## LETTERS

## **Europe-wide reduction in primary productivity** caused by the heat and drought in 2003

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Future climate warming is expected to enhance plant growth in temperate ecosystems and to increase carbon sequestration<sup>1,2</sup>. But although severe regional heatwaves may become more frequent in a changing climate<sup>3,4</sup>, their impact on terrestrial carbon cycling is unclear. Here we report measurements of ecosystem carbon dioxide fluxes, remotely sensed radiation absorbed by plants, and country-level crop yields taken during the European heatwave in 2003. We use a terrestrial biosphere simulation model<sup>5</sup> to assess continental-scale changes in primary productivity during 2003, and their consequences for the net carbon balance. We estimate a 30 per cent reduction in gross primary productivity over Europe, which resulted in a strong anomalous net source of carbon dioxide (0.5 Pg Cyr<sup>-1</sup>) to the atmosphere and reversed the effect of four years of net ecosystem carbon sequestration<sup>6</sup>. Our results suggest that productivity reduction in eastern and western Europe can be explained by rainfall deficit and extreme summer heat, respectively. We also find that ecosystem respiration decreased together with gross primary productivity, rather than accelerating with the temperature rise. Model results, corroborated by historical records of crop yields, suggest that such a reduction in Europe's primary productivity is unprecedented during the last century. An increase in future drought events could turn temperate ecosystems into carbon sources, contributing to positive carbon-climate feedbacks already anticipated in the tropics and at high latitudes<sup>1,2</sup>.

Europe experienced a particularly extreme climate anomaly during 2003, with July temperatures up to 6 °C above long-term means, and annual precipitation deficits up to 300 mm yr<sup>-1</sup>, 50% below the average. The presence of an extensive network of instrumentation for the monitoring of ecosystem fluxes at this time, with continuous records of CO<sub>2</sub>, water, and energy fluxes<sup>7,8</sup>, helped us to assess the impact of such an extreme event on the continental-scale carbon balance. We analysed CO<sub>2</sub> fluxes from 14 forest sites and one grassland site for 2002–2003 (Table 1). Flux records are generally not yet long enough to provide long-term average references, and therefore we used 2002 as a reference (see Methods). Hourly fluxes of photosynthesis (gross primary productivity, GPP) and total

ecosystem respiration (TER) are separated from CO<sub>2</sub> net fluxes (net ecosystem exchange, NEE), using the same method for each site<sup>9</sup>.

Given inter-site differences in drought duration and intensity, soil characteristics, vegetation state, and species-specific responses to climate variation, one would not expect a uniform response of GPP to the abnormal conditions of 2003. Yet, Table 1 (also Supplementary Fig. S1) clearly shows that nearly all sites experienced a significant GPP reduction in 2003. The GPP drop coincides with reduced evapotranspiration and soil drying due to the rainfall deficit (Supplementary Fig. S1). Generally, below a threshold of ~0.4 in relative extractable water, water stress occurs, causing both GPP and transpiration to decrease in response to stomatal closure 10,11. Particularly large reductions in GPP were found in temperate deciduous beech and northern Mediterranean forests (Hesse, Hainich, Roccarespampani, San Rossore), together with reductions in canopy conductance (in 2003, conductance reached only 15% of its 2002 value at Hesse). These productive temperate and Mediterranean forests were greatly affected by extreme drought and/or heat (Fig. 1). Moreover, the GPP did not entirely recover from the summer stress during the remainder of the growing season (Fig. 1). Southern evergreen forest sites El Saler (pine) and Puéchabon (oak) also experienced a reduction in GPP during the heatwave (Table 1). Southern forest sites with an herbaceous layer that normally dries in summer were less affected by the heatwave and drought (Pianosa).

Warmer temperatures are expected to increase both microbial and plant respiration. However, during the 2003 summer, TER fell in parallel with GPP at most sites (Table 1, Supplementary Fig. S1). A reduction in both plant respiration (due to diminished substrates) and microbial soil respiration (also due to drought) can explain such parallel TER and GPP responses. Possible artefacts of the method used to separate gross fluxes<sup>9</sup> can largely be ruled out because of the close correlation between the independent quantities TER and midday NEE, the latter dominated by GPP (Fig. 1). Overall, those forests where GPP strongly decreased also had reduced net carbon uptake (NEE), with Hesse and Tharandt even temporarily becoming net

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Site Code	Name	Vegetation, main genus	Country	Latitude	Longitude	July-September					Annual				
						ΔΤ	ΔΡ	ΔGPP	$\Delta TER$	ΔΝΕΡ	s.e.*	ΔGPP	ΔTER	ΔΝΕΡ	s.e.*
SA	El Saler	ENF, pine	SP	39.28	0.33	1.7	-34	-33	-63	30	7	-94	-460	366	43
CP	Castelporziano	EBF, oak	ΙT	41.71	12.38	3.5	-42	-47	-21	-26	11	-17	16	-33	86
RO	Roccarespampani	DBF, oak	ΙT	42.39	11.92	2.3	-118	-117	-89	-28	15	-130	-287	158	95
SR	San Rossore	ENF, pine	ΙT	43.71	17.28	1.8	-120	-87	-47	-40	11	-344	-292	-51	25
BX	Bray	ENF, pine	FR	44.72	-0.77	2.9	-4	29	21	8	14	180	-114	294	77
LA	Laqueuille	GRA, grass	FR	45.64	2.75	3.5	-15	-25	-19	-6	4	-†	-†	-†	-+
PI	Pianosa	OSH, juniper	ΙT	42.58	10.07	3.2	-69	5	9	-4	16	-†	-†	-†	-+
PU	Puéchabon	EBF, oak	FR	43.73	3.58	2.2	+3	-52	-24	-28	6	-206	-91	-115	32
HE	Hesse	DBF, beech	FR	48.67	7.08	2.0	-53	-115	-42	-73	9	-291	-187	-104	46
VI	Vielsalm	MF, beech and fir	BE	50.30	6.00	1.4	-18	-20	-37	+17	15	-95	-203	108	75
TH	Tharandt	ENF, spruce	GE	50.95	13.57	1.0	-121	-41	-10	-31	7	-208	-53	-155	53
HA	Hainich	DBF, beech	GE	51.07	10.5	1.8	-30	-82	-25	-57	6	-195	-125	-70	48
SO	Soroe	DBF, beech	DK	55.48	11.63	0.3	-57	-15	-14	-1	7	-158	-183	26	66
HY	Hyytiälä	FNF nine	FI	61.85	24.28	-01	-5	-3	10	-13	5	-52	48	-100	30

Table 1 | Changes in climate and ecosystem CO<sub>2</sub> fluxes between 2002 and 2003 at eddy covariance sites

The more positive GPP and NEE are, the larger is the carbon uptake from the atmosphere. For the July to September period, units are in  $g C m^{-2} month^{-1}$ , for the annual period in  $g C m^{-2} vear^{-1}$ . The more positive TER is, the larger is the carbon release. Changes in climate and CO<sub>2</sub> fluxes are reported for the averaging period of July to September, and for the whole year. The vegetation is coded according to the IGBP classification: ENF, evergreen needle-leaf forest; EBF, evergreen broad-leaf forest; DBF, deciduous broad-leaf forest; GRA, grassland; MF, mixed forest; OSH, open shrubland.

CO<sub>2</sub> sources to the atmosphere in August. Despite the general reduction of carbon sink of most European sites, it seems that several Mediterranean sites showed a smaller decrease in NEE, largely dominated by less respiration in 2003. Although the eddy-covariance data provide an unambiguous evidence for a spectacular reduction in GPP and in NEE in European forests in 2003 (Table 1) it is still too early to assess the impacts on the long-term carbon balance. Tree damage, changes in litterfall rates, and changes in the pool sizes of carbon reserves will have consequences beyond the duration of the extreme climate event<sup>12</sup>. Analysis of the responses to these disturbances should be carried out over the next few years.

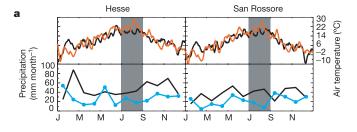
For croplands, we analysed harvest data from country-level statistics<sup>13</sup>. In each country, harvest was converted to crop net primary productivity (NPP), using allometric relationships<sup>14</sup>. Differences in crop NPP in 2003 versus 1998–2002 reflect the combined response of cultivated plants to climate stress and possible management adaptations to it (for example, increased irrigation). Nevertheless, the harvest data show a pronounced NPP decrease in 2003 (Supplementary Fig. S2) in those agricultural regions affected by heat (northern Italy, France) and by drought (Ukraine, Romania). A record NPP drop of 36% occurred in Italy for maize, a cereal grown in the Po valley where extremely high temperatures prevailed (see Fig. 2 and http://www.esa.int/export/esaEO/SEMZP6YO4HD\_index\_0.html). Winter crops (wheat) had nearly terminated their growth by the time of the heatwave and therefore suffered less NPP reduction than summer crops (corn) undergoing maximum foliar development (Supplementary Fig. S2). Mediterranean countries normally experience dry and hot summers, and therefore both irrigation and cultivation of drought-tolerant species reduced the impact of the climate conditions in these regions.

We next estimated the Europe-wide impacts of the anomalous 2003 climate on productivity, using a process-based ecosystem model<sup>5</sup>, which calculates phenology, carbon pool dynamics, and hourly fluxes of  $CO_2$ , energy and water vapour (see Methods). First, we ran the model at each eddy-covariance site (Supplementary Figs S1 and S3) to verify its ability to reproduce the observed GPP and TER anomalies (data-model average correlation  $R^2 = 0.6$  for 2003 versus 2002 anomalies). Second, we simulated the Europe-wide changes (Fig. 2) in carbon fluxes from 1900 to 2003 using reconstructed climate and weather analyses <sup>15,16</sup>.

We first verified the model-predicted changes in leaf area index (foliar surface per m<sup>2</sup>) against satellite observations of the fraction of absorbed photosynthetically active radiation (FAPAR) derived from the EOS-Terra-MODIS instrument<sup>17</sup>. Simulated and satellite-derived

patterns of FAPAR changes in 2003 versus 2000–2002 show good agreement over western Europe (Fig. 2e, f) with maximum reduction in satellite FAPAR over France (-8%) and Northern Italy (-15%). Over eastern Europe however, we simulated a larger FAPAR reduction than in the satellite observations.

Next, we mapped productivity changes. Although 2003 is not the driest year on record, the impacts of drought on GPP and NPP was amplified by high summer temperatures and soil water deficits carried over from the previous spring. For European forests, we calculate a mean reduction in NPP of 16 gC m<sup>-2</sup> month<sup>-1</sup> in the summer of 2003 compared to 1998–2002 (Fig. 2c), corresponding to



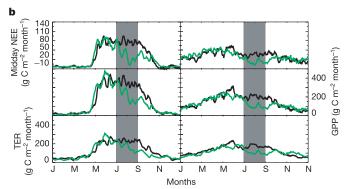


Figure 1 | Observed climate and ecosystem CO<sub>2</sub> fluxes during 2002 and 2003 at two forest sites. The two sites are a temperate deciduous beech forest in France (Hesse) and a southern evergreen pine forest site (San Rossore) in northern Italy. a, Climate fields. b, Ecosystem CO<sub>2</sub> fluxes. A five-day running average was applied to the original half-hourly flux and temperature data to remove diurnal variations. Precipitation values are monthly averages. Data for 2002 are in black and for 2003 in colour. The July to August period is shaded in grey.

<sup>\*</sup>Standard error (s.e.) estimates for the changes  $\Delta$ GPP and  $\Delta$ TER (see Methods for details).

<sup>†</sup>Non-reported values with more than 20% non-reliably filled gaps in 2002 or 2003.

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a GPP reduction of 28 g C m<sup>-2</sup> month<sup>-1</sup>. This finding is consistent with eddy-covariance observations (Table 1). Moreover, as observed at the eddy-covariance sites, a modelled soil water deficit extending from spring to autumn resulted in a significantly lower annual average NPP during 2003 (541 g C m  $^{-2}$  yr  $^{-1}$ ) compared to 1998–2002 (644 gC m  $^{-2}$  yr  $^{-1}$ ). Although our model does not include cropspecific parameterizations, the simulated NPP decrease at crop locations compares well with the crop harvest data (Supplementary Fig. S2). Overall, the NPP reduction in 2003 (Fig. 2c, d) follows the pattern of drought in Central and Eastern Europe, and of extreme summer heat in Western Europe. Accordingly, we find the largest NPP reduction in the Ukraine and Romania (-20%), France (-17%) and Italy (-12%), whereas NPP even increases in southern Sweden in response to moderate warming and no marked water deficits. Overall, the simulated GPP anomalies at the continental scale in 2003 correlate better with rainfall changes than with summer air temperature changes (Supplementary Fig. S4), indicating the dominant role of water limitations.

Modelled respiration (TER) fell over Europe in 2003 by  $77 \,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ , tailing off with a larger GPP reduction of  $195 \,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ , as observed at the eddy-covariance sites. In the

model, the response of TER can be attributed to reduced plant respiration (less assimilates from the GPP drop) and reduced heterotrophic respiration (high soil-water deficit over-compensating the built-in effect of warmer temperatures increasing decomposition according to  $Q_{10}$  relationships). ( $Q_{10}$  is the exponential factor of the temperature dependency of respiration.) Complementary measurements at Hesse confirm that pronounced soil water deficits compensated for the effect of warmer temperatures in reducing soil respiration. The parallel reduction in GPP and TER over western Europe  $(4.6 \times 10^6 \, \mathrm{km}^2)$  equates to a 2003 anomalous source to the atmosphere of  $0.5 \, \mathrm{Pg} \, \mathrm{Cyr}^{-1}$ , roughly undoing four years of net carbon storage<sup>6</sup>, although uncertainties in each number remain quite large (see Methods).

Finally, we analysed the 1900–2003 simulation to place the 2003 productivity reduction in context (Fig. 3). We find that 2003 has the lowest productivity of the past century (20% below the 1960–1990 average). This result is in good general agreement with crop harvest historical data<sup>13</sup>, especially for the summer crop maize. Such a crash in productivity during one year is large enough to alter the 'greening' detected from satellites, and interpreted as a mean NPP increase of 1% per year over Europe<sup>18</sup>.

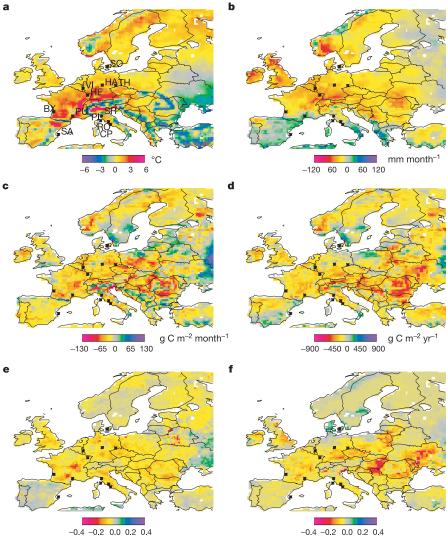


Figure 2 | European-wide anomalies of climate and net primary productivity (NPP) during 2003. All data compare 2003 and the average of 1998–2002. a, b, Climate. a, Changes in July–September air temperature. b, Changes in annual precipitation. c, d, NPP. c, Simulated changes in July–September NPP. d, Simulated changes in annual mean NPP.

**e**, **f**, Fraction of absorbed photosynthetic radiation. **e**, Observed changes in FAPAR from the MODIS–Terra–EOS satellite. **f**, Simulated changes in FAPAR. The location of eddy covariance sites is indicated by the black squares (see list in Table 1).

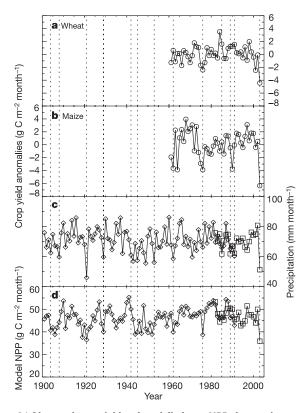


Figure 3 | Observed crop yield and modelled crop NPP changes in response to climate variability over France and Italy during the past 100 years.

a, Winter wheat yields. The trace shows area-weighted national yield records from ref. 13; a linear trend has been removed from the data to subtract the effects of improved agriculture and let appear the climate-induced variability. b, Same for maize. c, Annual precipitation over the same domain: diamonds are precipitation data from ref. 15 and squares from ref. 18.

d, Model-simulated NPP obtained by averaging all cropland grid points in France and Italy. Dashed vertical lines indicate the driest years of the past 100 years.

In conclusion, extreme events such as the 2003 European drought and heatwave have the potential to significantly alter long-term continental carbon balances. In Europe, more frequent extreme drought events3,4 may counteract the effects of the anticipated mean warming and lengthening of the growing season, and erode the health and productivity of ecosystems, reversing sinks to sources, and contributing to positive carbon-climate feedbacks. This study only attempts to quantify the short-term consequences of extreme climate conditions on productivity (Supplementary Figs S1 and S5), but the long-term impacts are likely to be significant as well<sup>19,20</sup>. In particular, we need to understand better the consequences of xylem embolism<sup>21</sup>, the effects of reduced carbohydrate pool sizes<sup>22</sup> on subsequent leaf and fine root production and turnover, and on the ability of plants to resist pathogen attacks23, the impacts on soil microbial dynamics, decomposition and nutrient-supply processes<sup>24</sup>, and shifting competitive abilities between plant species.

## **METHODS**

Eddy covariance data.  $CO_2$  fluxes were determined by the eddy-covariance technique using the same protocol as in ref. 8. We used quality-controlled half-hourly data screened out site-specifically for low nocturnal turbulence<sup>25</sup> ( $u^*$ -filtering) The choice of 2002 as a reference period is justified by the availability of high-quality data from numerous sites, and because 2002 was not a very abnormal year over most of Europe. For the July–September period, 2002 was not warmer than the average 1998–2002 at any site, but it was wetter in central Europe and northern Italy (Tharandt, Hainich, San Rossore) and drier at two southern sites (Bray, El Saler). The flux data were gap-filled<sup>9</sup> by replacing missing values with average measurements obtained under similar

meteorological conditions and during as small a time window as possible. The partitioning of NEE into GPP and TER was achieved through an algorithm9 that first establishes a short-term temperature dependence of TER from turbulent night-time data and then uses this relationship for extrapolating respiration from night-time to day-time. Day-to-day varying base rates of respiration were derived from  $u^*$ -filtered night-time fluxes, avoiding the confounding effect of covariance between general biological activity and temperature (http://gaia. agraria.unitus.it/database/eddyproc/). Uncertainties in the changes of GPP and TER between the years were estimated as a combination of errors arising from u\*-filtering, gap-filling and flux-partitioning. We assume that potential systematic errors affecting the absolute magnitude of the fluxes, as well as biases due to u\*-filtering cancel out by differencing between the years, because fluxes in both years should be affected similarly. Random errors of up to 50% for halfhourly fluxes diminish by integration over a month or a year. The bias of the gapfilling was estimated by introducing artificial gaps and was never higher than  $3 \text{ gC m}^{-2} \text{ month}^{-1}$ . At most 20% of the data were gap-filled, so this corresponds to an error of 0.6 g C m<sup>-2</sup> month<sup>-1</sup>. The uncertainty of the GPP versus TER partitioning is largely determined by the uncertainty of the temperature sensitivity  $(E_0)$  used to extrapolate from night to day. This uncertainty was estimated as the standard deviation of all  $E_0$  estimates for one year in ref. 9, assuming that the true value of  $E_0$  is constant over the year and all variability can be attributed to the estimation error. Clearly, because  $E_0$  can vary through the year, this is a conservative estimate of error. Errors for each year per site were summed for the difference between years, assuming that they are independent

Carbon flux model. Crop harvest-yield data are reported on a yearly basis<sup>13</sup>. Crop-specific factors<sup>11</sup> were used to convert harvested biomass into dry matter (~0.8 g), into carbon mass (~0.45 gC) and into crop NPP. The ORCHIDEE biosphere model<sup>5</sup> (http://www.ipsl.jussieu.fr/~ssipsl) explicitly calculates CO<sub>2</sub>, energy and H<sub>2</sub>O fluxes on a half-hourly basis, forced by air temperature, precipitation, air humidity and solar and thermal radiation data. Turbulent fluxes are coupled to the calculation of carbon pool dynamics internal to the ecosystem, for eight different plant functional types over Europe. Carbon dynamics include calculation of the growth onset and senescence periods, allocation of assimilates to the different plant organs, mortality, and litter and soil organic matter decomposition. No explicit nitrogen cycle is modelled. No adjustments are made to adapt the modelled response of the vegetation to extreme climate conditions. For point-wise simulations at eddy-covariance sites, the modelled carbon fluxes and stocks are spun up (200 years) to their equilibrium value, and then forced by in-situ meteorological records. By construction, the long-term modelled NEE is zero, unlike in the flux measurements. Yet, interannual variations of NEE, GPP and TER in response to climate can be safely analysed. For spatially explicit simulations of carbon and water fluxes, a vegetation map<sup>26,27</sup>, translated into the eight plant functional types, was held constant and ambient atmospheric CO2 was increased from 280 to 360 p.p.m. between 1900 and 2003. After 1,000 yr spin-up, ORCHIDEE was driven from 1900 to 2003 by monthly mean historical climate reconstructions over Europe<sup>15</sup> interpolated to half-hourly values using a weather generator over the period 1900–1990 at a spatial resolution of  $\sim$ 100 km, six-hourly meteorological re-analyses<sup>16</sup> provided by the European Centre for Medium-Range Weather Forecasts (ECMWF) at ~125-km spatial resolution over the period 1983-2001, and six-hourly ECMWF operational weather analyses at ~40-km spatial resolution over the period 2000-2003. Using distinct climate input data sets is necessary to span over the whole period of interest, but creates some differences in the simulated carbon quantities. We verified that the year-to-year variability of  $CO_2$  fluxes was, however, similar ( $\pm 10\%$ ) between simulations forced by distinct climate data sets during their period of overlap. Using another climate data set (NCEP), we found a difference of up to 50% in the modelled NPP reduction and of 5% in the NEE reduction. To evaluate the model results against satellite FAPAR, we converted leaf area index into FAPAR following ref. 28.

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- Cox, P. M., Betts, R. A., Jones, C. D., Spal, A. S. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408, 184–187 (2000).
- Dufresne, J. L. et al. On the magnitude of positive feedback between future climate change and the carbon cycle. Geophys. Res. Lett. 29(10), doi:10.1029/ 2001GL013777 (2002).
- Schär, C. et al. The role of increasing temperature variability in European summer heatwaves. Nature 427, 332–335 (2004).
- Meehl, G. A. & Tebaldi, C. More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305, 994–997 (2004).
- i. Krinner, G. et al. A dynamic global vegetation model for studies of the

- coupled atmosphere-biosphere system. *Glob. Biogeochem. Cycles* **19**, 1–33 (2005).
- 6. Janssens, I. A. et al. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic  $CO_2$  emissions. Science 300, 1538–1542 (2003).
- 7. Valentini, R. et al. Respiration as the main determinant of carbon balance in European forests. *Nature* **404**, 861–865 (2000).
- Aubinet, M. et al. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Adv. Ecol. Res. 30, 113–175 (2000).
- Reichstein, M. et al. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob. Change Biol. 11, 1–16 (2005).
- Granier, A., Bréda, N., Piron, P. & Vilette, S. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Modell. 116, 269–283 (1999).
- Reichstein, M. et al. Inverse modelling of seasonal drought effects on canopy CO<sub>2</sub>/H<sub>2</sub>O exchange in three Mediterranean Ecosystems. J. Geophys. Res. 108, 4716–4721 (2003).
- Irvine, J., Perks, M. P., Magnani, F. & Grace, J. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiol.* 18, 393–402 (1998).
- Food and Agriculture Organization Database (http://faostat.fao.org/faostat/ collections?subset=agriculture) (2004).
- 14. Goudriaan, J., Groot, J. J. R. & Uithol, P. W. J. in *Terrestrial Global Productivity* (eds Saugier, B. & Roy, J.) (Academic, 2001).
- Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M. & New, M. A comprehensive set of high resolution grids of monthly climate for Europe and the globe: the observed record (1901–2000) and 16 scenarios (2001–2100). Working paper 55 (Tyndall Centre for Climate Change Research, July 2004); available at (http://www.tyndall.ac.uk/publications/working\_papers/ wp55.pdf).
- Simmons, A. J. & Gibson, J. K. The ERA 40 Project Plan. ERA-40 Project Report Series No. 1, 1–62 (European Center for Medium Range Weather Forecasts (ECMWF). 2000).
- Myneni, R. B. et al. Global products of vegetation leaf area and fraction absorbed PAR from one year of MODIS data. Remote Sens. Environ. 83(1–2), 214–231 (2002).
- Nemani, R. R. et al. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300, 1560–1563 (2003).
- Barber, V. A. et al. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405, 668–673 (2000)
- 20. Elliot, K. J. & Swank, W. T. Impacts of drought on tree mortality and growth in

- a mixed hardwood forest. J. Veget. Sci. 5.2, 229-236 (1994).
- Tyree, M. T. & Sperry, J. S. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88, 574–580 (1988).
- Cherbuy, B., Joffre, R., Gillon, D. & Rambal, S. Internal remobilization of carbohydrates, lipids, nitrogen and phosphorus in the Mediterranean evergreen oak *Quercus ilex*. Tree Physiol. 21, 9–17 (2001).
- Boyer, J. S. Biochemical and biophysical aspects of water deficits and the predisposition to disease. Annu. Rev. Phytopathol. 33, 251–274 (1995).
- Schimel, J. S. et al. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. Soil Biol. Biochem. 31, 831–838 (1999).
- Reichstein, M. et al. Severe drought effects on ecosystem CO<sub>2</sub> and H<sub>2</sub>O fluxes at three mediterranean sites: revision of current hypothesis? Glob. Change Biol. 8, 999–1017 (2002).
- Büttner, G., Feranec, J. & Jaffrain, G. Corine Land Cover Update 2000. Technical Report 89 (European Environment Agency, 2000); available at <a href="http://reports.eea.eu.int/technical\_report\_2002\_89/en">http://reports.eea.eu.int/technical\_report\_2002\_89/en</a>).
- Mucher, C. A., Steinnocher, K. T., Kressler, F. D. & Heunks, D. Land cover characterization and change detection for environmental monitoring of pan europe. *Int. J. Remote Sens.* 21, 1159–1182 (2000).
- 28. Monsi, M. & Saeki, T. Über den Lichfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn. J. Bot.* 14, 22–52 (1953).

 $\begin{tabular}{ll} \textbf{Supplementary Information} is linked to the online version of the paper at www.nature.com/nature. \end{tabular}$ 

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