

Climate-Driven Increases in Global Terrestrial Net Primary Production from 1982 to 1999

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Recent climatic changes have enhanced plant growth in northern mid-latitudes and high latitudes. However, a comprehensive analysis of the impact of global climatic changes on vegetation productivity has not before been expressed in the context of variable limiting factors to plant growth. We present a global investigation of vegetation responses to climatic changes by analyzing 18 years (1982 to 1999) of both climatic data and satellite observations of vegetation activity. Our results indicate that global changes in climate have eased several critical climatic constraints to plant growth, such that net primary production increased 6% (3.4 petagrams of carbon over 18 years) globally. The largest increase was in tropical ecosystems. Amazon rain forests accounted for 42% of the global increase in net primary production, owing mainly to decreased cloud cover and the resulting increase in solar radiation.

Between 1980 and 2000, Earth experienced dramatic environmental changes (1). It had two of the warmest decades in the instrumental record (1980s and 1990s), had three intense and persistent El Niño events (1982 to 1983, 1987 to 1988, and 1997 to 1998), and saw noteworthy changes in tropical cloudiness (2) and monsoon dynamics (3). Meanwhile, atmospheric CO₂ levels increased by

9% [337 to 369 parts per million (ppm)] and human population increased by 37% (4.45 × 10⁹ to 6.08 × 10⁹). Changes in terrestrial net primary production (NPP) integrate these and other climatic, ecological, geochemical, and human influences on the biosphere. Several regional studies have reported increases in NPP (4–10), but a globally comprehensive analysis of the impacts of climatic changes on

NPP is lacking. For the northern mid-latitudes and high latitudes, these studies suggest that multiple mechanisms (e.g., nitrogen deposition, CO₂ fertilization, forest regrowth, and climatic changes) have promoted increases in NPP, whereas increases in the tropics have been primarily attributed to CO₂ fertilization. Here we analyze nearly two decades of recent global climatic data and satellite observations of vegetative activity and show that climatic changes have eased multiple climatic constraints to plant growth, increasing NPP over large regions of Earth.

Temperature, radiation, and water interact to impose complex and varying limitations on vegetation activity in different parts of the world (11). To provide a comprehensive interpretation of climate change impacts on plant growth, we first constructed a map of the relative contributions of climatic controls on global vegetation. We used long-term monthly climate statistics to build simple

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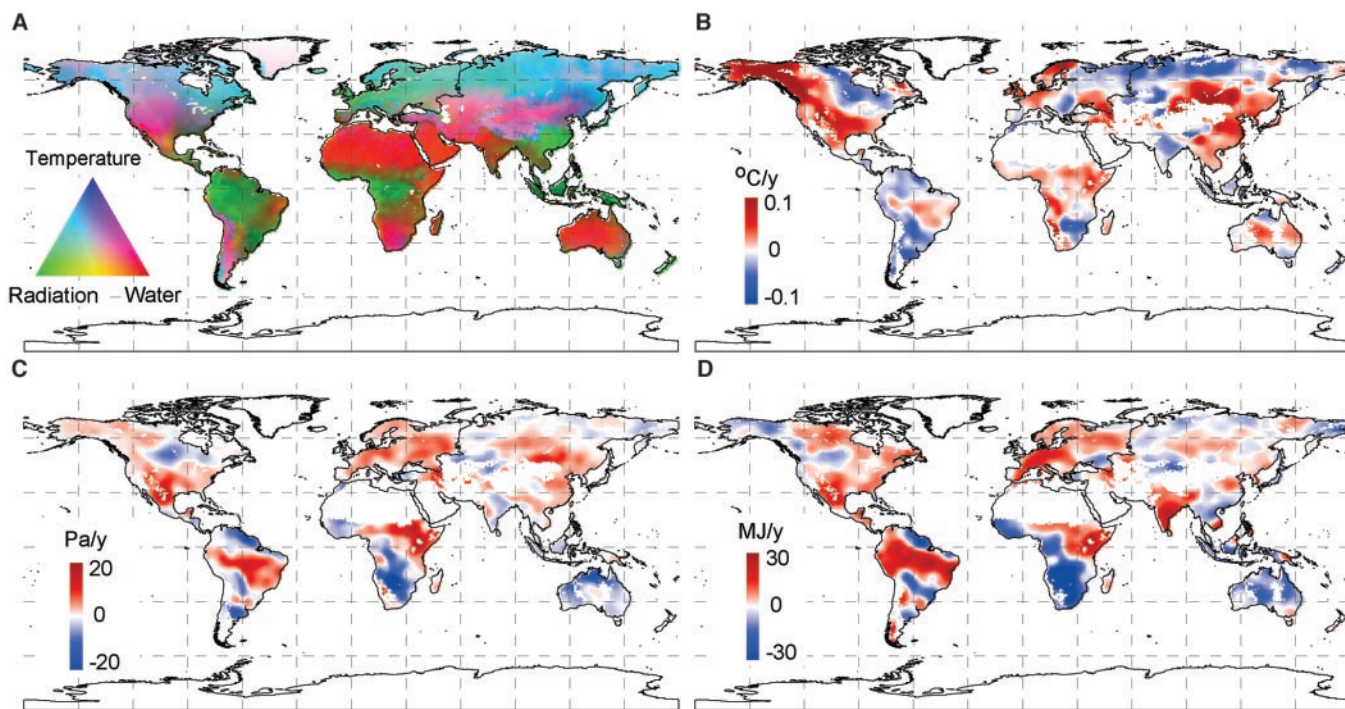


Fig. 1. (A) Geographic distribution of potential climatic constraints to plant growth derived from long-term climate statistics. (B to D) Recent climatic changes, estimated from reanalysis data from 1982 to 1999, in the growing season average temperature (B), vapor pressure

deficit (VPD) (C), and solar radiation (D). Reductions in VPD are indicative of increased water availability (C). The growing season is defined as those months with 1982 to 1999 average air temperatures above 0°C.

bioclimatic indices (12). From these indices, we estimated that water availability most strongly limits vegetation growth over 40% of Earth's vegetated surface, whereas temperature limits growth over 33% and radiation over 27% of Earth's vegetated surface (Fig. 1A). These factors tend to be colimiting. For example, cold winter temperatures and cloudy summers limit high-latitude Eurasian vegetation, whereas cold winters and dry summers limit vegetation in western North America. Tropical areas are never limited by low temperatures but may have either a sustained dry season or nearly perpetual cloud cover that limits solar radiation (13).

We have estimated the trends in these growth-limiting climate factors from 1982 to 1999 using daily reanalysis data from the National Center for Environmental Prediction (NCEP) (14). The observed trends were confirmed with independent data sets of ground- and satellite-based observations (figs. S1 to S3) (12). Air temperatures that regulate the growing-season dynamics have increased over temperature-limited regions of North America and northwest Europe (Fig. 1B), promoting earlier plant growth (7) and additional carbon sequestration (15). Changing monsoon dynamics produced wetter rainfall regimes and associated reductions in vapor pressure deficit (VPD) in water-limited ecosystems of Australia, Africa, and the Indian subcontinent (Fig. 1C) (3). Importantly, increasing incident solar radiation was evident over radiation-limited regions of Western Europe and the equatorial tropics (2, 16) (Fig. 1D).

Most of the observed climatic changes have been in the direction of reducing climatic constraints to plant growth. To quantify this effect, we used a biome-specific production efficiency model (PEM) (12, 17) that combines monthly estimates of satellite-derived vegetation prop-

erties with daily NCEP climate data to estimate monthly and annual NPP at $0.5^\circ \times 0.5^\circ$ resolution. The satellite-derived vegetation properties used were the fraction of absorbed photosynthetically active radiation (FPAR) and leaf area index (LAI) derived from remotely sensed normalized difference vegetation index (NDVI) and a biome map (18, 19). The PEM that we used is similar in logic to other PEMs (8, 13, 20) but has parameters derived from field studies and a global ecosystem process model (17, 21). To account for differences in satellite data processing, we used two independent data sets of LAI and FPAR derived from Global Inventory Monitoring and Modeling Studies (GIMMS) (22) and Pathfinder Advanced Very High Resolution Radiometer Land (PAL) (23) NDVI data sets (12).

From 1982 to 1999, modeled NPP increased the most (6.5%) in water- and radiation-limited regions, followed by temperature- and radiation-limited regions (5.7%) and temperature- and water-limited regions (5.4%). NPP increased significantly ($P < 0.01$) over 25% of the global vegetated area, with a mean rate of $6.3 \text{ g C m}^{-2} \text{ year}^{-1}$, and decreased significantly over only 7% of the area, with a mean rate of $4.2 \text{ g C m}^{-2} \text{ year}^{-1}$ (Fig. 2).

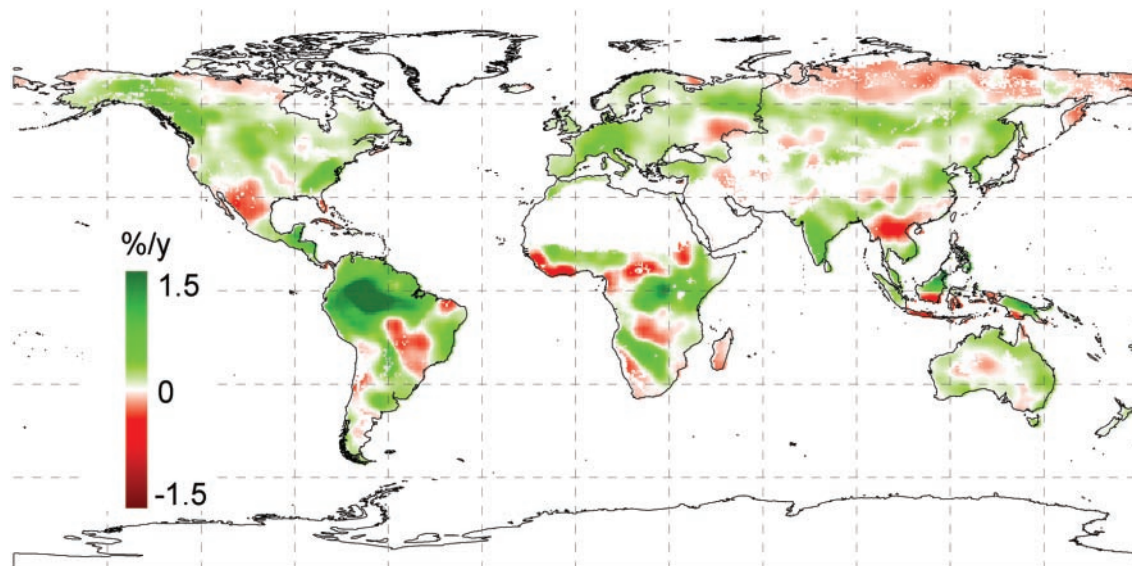
To isolate the role of climate from other mechanisms that could enhance carbon sequestration—such as CO_2 fertilization, nitrogen deposition, and forest regrowth—and to remove spurious trends in satellite data due to residual sensor-calibration effects, we alternately estimated NPP by assuming constant vegetation (1982 to 1999 monthly average FPAR and LAI) with changing climate or by assuming constant climate (average daily climate from 1982 to 1999) with changing vegetation. Changes in climate (with constant vegetation) directly contributed nearly 40% of the total increase in NPP from 1982 to 1996 (table S2). Changes in veg-

etation (with constant climate) over the same period contributed $\sim 60\%$ of total NPP increase, possibly as a result of climate-vegetation feedbacks, changes in land use, and growth stimulation from other mechanisms. Over parts of North America, Western Europe, the Amazon, south and central Africa, Australia, and the Indian subcontinent, changing climate alone produced persistent NPP increases (fig. S8).

Globally, NPP increased (Fig. 3) by 6.17%, 3.42 PgC over 18 years ($P < 0.001$), between 1982 and 1999. Ecosystems in all tropical regions and those in the high latitudes of the Northern Hemisphere accounted for 80% of the increase. Although terrestrial NPP accounts for only part of the biosphere-atmosphere carbon exchange, interannual variations of NPP are negatively correlated with global increases in atmospheric CO_2 growth rate ($r = 0.70$, $P < 0.001$). NPP anomalies attributable to climate alone (calculated with constant vegetation) explained nearly the same amount of variation in the NPP- CO_2 relation ($r = 0.71$, $P < 0.001$), indicating that climatic variability over land exerts a strong control over the variation in atmospheric CO_2 (fig. S9).

NPP responded differentially with respect to latitude to major climatic events such as El Niño and volcanic eruptions (Fig. 4). Globally, NPP declined during all three major El Niño events with corresponding increases in global CO_2 growth rate (24). El Niño events dominate tropical NPP variability, which has the highest association with global CO_2 growth rate ($r = 0.75$, $P < 0.001$). This response is likely because NPP and soil respiration are more tightly coupled in tropical climates compared with ecosystems in other latitudes. Soil carbon residence times range from less than 4 years in hot, wet tropical areas to greater than 1000 years in cold boreal or dry desert conditions (25). A strong decline in NPP after the Mount Pina-

Fig. 2. Spatial distribution of linear trends in estimated NPP from 1982 to 1999. NPP was calculated with mean FPAR and LAI derived from GIMMS and PAL data sets.



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tubo eruption (1991) was evident only at the high latitudes of the Northern Hemisphere. Cooler temperatures resulting from this eruption decreased the growing-season length there (15), but cooling, in association with favorable radiation regimes for photosynthesis (26), promoted plant growth in low-latitude ecosystems by reducing evaporative demand and respiration losses.

An increase in NPP of only 0.2% per 1-ppm

increase in CO₂ could explain all of the estimated global NPP increase of 6.17% over 18 years and is within the range of experimental evidence (27). However, NPP increased by more than 1% per year in Amazonia alone, which accounts for 42% of the global NPP increase between 1982 and 1999. This result cannot be explained solely by CO₂ fertilization. We suggest that increases in solar radiation, owing to declining cloud cover in these predominantly radiation-limited for-

ests, is the most likely explanation for the increased tropical NPP (28, 29). Because there is no evidence of trends in rainfall or streamflows (30) concurrent with these declines in cloud cover in this region, it is likely that rainfall patterns have changed.

Quantifying trends in NPP, as we have sought to do here, is necessary but not sufficient for understanding land surface net ecosystem exchange of CO₂. The same climatic changes that have caused decadal-scale increases in NPP can also change aboveground and belowground carbon allocation, decomposition rates, disturbance regimes, and other processes that cycle carbon between terrestrial ecosystems and the atmosphere. Atmospheric CO₂ inversion models show that northern mid-latitude ecosystems have recently been consistently large carbon sinks, and the tropics are either neutral or small sources, albeit with high uncertainty (1). Our satellite-based estimates of NPP, by contrast, show significant growth stimulation in both the tropics and the northern high-latitude ecosystems. Assuming that carbon emissions, including those from biomass burning and land-use changes, are properly accounted for in the atmospheric inversions, this spatial discrepancy means that respiration as well as NPP is a major driver of terrestrial carbon-sink dynamics. Global climate models project, in response to increasing greenhouse gases, an intensified hydrologic cycle altering the patterns of temperature, humidity, cloud cover, and rainfall (1). Our ability to predict the future of terrestrial ecosystems is contingent upon how well we can interpret such changes in the context of multiple limiting factors to biogeochemical cycling.

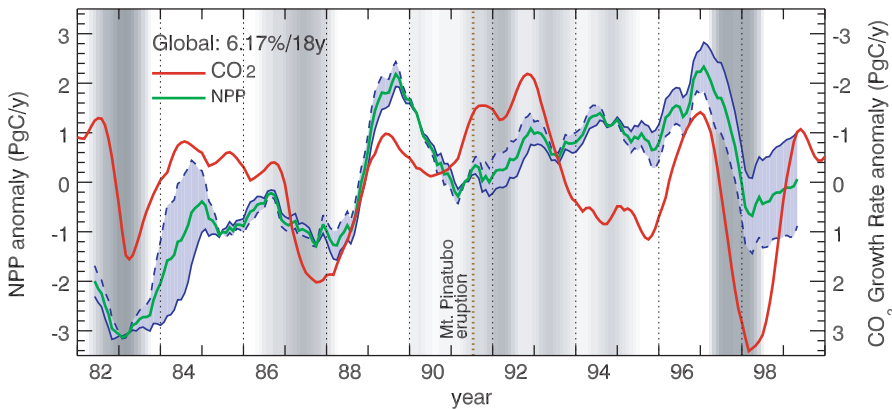
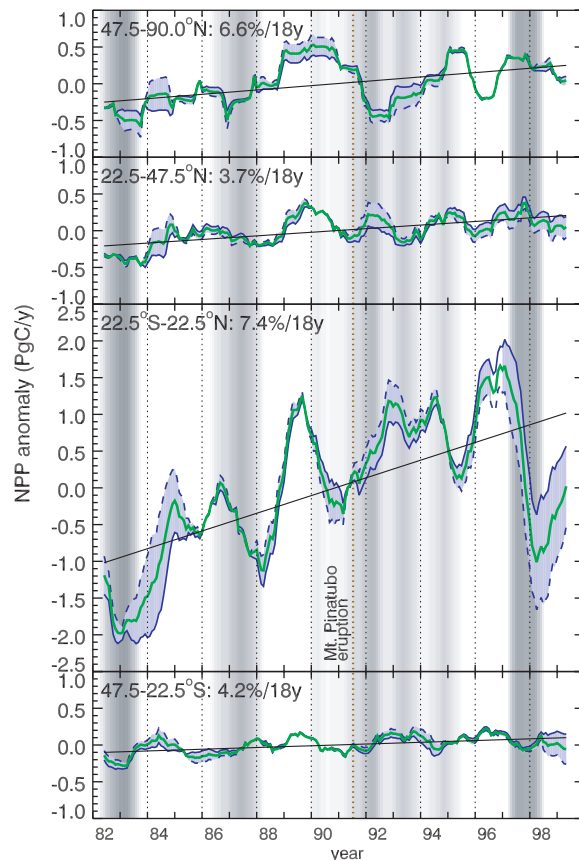


Fig. 3. Interannual variations from 1982 to 1999 in global NPP in relation to atmospheric CO₂ growth rate. Trends in global NPP anomalies are shown for GIMMS (solid blue line), PAL (dashed blue line), and their average (green line). CO₂ growth rate (inverted) is shown in red. Growth rates in ppm were converted to Pg of carbon with a conversion factor of 2.12 Pg per ppm (24). Mean NPP was 54.5 PgC year⁻¹. Mean CO₂ growth rate was 3.2 PgC year⁻¹. A multivariate ENSO (El Niño–Southern Oscillation) index (MEI) (37) is shown in gray scale, where darker shades represent higher MEI values.

Fig. 4. Interannual variations in NPP distributed by latitudinal zones. Zonal NPP anomalies in each zone are shown for GIMMS (solid blue line), PAL (dashed blue line), and their average (green line).



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Supporting Online Material

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Materials and Methods

Figs. S1 to S9

Tables S1 and S2

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Glacial Refugia: Hotspots But Not Melting Pots of Genetic Diversity

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Glacial refuge areas are expected to harbor a large fraction of the intraspecific biodiversity of the temperate biota. To test this hypothesis, we studied chloroplast DNA variation in 22 widespread European trees and shrubs sampled in the same forests. Most species had genetically divergent populations in Mediterranean regions, especially those with low seed dispersal abilities. However, the genetically most diverse populations were not located in the south but at intermediate latitudes, a likely consequence of the admixture of divergent lineages colonizing the continent from separate refugia.

During the long glacial episodes of the Quaternary, European forests were considerably more restricted than in the present interglacial.

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cial, because the Mediterranean Sea in the south and unsuitable environment in the north restricted temperate tree and shrub taxa to the Iberian, Italian, and Balkan peninsulas. For instance, at the time of the last glacial maximum, 25,000 to 17,000 years ago, networks of fossil pollen data and macrofossil remains such as charcoals indicate that several tree species were localized in small favorable spots within the Mediterranean region but also at the southern edge of the cold and dry steppe-tundra area in eastern, central, and southwestern Europe (1–5). After climate warming, some of these surviving populations expanded, whereas others remained trapped and either became extinct or persisted by shifting altitude (2, 6). As a consequence of prolonged isolation, extant tree populations situated close to refugia should be highly divergent, especially if they were not the source of the expansion. Another related prediction is that intraspecific diversity should decline away from refugia, as a consequence of successive founder events during postglacial colonization (7, 8). However, species attributes such as colonizing ability may alter these predictions (9). Furthermore, the individualistic migration behavior of tree species during interglacial periods (6, 9) and the presence of more northern refugia (4, 5) may have blurred this pattern. In Europe, range-wide genetic surveys of a few well-investigated

tree species have been performed (10–12), but it is difficult to generalize from these studies. To get a broader picture and to test the previous predictions, we gathered data from several woody angiosperm taxa across Europe using standardized sampling and molecular screening techniques. Such knowledge on the genetic consequences of the recent history of woody plant species may be critical for the conservation and sustainable management of their genetic resources.

Plastids are generally maternally inherited in angiosperms and, therefore, moved by seeds only. Because colonization of new habitats occurs through seeds, chloroplast DNA (cpDNA) markers provide information on past changes in species distribution that is unaffected by subsequent pollen movements (13). We have investigated patterns of cpDNA diversity in 22 woody species. These were sampled in the same 25 European forests selected on the basis of their high species richness and limited human influence (table S1). About 10 individuals per species were sampled from each forest, following a standard procedure (14). Polymorphisms were detected by polymerase chain reaction (PCR) techniques (14) in all 22 species [4 to 50 haplotypes per species, mean 16.9 (Table 1)]. The degree of subdivision of cpDNA diversity (G_{ST}) was estimated for each species (15, 16). This measure partly reflects the dispersal ability of the species considered, although long-term range fragmentation should also play a role. Low G_{ST} values (indicative of high levels of gene flow through seeds) were found in *Salix* and in *Populus* (0.09 to 0.11), characterized both by light, wind-dispersed cottony seeds. The species characterized by animal-ingested seeds also tended to have below-average values. In contrast, species with animal-cached seeds (i.e., nuts) exhibited higher than average values (Table 1).

To compare forests with each other, we calculated the mean number of haplotypes and within-population gene diversity by averaging across species in each forest (table S2). We also calculated a measure that expresses the average genetic divergence of the forest from all remaining populations (17) (table S2). The highest values were observed in Corsica, Italy, and the Balkans, including Croatia and Romania, whereas average or below-average values were