growth, and mortality within forests (e.g. Watt 1947; Bray 1956).

The FORENA model consists of response functions that apply to all species, and parameters which define the limits of response functions for individual species. The response functions (Fig. 1) include variables intrinsic to the species (maximum potential growth rate, mortality), or to the stand (shading, crowding), and variables extrinsic to the stand (variance in summer warmth, winter cold, soil moisture). The parameters were assembled from common silvics manuals (Fowells 1965; Harlow et al. 1979) to char-

acterize the limits to establishment, growth, longevity, and mortality of each of 72 tree species (Table 4 in Solomon et al. 1984). The extrinsic variables are mapped from data sets in Olson et al. (1980) and Hare and Thomas (1979), and the matching tree distributions are mapped in Little (1971, 1977).

FORENA calculates the annual establishment of new seedlings, the growth of each tree present, and the mortality of trees on a $1/12$ ha plot, based on plot conditions. These conditions include shading at 0.1 m vertical intervals, determined from light attenuation (Monsi et al. 1973) through the leaf area generated by trees growing above each level. Leaf area in turn is calculated from empirical equations in Sollins et al. (1973) that relate the leaf areas of trees to their diameters. Temperature affects growth as annual growing degree days (heat sums above a minimum temperature of 5° C; Hare and Thomas 1979). Degree days are stochastic variables, provided as sums of monthly random values drawn from predefined means and standard deviations. The stochastic January temperature values used to calculate degree days also provide a lowest annual winter temperature. Annual drought days (days of each growing season in which soil moisture is below the wilting point of -15 bars) are also stochastic variables, calculated from a soil column of predefined depth and soil moisture capacity, into which the monthly precipitation enters, and from which it leaves either as runoff (when soil moisture capacity is exceeded) or as evapotranspiration, determined by the monthly temperature (Thorntwaite and Mather 1957).

During each simulated year, the model applies the shading, crowding, winter cold temperature, drought days and degree days on the plot, to the optimum growth each tree can achieve at its respective age (Fig. 1), and reduces that year's annual growth of each tree accordingly. The model randomly selects trees for death according to the age-dependent mortality function (Fig. 1) and a second, age-independent mortality criterion (below). It plants a new cohort of seedlings, the species and amount being selected stochastically. The available species pool each year depends on the plot conditions that year, including light levels, presence of leaf litter (from plot leaf area), and of mineral soil (from death of a large tree), and death of an individual of species capable of sprouting from roots when above-ground parts are lost.

Data from field and laboratory literature parallel the simulated optimum growth (Fig. 1; see Doyle 1983) and age-independent mortality (Nichols 1968; 2 consecutive years of growth less than 10% of each species' optimum growth at that age raises the probability of mortality to an arbitrary 0.368). Documented responses also parallel those of growth to shading (Kramer and Decker 1944), soil moisture (Bassett 1964), and temperature during growing seasons (Larcher 1969) and winter (Sakai and Weiser 1973) (Fig. 1). In contrast, lack of field data forced the use of intuition in routines to mimic effects of crowding (an hypothesized proxy for nutrient competition) as a negative linear function of tree density (Fig. 1; Shugart and West 1977), and of age-dependent mortality as a negative exponential function of tree age (Fig. 1; Botkin et al. 1972).

Simulation conditions

The model FORENA was used to simulate effects of CO₂-induced climate change on forest growth at 21 locations

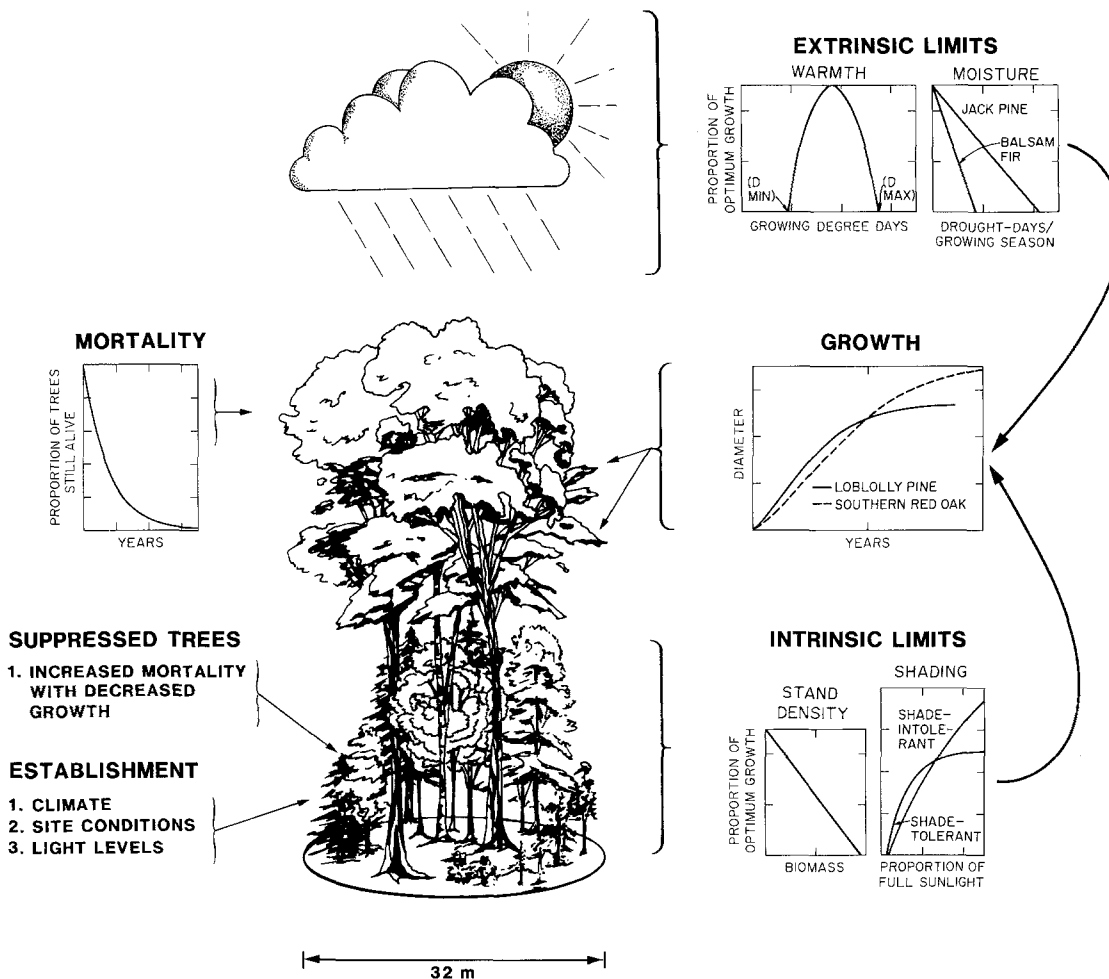


Fig. 1. Diagrammatic representation of important processes in forest gap dynamics simulated by FORENA. Extrinsic stochastic variables and intrinsic deterministic variables control growth differently (right), depending on tree species, age, and height, and numbers of trees on the plot (center). Trees die as they age or stop growing (left center), and are replaced by stochastic seed sources, depending on site conditions (left bottom). From Solomon and Webb 1985

in eastern North America (Fig. 2). In addition to the assumptions inherent in the model described above, the simulations were run under the following conditions.

1. All forests began on a cleared plot, growing undisturbed for 400 years with modern climate (defined in item 6, below). The lack of disturbance is not realistic in forests of eastern North America (e.g. White 1979). The mature, undisturbed forests simulated may be more sensitive to environmental changes than would irregularly disturbed forests.

2. At all times during each simulation, 72 tree species were available for selection to enter the plot as 1.5 cm diam saplings. This assumption simplifies the problem of estimating which species would enter a plot during changing climate, but it eliminates any transients relating to slow tree immigration.

3. The scenario of CO_2 -induced climate change included three phases.

- (a). The forests underwent climate change beginning at year 400, reaching the climate of a CO_2 doubling ($2 \times \text{CO}_2$) by year 500, with linear interpolation of changing climatic means each year between years 400 and 500.

- (b). The forests underwent continued climate change after year 500. By year 700, climate matched that from a CO_2 quadrupling ($4 \times \text{CO}_2$), with linear interpolation of

changing climatic means each year between years 500 and 700.

- (c). Climate stabilized at year 700 and the simulation continued another 300 years thereafter. The foregoing chronology is based on current estimates of the likely future CO_2 increases, and it assumes that CO_2 -induced climate changes will be incremented linearly. A doubling of atmospheric CO_2 is quite plausible within 100 years at current rates of increase (Gammon et al. 1985) but there is no basis for suggesting when, if ever, it will quadruple. There is good evidence that the CO_2 increase will not be linear (e.g. Gammon et al. 1985), but no information exists to estimate how the climate will respond to either a linear or the more probable geometric increase in CO_2 .

4. The climate scenarios for each site, from Mitchell (1983) and Mitchell and Lupton (1984), are similar to those of Manabe and Stouffer (1980), whose GCM Mitchell modified and used. The advantages of Mitchell's work are that temperature and precipitation are illustrated by season, simulated on realistic geography, and include both $2 \times \text{CO}_2$ and $4 \times \text{CO}_2$ conditions from the same model. The climate changes (Figs. 16 and 17 in Solomon et al. 1984) included increased temperature changes with latitude (range 1 to 7.5°C), winter temperature increases (range 2 to 6°C at $2 \times \text{CO}_2$; 2.5 to 7.5°C at $4 \times \text{CO}_2$) of greater magnitude

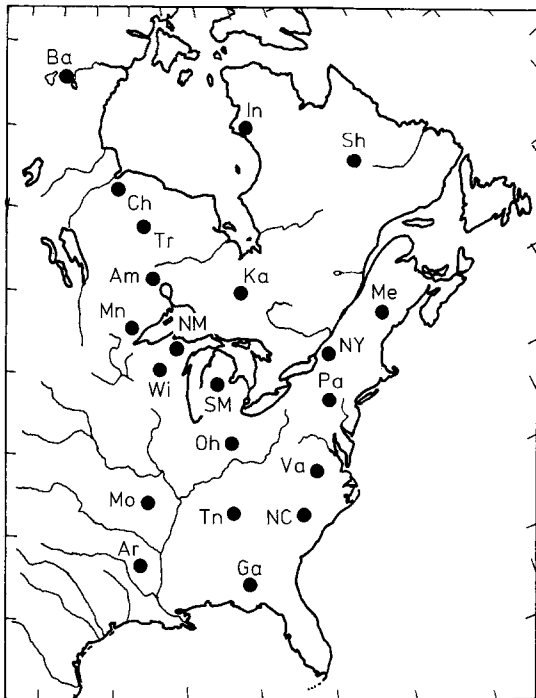


Fig. 2. Locations used to simulate forest response to CO₂-induced climate change, including Baker Lake, North West Territories (*Ba*); Churchill, Manitoba (*Ch*); Trout Lake, Ontario (*Tr*); Inoucdjouac, Quebec (*In*); Armstrong, Ontario (*Am*); Kapuskasing, Ontario (*Ka*); Shefferville, Quebec (*Sh*); Northeast Division, Minnesota (*Mn*); West Upper Division, Michigan (*NM*); Northcentral Division, Wisconsin (*Wi*); Central Lower Division, Michigan (*SM*); Northern Division, Maine (*Me*); St Lawrence Valley Division, New York (*NY*); Upper Susquehanna Division, Pennsylvania (*Pa*); West Central Division, Ohio (*Oh*); Eastern Piedmont Division, Virginia (*Va*); Southern Piedmont Division, North Carolina (*NC*); Cumberland Plateau Division, Tennessee (*Tn*); Southwest Division, Georgia (*Ga*); West Ozarks Division, Missouri (*Mo*); and South Central Division, Arkansas (*Ar*).

than summer increases (range 1 to 3° C at 2 X CO₂; 2.5 to 5° C at 4 X CO₂), summer precipitation decrease near the Great Plains (range 0 to -1 mm/day at 2 X CO₂ and at 4 X CO₂), increase along the U.S. east coast (range 0 to 1 mm/day at 2 X CO₂; 0 to 2 mm/day at 4 X CO₂), and no change in winter precipitation except for a decrease in the southern U.S. (range 0 to -1 mm/day at 2 X CO₂; 0 to -2 mm/day at 4 X CO₂).

5. Standard deviations of monthly temperature and precipitation are not changed by CO₂-induced climate shifts.

The assumption is important because, like reality, the model directly generates forest dynamics with climate variance, not with climate means. The assumption of unchanging variance is questionable at best because warmer climate usually contains lower temperature variance (Wigley et al. 1980; Palutikof et al. 1984), while precipitation variance may be inversely related to precipitation amounts (e.g. Green and Sellars 1964). Since there is no basis for quantitative estimates of any change in climate variance, none was simulated.

6. Monthly temperatures, precipitation, and their standard deviations during the initial 400 years at U.S. sites were from climatic divisions, 1941 to 1970 (Olson et al. 1980). Canadian site means are from records of nonuniform length at individual meteorological stations (Hare and Thomas 1979), and standard deviations are from the nearest U.S. division, taken unchanged for temperature, or as a percentage of the mean for precipitation. The soil used at all sites was a 100-cm deep mesic silt-loam, with 17% available water capacity, 35.5% field capacity, and 18.5% wilting point. The soil was chosen to minimize the effects of precipitation deficits on simulated forests because precipitation is among the variables which GCMs simulate most poorly (Manabe 1983).

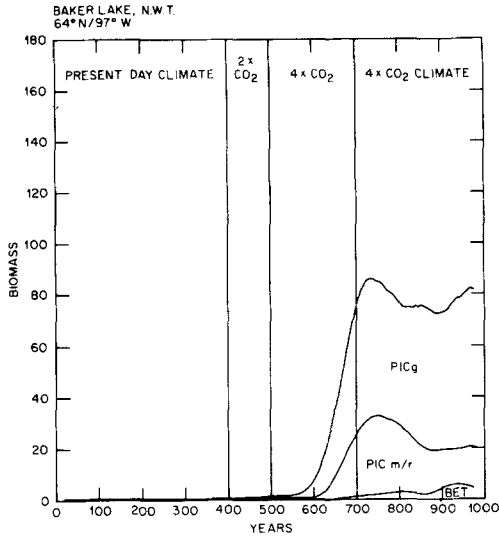
7. Model output at each of 21 sites (Fig. 2) consisted of values every five years. Runs at each site were replicated ten times and averaged. The only difference between simulations from one site to another was the entry of different monthly climate variables, latitude (used to calculate evapotranspiration), and new monthly climate means at 400 to 500 and 500 to 700 years. The model interpolated mean climate values for each year between 400 and 700 years, except that the growing season (used to calculate soil moisture effects) was shifted at 450, 550, and 750 years.

Simulation model validity

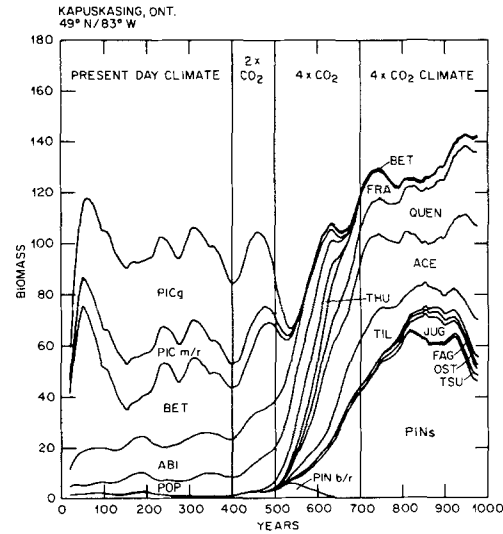
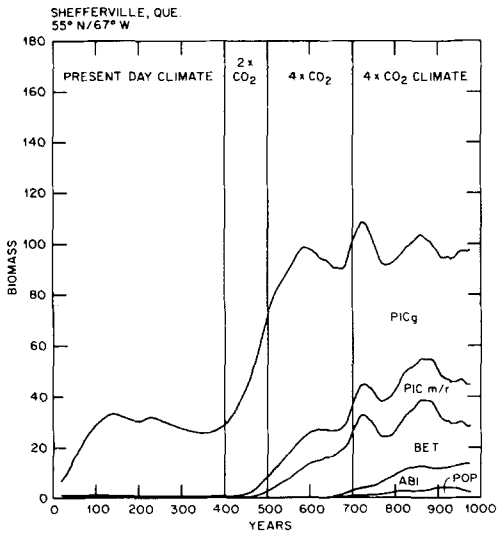
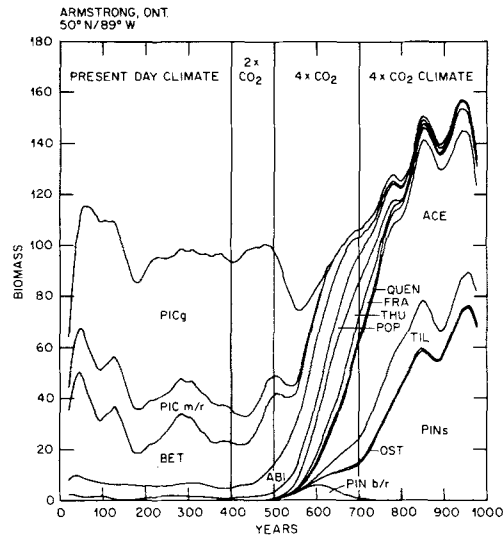
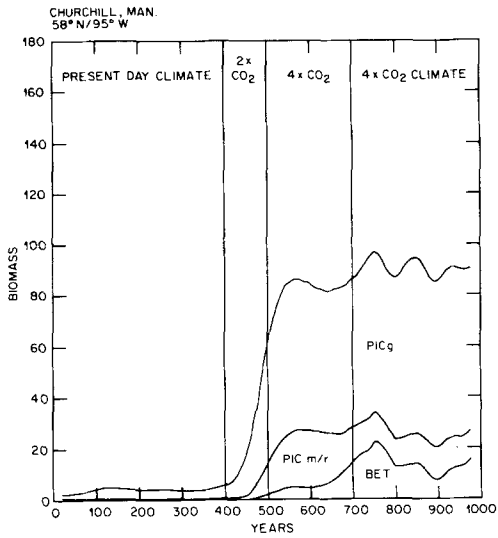
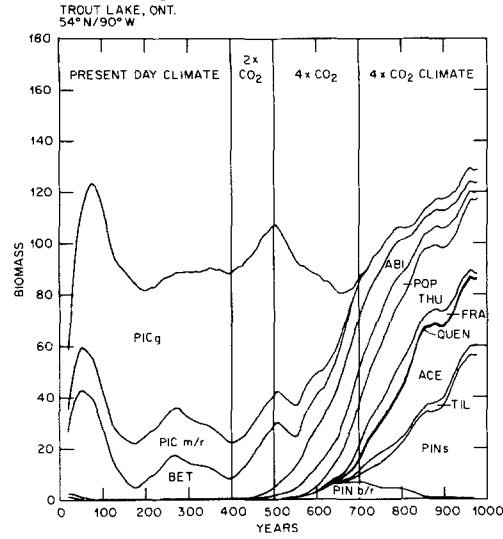
The validity of the FORENA model (without current age-independent mortality routine) has been tested with independent forest composition data, defined by fossil pollen deposited during the past 10,000 years, and during full-glacial time, 16,000 years ago (Solomon and Shugart 1984). The model results are consistent with long-term variations measured in forests, including long temporal sequences and spatial patterns (Solomon and Webb 1985). The model also reproduces the specific forest responses to unique climate configurations which occurred in the past, which do not occur today, and are suggested by climate models for future CO₂-induced warming (Solomon and Tharp 1985). These

Fig. 3. Simulations of 1000-year biomass dynamics, including CO₂-induced climate change, at three sites in tundra or tundra-boreal forest mosaic (column 1) and three sites in northern boreal forest regions (column 2). Ordinate is in megagrams of biomass per hectare. See text for simulation conditions at years 0–400, 400–500, 500–700, and 700–1,000. Tree taxon abbreviations used in Figs. 3 to 5 include: ABI, *Abies balsamea* (balsam fir) and *A. Fraseri* (Fraser fir); ACE, *Acer saccharum* (sugar maple), *A. rubra* (red maple), and *A. saccharinum* (silver maple); AES, *Aesculus octandra* (yellow buckeye); BET, *Betula lenta* (sweet birch), *B. papyrifera* (paper birch), *B. alleghaniensis* (yellow birch), and *B. populifolia* (gray birch); CAR, *Carya cordiformis* (bitternut hickory), *C. tomentosa* (mockernut hickory), *C. glabra* (pignut hickory), *C. ovata* (shagbark hickory), *C. laciniosa* (shellbark hickory), and *C. texana* (black hickory); CAS, *Castanea dentata* (American chestnut); CEL, *Celtis laevigata* (sugarberry); FAG, *Fagus grandifolia* (American beech); FRA, *Fraxinus pennsylvanica* (green ash), *F. americana* (white ash), *F. nigra* (black ash), *F. quadrangulata* (blue ash); ILE, *Ilex opaca* (American holly); JUG, *Juglans cinerea* (butternut), *J. nigra* (black walnut); LIQ, *Liquidambar styraciflua* (sweetgum); LIR, *Liriodendron tulipifera* (yellow-poplar); NYS, *Nyssa sylvatica* (black gum); OST, *Ostrya virginiana* (eastern hornbeam) and *Carpinus caroliniana* (American hornbeam); PICg, *Picea glauca* (white spruce), *P. mariana* (black spruce) and *P. rubens* (red spruce); PINb/r, *Pinus banksiana* (jack pine), *P. resinosa* (red pine), *P. echinata* (shortleaf pine), *P. taeda* (loblolly pine), *P. virginiana* (Virginia pine), and *P. rigida* (pitch pine); PINs, *Pinus strobus* (white pine); POP, *Populus balsamifera* (balsam poplar), *P. grandidentata* (bigleaf aspen), *P. tremuloides* (trembling aspen); PRU, *Prunus serotina* (black cherry); QUEN, (northern) *Quercus alba* (white oak), *Q. coccinea* (scarlet oak), *Q.*

TUNDRA-WOODLAND



N. BOREAL FOREST



pinus (chestnut oak), *Q. rubra* (northern red oak), *Q. velutina* (black oak), *Q. macrocarpa* (bur oak), *Q. borealis* (gray oak), and *Q. ellipsoidalis* (northern pin oak); QUEN, (southern) *Quercus falcata* (southern red oak), *Q. lyrata* (overcup oak), *Q. marilandica* (blackjack oak), *Q. muehlenbergii* (chinkipin oak), *Q. nuttallii* (Nuttall's oak), *Q. palustris* (pin oak), *Q. shumardii* (Shumard's red oak), *Q. stellata* (post oak), and *Q. virginiana* (live oak); THU, *Thuja occidentalis* (northern white cedar), *Juniperus virginiana* (red cedar), and *Larix laricina* (tamarack); TIL, *Tilia americana* (American basswood) and *T. heterophylla* (white basswood); TSU, *Tsuga canadensis* (eastern hemlock); ULM, *Ulmus americana* (American elm) and *U. alata* (winged elm).

and earlier long-term simulation studies (Solomon et al. 1980, 1981) developed the model capability to reproduce temporal sequences of changing communities. This development, in turn, led to modeling the temporal dynamics of changing communities of different forests within a large region (Solomon et al. 1984).

The spatial aspects of forests were reproduced remarkably well, based on comparison of simulations during the first 400 years at each site, with potential vegetation described for the sites (U.S. by Kuchler 1964; Canada by Rowe 1972). The model was physiognomically correct, simulating stunted woodland where scattered trees grow, simulating forests where forests grow, and simulating growth of nothing where trees are absent on the modern landscape (the latter capability being absent in both JABOWA and FORET).

Major ecosystems, such as those defined by Braun (1950), were also correctly simulated. The 72 tree species at 21 sites provided over 1,500 opportunities for model responses to be wrong at the species level (species growing where or when they should not, or not growing where and when they should; species growing in too great or too little abundance). A detailed survey of the model results, however, yielded fewer than 150 such occurrences, even with a broad definition of "wrong" (Kuchler's "dominants" and Rowe's "characteristic species," >10% of simulated stand biomass; Kuchler's "other components" and Rowe's "common species," 1–10% of simulated biomass; all other species, <1% of simulated stand biomass). In short, the model is reasonably valid for the purpose of this investigation, although the model must be viewed as being no more than an abstraction, and its picture of the future as only an hypothesis, not a prediction.

Results

The results are subdivided into examinations of today's northern boreal forests dominated by conifers, the transition forests of mixed deciduous and coniferous trees, and the temperate deciduous forests. Figs. 3 to 5 illustrate the species dynamics simulated at 18 of the 21 sites (data at Inoucdjouac Quebec, northeast Pennsylvania, and southwest Georgia [Fig. 2] not shown). The 72 species simulated are grouped into 28 taxa. The species important in taxon descriptions, but which could not be included legibly in Figs. 3–5 are mentioned in the text. Common and scientific names are provided in the legend of Fig. 3.

Northern conifers: Tundra-woodland and northern boreal forest (Fig. 3)

Modern forests. The simulations in tundra-woodland and north boreal forests (initial 400 years, Fig. 3) reproduced the floristically simple forests growing there today. The model grew no trees on the modern tundra (Inoucdjouac, not shown, and Baker Lake). It is important to note that the model takes no cognizance of the presence of permafrost in these regions. The lack of a modeled soil energy balance precludes more precise uses of the model in these low-arctic areas. A recent stand simulator deals with the unique complexities along tundra-forest borders of low sun angles interacting with high fire frequencies, effects of tree species on permafrost growth and of permafrost on tree species succession (Moorhead 1985).

A few stunted trees grew at the tundra-forest transition (Churchill, Shefferville), and *Picea glauca* (PICg), *P. mariana* (PICm/r), and *Betula papyrifera* (BET) grew in the northern boreal forest regions (Trout Lake, Armstrong). In more central boreal forest (Kapusksing), these species were joined by *Abies balsamifera* (ABI) and *Populus balsamifera* (POP) to mimic the actual undisturbed forests on well-drained mesic soils. *Pinus banksiana* (PINb/r) was absent from these simulations. In reality, it rarely grows in the mesic soil or in the undisturbed forests simulated here although it dominates many forests of the region (Rowe 1972).

Future Forests. The community response to CO₂-induced climatic change along the tundra-forest border was relatively simple (Fig. 3, column 1). Trees did not grow at Inoucdjouac (not shown), 300 km north of the present boreal forest along eastern Hudson Bay (Fig. 2), even with 4 X CO₂ climate. The 4 X CO₂ climate was required for growth of *Picea glauca* (PICg) and *P. mariana*, with a small amount of *Betula papyrifera* (BET), all in the form of a closed-canopy forest at Baker Lake, 350 km north of boreal forest to the west of Hudson Bay (Fig. 2). The 2 X CO₂ climate allowed closed forest to replace open parkland at Churchill and Shefferville. Even under a stable 4 X CO₂ climate, winter temperature tolerances and summer heat sum requirements kept simulated deciduous forest species from competing at these high latitudes.

Responses to CO₂-induced warming were more complex in the northern boreal forest region (Fig. 3, column 2). Initial response to 2 X CO₂ climate at Trout Lake was an increase in total stand biomass as *Picea glauca* (PICg) and *Betula papyrifera* (BET) grew more rapidly. The enhancement of the birch may result from the cyclic behavior it showed at all sites in the absence of climate change, a function of its intrinsic rapid growth, short life span, and the wide environmental tolerances of its seedlings. In contrast, the *Picea glauca* increase appears to result from the simulated climate shift toward spruce's temperature optimum. *P. glauca* began to decline during the 2 X CO₂ warming, sequentially from south to north.

A striking feature of simulated boreal forest behavior was the time-transgressive shift of species composition in response to time-constant climatic change. That is, the species involved were essentially the same from site to site. However, the time at which ecological stability was achieved differed from place to place. The vegetation composition stabilized by year 700 at Kapuskasing, by year 850 at cooler, drier Armstrong, and probably not by year 1,000 at the coldest, driest site at Trout Lake. This lag response appears to be a simple function of the ecological amplitude of the species available to grow. *Acer saccharum*, for example, could grow at the southern sites early in the climate scenario, but not at the northern sites until much later. In the meantime, there simply were no species adapted to the intermediate climate variables at the northern sites.

The total stand biomass was 30–50% greater in the modeled boreal forest following simulated climate change than it was previously because of the influx of larger deciduous tree species from the south. However, interpretation of the biomass enhancement requires caution because modeled tree geometry is rudimentary (all species use the same non-linear function of age for diameter). Preceding establishment of the deciduous forests, the boreal elements died

S. BOREAL FOREST

N. DECIDUOUS FOREST

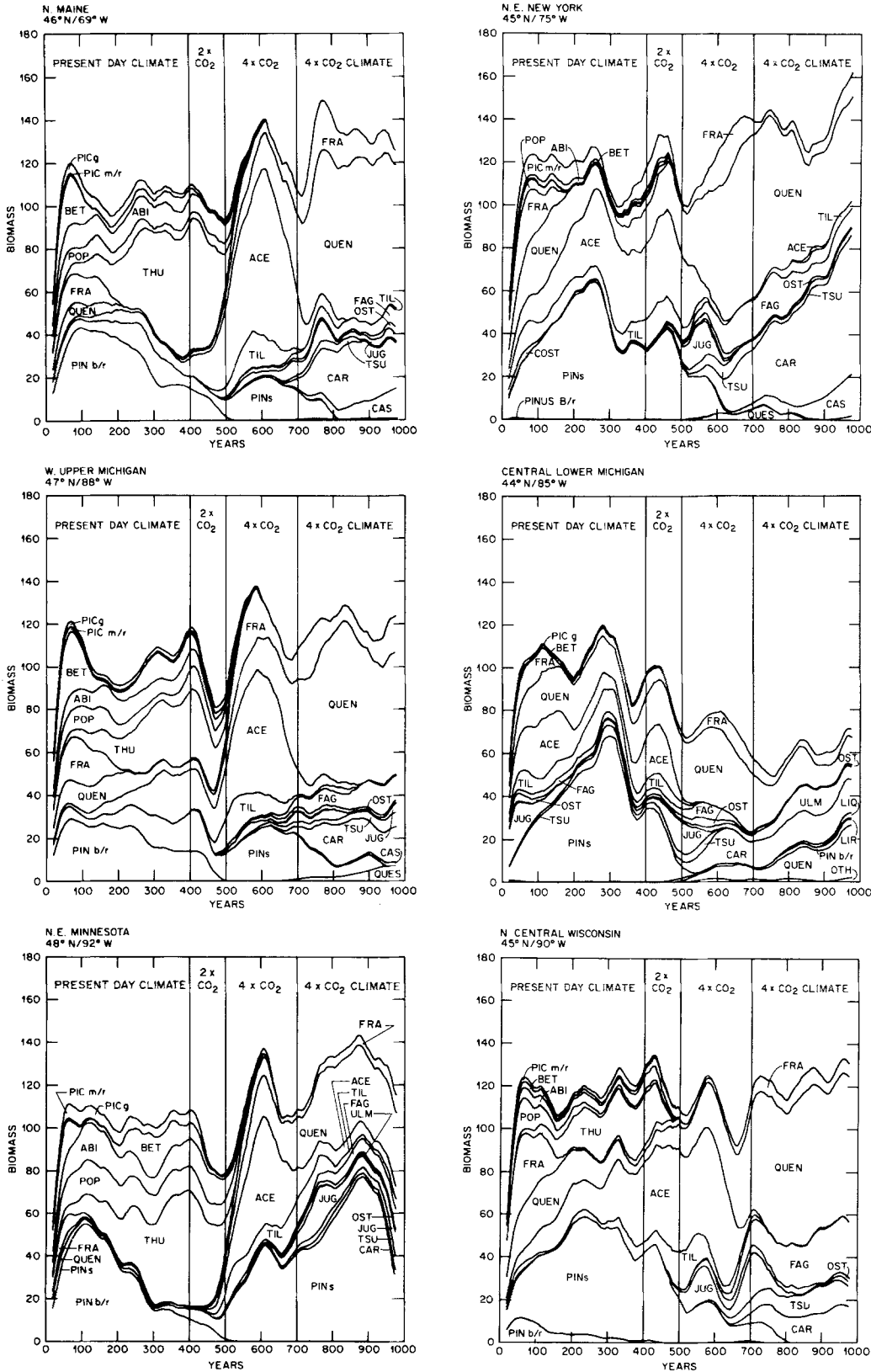


Fig. 4. Simulations of 1,000-year biomass dynamics, including CO₂-induced climate change, at three sites in southern boreal forest (column 1) and three sites in northern deciduous forest regions (column 2). Ordinate is in megagrams of biomass per hectare. See text for simulation conditions at years 0–400, 400–500, 500–700, and 700–1,000. Tree taxon abbreviations are given in legend of Fig. 3.

back, most clearly to the east (Kapuskaing). The community replacement dynamic which was simulated appears to consist of rapid extinction of local species, and subsequent gradual replacement by new species in which loss preceded gain by 50 to 100 years.

Transition forests: Southern boreal and northern deciduous forests (Fig. 4)

Modern forests. Today's coniferous-deciduous transition forests contain more complex species composition and interactions than the boreal forests, because the deciduous species from the south mix with boreal species from the north, each in a peripheral portion of their respective geographical ranges. Yet, simulated species composition and species frequencies (Fig. 4) were quite realistic through the first 400 years at all sites (e.g. see Curtis 1959, Braun 1950). Shade-intolerant species gained prominence first: *Betula papyrifera* (BET), *Fraxinus pennsylvanica* (FRA), *Pinus resinosa* (PINb/r), and *Populus balsamifera* (POP) to the north (Fig. 4, column 1), and *F. pennsylvanica* with *Quercus borealis* (northern small variety of *Q. rubra*, e.g. Britton and Brown 1913), *Q. ellipsoidalis* (QUEN), and *Populus tremuloides* (POP) to the south (Fig. 4, column 2). These species were subsequently outcompeted by the slower-growing and/or long-lived, and more shade-tolerant *Pinus strobus* (PINs) and *Thuja occidentalis* (THU), and by *Acer saccharum* (ACE) and *Quercus rubra* (QUEN), which have still stronger tolerance for shade. As on the modern landscape, the important spruce simulated at western sites was *Picea glauca* (PICg), while that at eastern sites was *Picea rubens* (PICm/r). *Pinus resinosa* (PINb/r) was favored in competition with *P. banksiana* (PINb/r), again due to effects of the mesic soils.

Anomalous tree species behavior is particularly evident in the biomass of *Thuja occidentalis* which constituted the majority of the three species labelled THU (*Juniperus virginiana* and *Larix laricina* are the other two) and which peaked later than it should and was probably too plentiful. This was due in part to the species' narrow tolerances for soil chemistry and drainage, which the model does not consider and which therefore allow the species to be simulated as a dominant on well-drained, commonly lime-poor soils where it normally is less abundant.

Future forests. Initial community response to simulated climate induced by 2 X CO₂ was a clear expression of the dieback phenomenon among many, but not all species in the southern boreal forests (Fig. 4, column 1). It was most pronounced at the dry western sites (northeastern Minnesota, western Upper Michigan). As warming continued, the community structure slowly recovered, first with expansion of *Acer saccharum* (ACE), *Tilia americana* (TIL), *Fraxinus pennsylvanica* (FRA), and *Pinus strobus* (PINs), then with various *Quercus* (QUEN) and *Carya* (CAR) species. This pattern of rapid dieback and slower recovery may merely reflect the fact that tree mortality takes less time than tree growth to maturity. At all three sites, the dieback separated the deterioration of dominant conifer species from the influx of an *Acer-Tilia* community. As warming continued, and apparently before community equilibrium was reached, the *Acer-Tilia* community itself underwent a second dieback (600 to 700 years) and was replaced by *Quercus-Carya* communities on the east (northern Maine, northwestern Michi-

gan) and a community of *Quercus* (*Q. velutina*, *Q. macrocarpa*, *Q. rubra*) and *Pinus strobus* on the west (northeastern Minnesota).

Overall stand biomass at all three southern boreal forest sites was about the same or slightly greater after the climate stabilized at 4 X CO₂ than it was before warming. The biomass enhancement from increased boreal forest growth and its replacement of tundra, visible at sites further north, was beginning to disappear before complete reversal occurred in deciduous forests to the south (see below).

Simulations at the northern deciduous forest sites (Fig. 4, column 2) illustrate many of the same phenomena already discussed. A mild double dieback is apparent in the Wisconsin diagram, from loss of *Thuja occidentalis* (THU) and *Pinus strobus* (PINs) at about 500 years, and from loss of *Acer saccharum* (ACE) at about 650 years. Only single diebacks appear during 4 X CO₂ warming at the other two sites. At the New York site, the dieback involved biomass changes no greater than those expected under unchanging climate. The central Lower Michigan site illustrates a continuous biomass decline from ca. 450 to 750 simulated years, as continuous warming forced the appearance then disappearance of many tree species (e.g. *Juglans cinerea*, *J. nigra* [JUG], *Fagus grandifolia* [FAG], *Tsuga canadensis* [TSU], several species of *Quercus* [QUEN], etc.).

Temperate forests: Western and eastern deciduous forests (Fig. 5)

Modern forests. The simulations of modern western and eastern deciduous forests (Fig. 5) accurately reflected the effects of both larger characteristic species (increasing the stand biomass) and increased species diversity (increased numbers of taxa). The simulations also appear realistic in terms of known forest composition and dynamics (Braun 1950). Dominant species reached maximum numbers in the mixed mesophytic forests (Virginia and Tennessee), with 18 species providing at least 1% of the biomass each and no species exceeding a 26% share of the stand biomass during the 400-year simulations. The actual species most characteristic of the mixed mesophytic forest (Braun 1950). *Tilia heterophylla* (TIL) and *Aesculus octandra* (AES), reach maximum proportions in the Appalachian Mountain region (eastern Tennessee and Kentucky, West Virginia and western Virginia) and are scarce or absent elsewhere (Little 1971; Braun 1950).

Quercus and *Carya* species dominate the simulated and the actual western forests, with decreasing tree density near the prairie-forest border (simulated in Missouri and Arkansas). In both simulated and real forests, *Quercus stellata* and *Q. shumardii* (QUES), *Celtis laevigata* (CEL), *Quercus velutina* and *Q. rubra* (QUEN), and *Carya ovata* (CAR), are more common on the more arid western sites (AR, MO), and *Nyssa sylvatica* (NYS), *Acer rubrum* (ACE), and *Carya glabra* (CAR) are more common on the more mesic eastern sites (North Carolina and Virginia).

Anomalous behavior of simulated modern species included that of *Castanea dentata* (CAS), which underwent blight from 1904 to its virtual extinction as a forest tree by ca. 1940 (Diller and Clapper 1965). Before the blight, however, *Castanea* reached maximum proportions of forest biomass in the locations in which it is simulated to be most

W. DECIDUOUS FOREST

E. DECIDUOUS FOREST

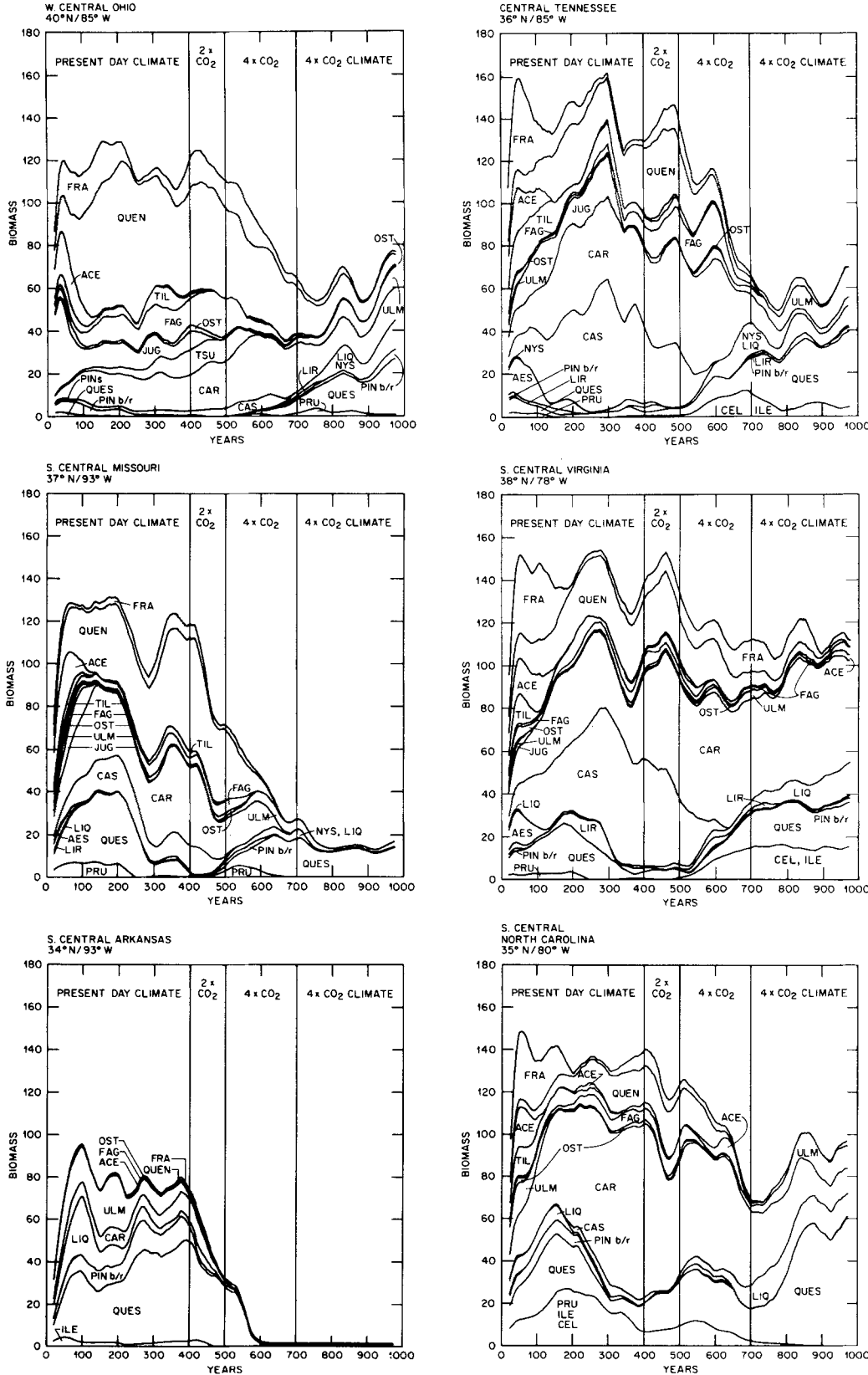


Fig. 5. Simulations of 1,000-year biomass dynamics, including CO₂-induced climate change, at three sites in western deciduous forest (column 1) and three sites in eastern deciduous forest regions (column 2). Ordinate is in megagrams of biomass per h. See text for simulation conditions at years 0-400, 400-500, 500-700, and 700-1,000. Tree taxon abbreviations are given in legend of Fig. 3

abundant. *Fagus grandifolia* (FAG) and *Tsuga canadensis* (TSU) should have reached maxima at sites further north than they did in simulations, and *Acer saccharum* (ACE) should have dominated further south as well as in the northern hardwoods (Braun 1950). There was probably less simulated biomass of southern species of *Pinus* (*P. echinata*, *P. taeda*, *P. virginiana*; PINb/r) everywhere, and more simulated *Carya* (CAR) in the Southeast than there should have been. However, the simulated pines in particular, are ambiguous because the pines primarily occupy recently cleared land and poor or sandy soils (Fowells 1965), neither of which was simulated but both of which are abundant in the study area.

Future forests. The deciduous forest response to climate change induced by CO₂ was remarkably uniform. Biomass declined at all sites simulated (including Pennsylvania, not shown), some time after CO₂ doubling at all but the westernmost (south central Missouri and Arkansas) and southernmost sites (southwestern Georgia, not shown). There, biomass decline began with the warming at year 400 and nonforest (prairie) vegetation was the eventual outcome of the simulations. The two western sites (Missouri and Arkansas) occur in modern xeric (dry) forests with prairie openings, where loss of forest is to be expected under future warming, as occurred in the past (e.g. see King 1981). The nonforest vegetation simulated at the southernmost southwest Georgia site (not shown) may be an artifact of the lack of more subtropical species in the model. Alternatively, the model simulated soil moisture there similar to conditions in modern western Texas where too little moisture falls for trees to grow.

The biomass declines at the other deciduous forest sites in North Carolina, Virginia, Tennessee, Ohio (Fig. 5), and Pennsylvania (not shown), do not appear to result from effects of warming or precipitation alone. The model generally simulates increases in stand biomass with increased temperature, and precipitation under CO₂-induced climate change is projected to be little different or slightly greater than today's at the deciduous forest simulation sites. However, simulated evapotranspiration and hence, moisture stress (days of soil moisture below the wilting point), increased at the sites an average of eight times, from four to 32 days a year, or from 2–14% of the average growing season length, between years 400 and 700. The moisture stress reduced stand biomass by reducing potential growth rates, particularly of rapidly growing species (*Castanea* [CAS]; *Quercus alba*, *Q. velutina*, *Q. prinus* [QUEN]). Moisture stress also conferred competitive advantages to other species, many of which are smaller and more slowly growing (*Q. muehlenbergii*, *Q. stellata*, *Q. virginiana* [QUES]; *Nyssa sylvatica* [NYS]; *Celtis laevigata* [CEL] and *Ilex opaca* [ILE]).

Discussion

The simulation model described above was developed gradually during the past 15 years, and development will most likely continue for some time in the future. Despite the development work to date, the model used in the simulation experiments (Solomon et al. 1984; Solomon and West 1984) does not consider certain processes that are likely to be important under CO₂-induced climate change. Effects of the major variables, temperature and precipitation, appear

adequate, although Tharp's (1978) treatment of overabundance of precipitation (flooding) remains to be incorporated in the present model structure if lowland forests of the whole landscape are to be treated.

A variable which could ameliorate negative effects of tree response to climate changes, CO₂ fertilization, was mentioned in the introduction. Certain versions of the forest-stand models have incorporated the concepts (Botkin et al. 1973; Shugart et al. 1984) or the few available data (West and Solomon 1984) on effects of CO₂ fertilization. These model experiments indicate that the primary nature of direct CO₂ response could involve accelerated growth of trees and increased rates of forest succession, and reduced impacts of the environmental changes simulated without CO₂ fertilization (e.g. forest dieback and recovery; invasion of boreal forests by deciduous species, etc.; West and Solomon 1984). Even with unrealistically high growth enhancement, hypothetical tree growth and forest community productivity did not exceed about 15–20% of current values (Shugart et al. 1984).

If carbon fertilization is to be of significance in the future, there is little evidence of it as yet. CO₂-induced tree growth enhancement from the approximately 25% increase in atmospheric CO₂ concentration during the past 100 years may be visible in tree rings of high altitude montane conifers (LaMarche et al. 1984). Yet, recent tree growth reduction seems to be the rule at lower altitudes where forests grow (e.g. Johnson 1983; McLaughlin et al. 1983b), and dieback of species and forests is a more immediate concern (Plochmann 1984). The 0.5 to 0.6° C increase in mid-latitude temperature during the past 100 years (Hansen et al. 1985) may be contributing to the growth reduction.

Additional processes not modeled in the simulation experiments are the effects of other atmospheric pollutants and secondary effects of chronic diseases and predators. A large-scale regional research program is under way to determine the chronic effects of acidic precipitation upon forests, based on field studies and forest-stand models (e.g. see McLaughlin et al. 1983a; Dale and McLaughlin 1984). This effort could be extended to include insects, pathogens, and other air pollutants, as well as climate change. The net effect of simulating these growth-reducing forces may be to enhance simulated tree growth losses and mortality under CO₂-induced climate change.

The lack of plant migration effects in the simulation model reduces the impacts of growth losses due to rapid climate change. If tree migration occurs in the future even as quickly as rates measured during preindustrial times (unlikely due to land-use which dissects landscapes into forest islands; e.g. Johnson et al. 1982), declines in stand productivity will be increasingly apparent with time, as fewer and fewer tree species are available to grow under the steadily more extreme conditions.

On the other hand, the implications of land-use history to the age structure of actual forest stands also are not considered in the simulations. Instead, the simplistic assumption was made that all forest stands had been undisturbed for hundreds of years before the climate began to change. The immediate loss of senescent trees in the resulting simulations (e.g. Solomon and West 1985) would be less important to mid- and high-latitude forests on the real landscape under CO₂-induced climate change. This characteristic might, in turn, ameliorate the initial dieback phenomenon apparent at several sites simulated.

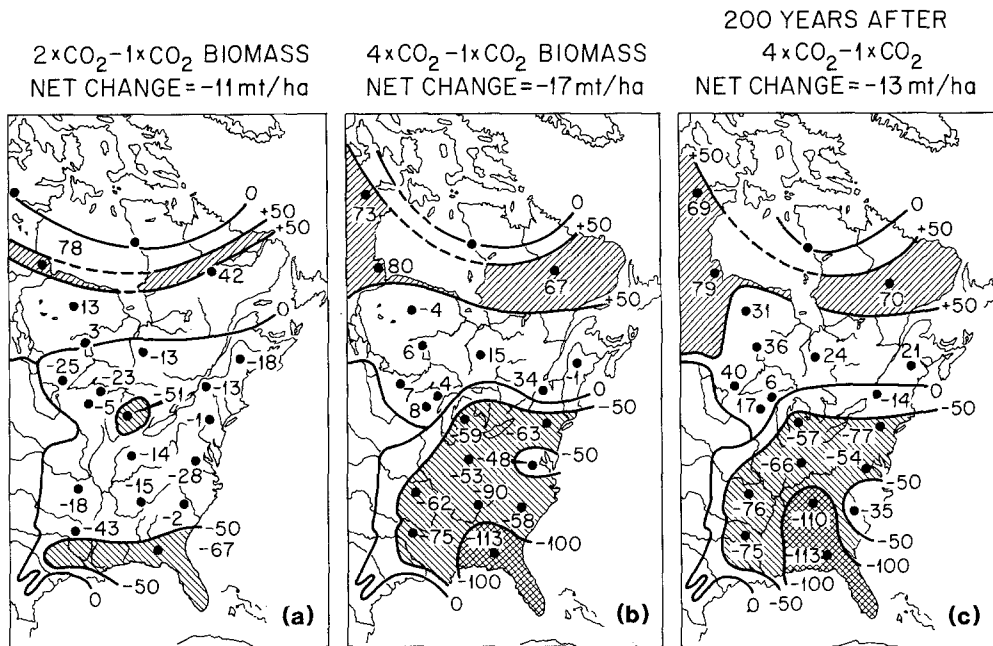


Fig. 6a-c. Carbon storage dynamics (in megagrams per hectare) simulated at 21 sites in eastern North America. Values on the maps at each of the 21 sites simulated represent live, aboveground stand biomass gain or loss in megagrams per hectare. Maps show carbon storage differences between contemporary climate and **a** 2 X CO₂-climate, **b** 4 X CO₂-climate, and **c** 200 years after 4 X CO₂ climate stabilizes

Even considering these difficulties, certain results from the simulation experiments appear to be realistic enough to warrant further study. In general, these include slower growth by most deciduous species throughout much of their geographic ranges in current deciduous forest regions of the eastern United States. This growth reduction may be similar to that recently documented by McLaughlin et al. (1983b). Initial warming could produce a dieback of many dominant temperate tree species, particularly those of narrow ecological amplitude (e.g. *Quercus coccinea*, *Picea rubens*, *Aesculus octandra*, *Pinus resinosa*) and of rapid growth rates (*Juglans cinerea*, *Aesculus octandra*, *Tilia americana*). Further north, deciduous tree species eventually may invade present-day southern boreal forests, but not before boreal species have virtually disappeared there.

If there occurs an extinction of boreal trees, followed by deciduous species invasion, the changeover is likely to be time-transgressive. It occurred first in simulations in the south and later in the north, independent of any migrational lags, which were not simulated. Some of these intrinsic lags required up to 300 years after the climate change ceased, a property of transient forest response similar in time scale to that seen in oceans (e.g. see Schneider and Thompson 1981). Only the least compositionally complex forests (northern boreal forests, arid western woodland) behaved as one might expect without using a stand-simulation model; i.e. boreal forest invaded present tundra; dense, closed forest replaced open northern boreal woodland; and dying trees were not replaced by trees of any species in dry western woodlands, suggesting the dominance of prairie grasses there.

The simulation experiments can suggest certain features of the role future forests may play as sources or sinks of CO₂ in the global carbon cycle. For example, consider aboveground carbon storage differences, mapped for specified points in time during continuous climate change (Fig. 6). By the time simulated doubling of CO₂ occurred (Fig. 6A) the aboveground biomass in the northern portion of the subcontinent had become a carbon sink, and the

southern portion, a carbon source, with carbon balance achieved at 50° N latitude. The modern forest-prairie border constituted an assumed western limit to carbon losses and gains in closed-canopy forests, because trees are absent on prairies today and, probably, in the future (see S. Central Missouri, S. Central Arkansas, Fig. 5).

The strongest aboveground carbon sinks at the 2 X CO₂ point in the simulations (Fig. 6a) were found along the northern boreal forest border where forest invaded tundra. The greatest carbon sources were in the southern U.S. where present-day forests are under moisture and temperature stress. Overall, the 21 sites simulated were cumulative carbon sources, losing about 10% of the live biomass stored before CO₂-induced changes occurred in climate.

By the time CO₂ quadrupled (Fig. 6b), total carbon further declined an average of 5% more per site. The strong northern carbon sinks and southern carbon sources intensified and increased in areal cover. Meanwhile, the carbon balance line migrated southward by 5° of latitude (550 km). Some 200 years after climate change ceased at the 4 X CO₂ level (Fig. 6c), carbon storage dynamics continued. Carbon sources intensified in the southeast (possibly for lack of appropriate simulated subtropical species), and the high-density northern carbon sinks expanded southwestward. Although the carbon-balance line appeared to have undergone little geographic change, carbon storage increased about 3% at the 21 sites during the 200-year period since climate stabilized. The continuation of obvious changes in storage dynamics of live carbon long after climate stabilization is a property of the global carbon cycle previously considered mainly in relation to soil organic matter pools and to the atmosphere-ocean interface. It must now be seriously considered among living terrestrial components as well.

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