

Response of northern forests to CO₂-induced climate change

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Climate changes resulting from increases in atmospheric CO₂ are expected to alter forest productivity and species distributions. But forest response to climate change depends in part on changes in soil water and nitrogen availability which limit tree growth. Here we report an investigation into the possible responses of north-eastern North American forests to a warmer and generally drier climate by driving a linked forest productivity/soil process model with climate model predictions corresponding to a doubling of CO₂. The greatest changes occurred at the current boreal/cool temperate forest border. Simulated productivity and biomass increased on soils that retained adequate water for tree growth and decreased on soils with inadequate water. Simulated changes in vegetation composition altered soil nitrogen availability, which in turn amplified the vegetation changes. The simulated responses of the forests were results of a positive feedback between carbon and nitrogen cycles, bounded by negative constraints of soil moisture availability and temperature.

General circulation models suggest a 2–4 °C mean rise in global temperature with CO₂ doubling, with greater warming in higher latitudes than near the equator^{1–5}. This doubling is expected to occur over the next one hundred years, although precise estimates of the doubling time vary according to model assumptions⁶. Several geographically explicit vegetation models suggest profound changes in the distribution of major biomes, particularly in north temperate and boreal regions, as temperature adjusts to this doubling of atmospheric CO₂^{7–10}.

As large fractions of terrestrial biomass are in forests¹¹, it is important to consider the potential responses of these carbon pools to enhance atmospheric CO₂ levels. The differing abilities of soils to hold water have been implicated as an important but poorly understood factor that will control the response of terrestrial ecosystems to CO₂-induced climate change¹². Different tolerances of tree species to drought result in their segregation along moisture gradients in the landscape; this in turn causes different rates of nitrogen and carbon cycling because species differ in growth rates, nitrogen uptake, return in litter, and release of nitrogen and carbon from decomposing litter^{13–16}. The carbon and nitrogen cycles are strongly and reciprocally linked: soil nitrogen availability strongly limits net primary production^{14,17–20} and in turn it is partially controlled by the carbon chemistry, particularly the lignin content, of decomposing litter^{21–23}. Insofar as nitrogen and water are two of the chief limiting factors to forest growth in eastern North America, the responses of trees to drought and the resulting feedbacks between vegetation and soil may control the carbon balance of a large part of the North American continent.

We examined the sensitivity of potential forest responses not only to climate changes which may occur under enhanced CO₂, but also to soil water-holding capacity and the subsequent positive feedbacks that are initiated as a result of changes in the nitrogen cycle. Previous estimates of the transient response of eastern North American forests to CO₂-induced climate changes^{9,10,24,25} have not considered concomitant changes in soil water and nitrogen availability and their interaction with corresponding shifts in vegetation zones.

Rapid changes in photosynthesis and water-use efficiency owing to changes in stomatal control under enhanced CO₂ have been observed in laboratory experiments^{26–31}. But, these physiological processes take place in a context of long-term and large-

scale ecosystem dynamics which pose formidable problems in deriving realistic estimates of forest growth from the few short-term studies now available²⁴. Instead of developing a model to extrapolate from rapid, small-scale physiological processes to ecosystem and global scales, a more feasible approach is to use a quantitative model of forest dynamics appropriate to the scale of a dominant canopy tree (~200 yr and 0.1 ha). At this scale, the effect of fast, single-leaf physiological dynamics is minimized, and competition, climate fluctuations, and plant-soil interactions dominate integration of these rapid single-leaf dynamics into growth of annual rings. This is the scale at which the forest environment, species composition, and associated soil properties change.

Our model simulates the annual establishment, growth, and death of individual trees and decay of cohorts of litter from these trees in a forest plot^{15,16}. Temperature and soil water availability are constraints to population dynamics and their feedback with soil nitrogen availability and light extinction through the canopy. Monthly temperatures and precipitation, mortality, recruitment, and initial tree size vary stochastically about mean values. The model has been extensively validated against independent data of biomass, productivity, species composition, nitrogen cycling, and soil organic matter dynamics in old growth and successional conifer and deciduous forests in eastern North America^{16,32,33}.

Simulations were run for eleven sites using realistic climate projections, on each of two contrasting soil types, to explore the range of potential forest response. We examine in detail the forest response at four sites with initially different climates and different transient responses: (1) Shefferville, northern Quebec (55°N, 66°W; northern interior boreal forest), (2) Kapuskasing, south-central Ontario (49°N, 83°W; southern interior boreal forest), (3) northeastern Minnesota (47°N, 92°W; sub-boreal/prairie border) and (4) northern Maine (47°N, 67°W; maritime subboreal/northern hardwoods).

Current mean monthly temperatures, precipitations, and their standard deviations are from compiled statistics^{34,35}. Changes in monthly temperature with a doubling of CO₂ were calculated by fitting a sine wave through projections for January and July temperatures³. Changes in monthly precipitation were calculated by proportioning projected winter and summer changes in precipitation⁴ across the year. Two contrasting soils, sand and silty clay loam, were selected to give estimates of the potential range of soil water availability at each site. Available soil water is assumed to be 18.3 cm m⁻¹ soil depth for the silty clay loam (field moisture capacity at -0.033 MPa is 38.3 cm, wilting point at -1.5 MPa is 20.0 cm) and 10 cm m⁻¹ soil depth for the sand (field moisture capacity, 15 cm and wilting point, 5.0 cm). Each model run began with no vegetation or forest floor present. Initial soil carbon and nitrogen contents were set at 90% of those reported for boreal wet forest and cool temperate moist forest³⁶ to account for the initial lack of a forest floor. Because of the stochastic nature of processes described above, the annual results of 20 model runs were averaged for each soil on each site. This averaged output can be thought of as corresponding to a random sample of 20 stands in a region of homogeneous climate and soils. The model was run for 200 years at each site under current climate, which was then altered linearly over the next hundred years to reach simulated 2 × CO₂ climate for each site⁴, then run for 200 more years with the new climate.

Responses to climatic change at each site are strongly dependent on latitude and changes in the water balance (Table 1, Fig. 1). For far northern Quebec (Fig. 1a–d), the increase in growing degree days was not sufficient to cause simulated boreal forests to be replaced by northern hardwoods. As temperature warmed to optimal levels for spruce, productivity and biomass increased. With climatic warming, there was no decrease in soil water availability on both soils, and therefore only small differences between them in simulated responses of forests.

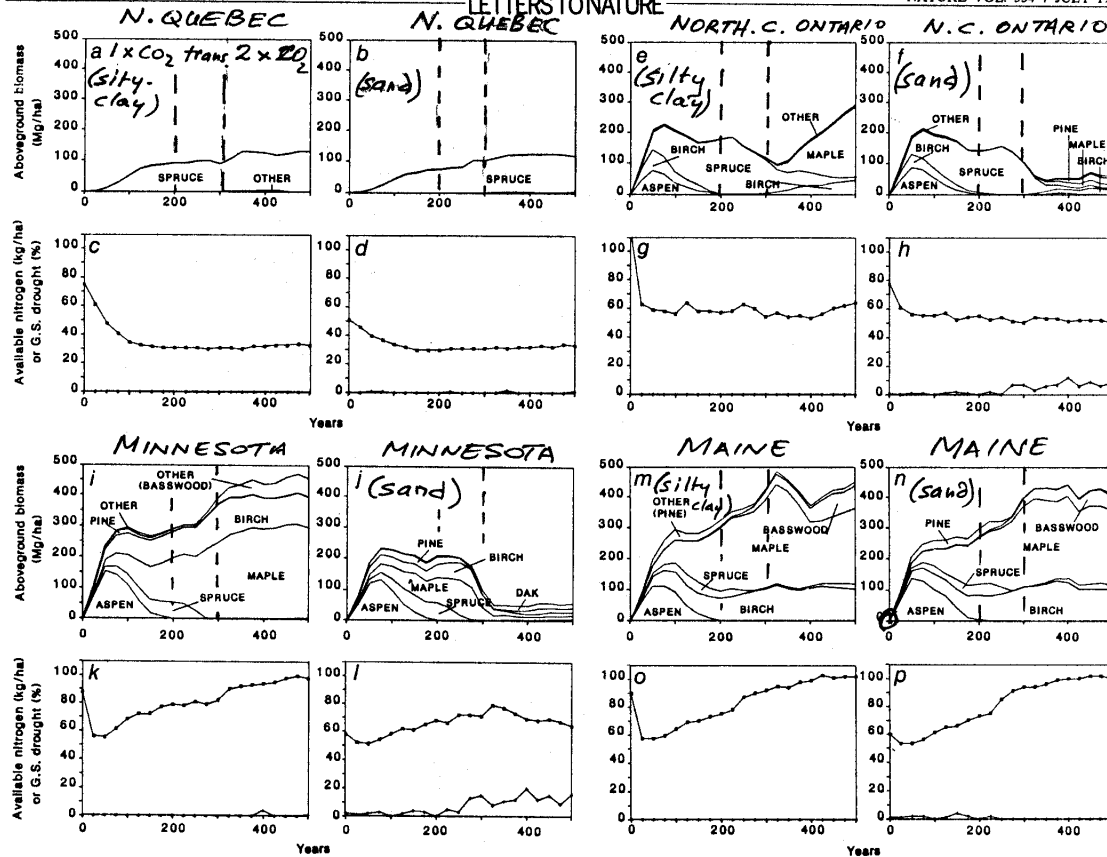


Fig. 1 Simulated changes in biomass, species composition, soil nitrogen availability (square symbols) and the proportion of the growing season (g.s.) that soil water is below wilting point (crossed symbols) for four northern forests, given a doubling of CO_2 . a-d, Shefferville, Quebec; e-h, Kapuskasing, Ontario; i-l, northeastern Minnesota; m-p, Maine. a, c, e, g, i, k, m and o, Silty clay loam soil type; b, d, f, h, j, l, n and p sand. Horizontal axes represent model runs for 200 years at each site under current climate, which is then altered linearly over the next hundred years to reach simulated $2 \times \text{CO}_2$ climate, then run for 200 more years with the new climate.

The situation is drastically different for those sites in southern boreal and northern hardwood forests, which are located in a band from the Western Great Lakes area eastwards to the Atlantic Ocean (Fig. 1e-p). In this area, major shifts in biomes were simulated with warming towards the climatic optima of less cold-hardy species. In most cases, carbon in aboveground biomass changed more than carbon stored in soil (Table 1).

At the current boreal/northern hardwood border, changes in the water balance had a major effect on simulated species composition and carbon balance. In general, on soils where there was no decrease in soil water availability with a doubling of CO_2 , the current mixed spruce-fir-northern hardwood forest was replaced by a more productive northern hardwood forest. This forest was more productive for two reasons. First, in the model, northern hardwoods have a faster intrinsic growth rate and can attain a greater biomass than either spruce or fir. Second, the warmer climate, as well as the higher nitrogen and lower lignin contents of northern hardwood litter, enhance soil nitrogen availability and this enhancement amplifies the effect of warming on productivity. This enhancement of productivity and/or nitrogen availability is particularly noticeable in the simulations for silty clay loams in Ontario (Fig. 1e and g) and northeastern Minnesota (Fig. 1i and k) and both soils in Maine (Fig. 1m-p).

Where there were increases in the proportion of the growing

season with soil water below wilting point, the simulated mixed spruce-fir/northern hardwood forests were replaced by a stunted pine-oak forest of much lower carbon storage (Fig. 1f, h, j and l). The most extreme examples are the simulations on sands, where the pine-oak forest under a doubling of CO_2 contains the aboveground biomass characteristic of savannas. But this pattern also occurred to a lesser degree on silty clay loams in northern Wisconsin, southern Michigan, and northern New York (Table 1). Although the warmer temperatures would increase decomposition rate and nitrogen mineralization, the higher lignin and lower nitrogen contents of oak and particularly pine litter compensated for this and reduced decomposition. Generally, as a result, no change or local decreases in soil nitrogen availability occurred.

These simulations assume no direct effect of increased CO_2 concentrations on growth or water use efficiency through changes in stomatal control, which may partially compensate for increased drought²⁶⁻³¹. Although some species more than double their water use efficiency with a doubling of CO_2 (ref. 30), most have a smaller response and others have no response³¹. Some of our simulations forecast three-fold to fourfold increases in the proportion of the growing season during which soil moisture is below the assumed -1.5 MPa wilting point; the reported changes in water-use efficiency under increased CO_2 may not be sufficient to compensate for such large increases in

Table 1 Net changes in climate, soil, and ecosystem properties 200 years after CO₂ doubling ends (year 500) compared with 200-year-old forests under present climate

Site	Latitude	Longitude	Growing season		Growing season		Above ground		Soil organic		Soil nitrogen	
			degree days		drought		biomass		matter		availability	
			200	500	(%)	(%)	(Mg ha ⁻¹)	(Mg ha ⁻¹)	(Mg ha ⁻¹)	(kg ha ⁻¹)	(kg ha ⁻¹)	(kg ha ⁻¹)
			200	500	200	500	200	500	200	500	200	500
North Manitoba	59°N	94°W										
sicl			443	711	0	0	4	89	91	164	23	26
sand			443	711	0	5	2	83	135	195	23	25
North Quebec	55°N	66°W										
sicl			496	727	0	0	93	132	164	207	31	33
sand			496	727	0	1	75	118	190	234	30	33
North West Ontario	54°N	90°W										
sicl			875	1,290	0	0	162	152	280	205	51	40
sand			875	1,290	0	3	128	111	286	236	47	40
Western Ontario	50°N	89°W										
sicl			995	1,515	0	0	164	145	274	156	53	43
sand			995	1,515	0	1	152	131	293	210	53	42
South central Ontario	49°N	83°W										
sicl			1,153	1,716	0	0	179	293	254	306	57	64
sand			1,153	1,716	0	8	142	61	273	268	55	50
North East Minnesota	47°N	92°W										
sicl			1,561	2,095	0	1	292	455	322	419	79	98
sand			1,561	2,095	0	16	211	57	322	309	69	64
North Michigan	47°N	88°W										
sicl			1,611	2,142	0	0	346	357	334	388	80	99
sand			1,611	2,142	0	4	255	206	334	361	72	86
North Wisconsin	46°N	90°W										
sicl			1,780	2,318	0	4	440	248	378	406	89	98
sand			1,789	2,318	0	31	384	11	373	250	87	54
South Michigan	44°N	85°W										
sicl			2,183	2,780	0	7	345	239	328	374	85	92
sand			2,183	2,780	12	36	27	3	210	129	50	32
North New York	45°N	75°W										
sicl			1,991	2,643	0	3	407	277	375	390	93	98
sand			1,991	2,643	8	32	102	23	269	225	63	53
North Maine	47°N	67°W										
sicl			1,606	2,102	0	0	324	456	320	385	75	102
sand			1,606	2,102	0	0	295	417	341	380	73	100

Results are means of 20 model runs for each site in which monthly temperatures and precipitation, tree mortality, and the birth of new trees vary stochastically. Sicl: silty clay loam.

water stress¹⁰. In any case, the current modelling effort provides an ecosystem context to evaluate the direct effects of enhanced CO₂ on tree physiology.

Our results are consistent with current systems theory³⁷. According to this theory, positive feedbacks amplify system responses to changes in negative feedbacks or constraints. Thus, responses of boreal and north temperate forests to CO₂-induced climate change may depend on the balance between changes in the hydrological cycle that constrain the forest response, and the positive feedbacks between the carbon and nitrogen cycles that amplify this response. If the vegetation response to drought decreases nitrogen availability, then the positive feedback between the carbon and nitrogen cycles weakens, resulting in a decline in productivity. Conversely, if climate change alters forest composition, thus enhancing growth of species which can further enhance soil nitrogen availability through the chemistry of their litter, then the same positive feedback results in an increased productivity.

Therefore, interactions between vegetation and water and nitrogen availabilities may produce a bifurcation in the forest ecosystem response, that is, increased productivity where soil water is not limiting and nitrogen availability is enhanced, and decreased productivity where water and nitrogen become more limiting. Forest responses to climate change are as sensitive to the indirect effects of climate and vegetation on soil properties as they are to the direct effects of temperature on tree growth. The heterogeneity of the landscape, particularly the distribution

of various soils, becomes an important factor determining forest responses to climate change, because these bifurcations can occur within, as well as between, biomes.

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