LETTERS

Prolonged suppression of ecosystem carbon dioxide uptake after an anomalously warm year

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Terrestrial ecosystems control carbon dioxide fluxes to and from the atmosphere[1,2] through photosynthesis and respiration, a balance between net primary productivity and heterotrophic respiration, that determines whether an ecosystem is sequestering carbon or releasing it to the atmosphere. Global[1,3–5] and site-specific[6] data sets have demonstrated that climate and climate variability influence biogeochemical processes that determine net ecosystem carbon dioxide exchange (NEE) at multiple timescales. Experimental data necessary to quantify impacts of a single climate variable, such as temperature anomalies, on NEE and carbon sequestration of ecosystems at interannual timescales have been lacking. This derives from an inability of field studies to avoid the confounding effects of natural intra-annual and interannual variability in temperature and precipitation. Here we present results from a four-year study using replicate 12,000-kg intact tallgrass prairie monoliths located in four 184-m^3 enclosed lysimeters[7]. We exposed 6 of 12 monoliths to an anomalously warm year in the second year of the study[8] and continuously quantified rates of ecosystem processes, including NEE. We find that warming decreases NEE in both the extreme year and the following year by inducing drought that suppresses net primary productivity in the extreme year and by stimulating heterotrophic respiration of soil biota in the subsequent year. Our data indicate that two years are required for NEE in the previously warmed experimental ecosystems to recover to levels measured in the control ecosystems. This time lag caused net ecosystem carbon sequestration in previously warmed ecosystems to be decreased threefold over the study period, compared with control ecosystems. Our findings suggest that more frequent anomalously warm years[9], a possible consequence of increasing anthropogenic carbon dioxide levels[10], may lead to a sustained decrease in carbon dioxide uptake by terrestrial ecosystems.

Ecosystem biogeochemical processes that modulate CO_2 exchange between land and atmosphere respond to climate variability at different timescales. Well known and characterized are the effects of seasonal changes in terrestrial net primary productivity (NPP) on NEE (the instantaneous net ecosystem CO_2 flux) that cause intra-annual fluctuations in global atmospheric CO_2 levels[1]. Less well quantitatively understood, however, are potential delayed or lagged effects of interannual climate variability—particularly climatically anomalous years—on net ecosystem productivity (NEP, the annual sum of NEE) that in turn help to determine interannual rates of change of atmospheric CO_2 concentration (refs 11, 12). This inadequate quantitative understanding of lagged responses to climatically anomalous years is of particular concern because, as a consequence of increasing anthropogenic CO_2 concentrations (ref. 10), the frequency and intensity of extreme years are increasing[9].

Although statistical and process modelling of global and site-specific temperature, precipitation, [CO_2] and NEE data at intra-annual and interannual timescales suggest a strong temporal correlation between climate variability, vegetation and growth rate of atmospheric CO_2 concentration (refs 1, 11, 12), interannual variability in both temperature and precipitation makes a quantitative examination of underlying ecosystem control mechanisms by using field data difficult. The EcoCELL facility at the Desert Research Institute uniquely enables: (1) tests of the effects of variability in a single climate factor at interannual timescales while simulating natural diel and seasonal climate variation; (2) continuous monitoring of NEE and ecosystem processes that determine NEE for multiple years; and (3) the study of intact soil monoliths with their native plant communities[7,8].

Key objectives of the present study were to quantify, first, how exposure to an anomalously warm year affects ecosystem processes that determine NEE and NEP, and thus annual net C sequestration, at intra-annual and interannual timescales; second, how intra-annual responses and feedbacks shape interannual responses; and third, the environmental factors and feedbacks that affect these processes. We used tallgrass prairie as a model ecosystem (see Methods).

During the course of the study, the intact natural ecosystems used in the EcoCELLs behaved largely in a fashion representative of natural tallgrass prairie ecosystems in the field. Plant canopies developed and senesced in a pattern (Fig. 1e) that followed seasonal changes in air temperature, daytime vapour pressure deficit (VPD) and rainfall (Fig. 1a, b, d). NEE and evapotranspiration closely followed patterns in plant canopy greenness (Fig. 1c, e, f).

In the treatment year, ecosystems exposed to temperatures 4 °C higher responded with a 7–10-day earlier start of the growing season, resulting in a more rapid rise in NEE and evapotranspiration in early spring (mid March to early April 2003; Fig. 1c, f). Mean daytime VPDs in warmed EcoCELLs immediately doubled when temperatures were raised, and this increased evapotranspiration in early spring 2003 (Fig. 1b, c). By the end of April 2003, NEE peaked almost 35 days earlier in warmed temperatures than in control temperatures (Fig. 1f). This coincided with an increase in mean daytime VPD, a disappearance of the treatment effect on evapotranspiration, a decline in soil water content (SWC) in surface horizons, and a slowing of plant canopy development (Fig. 1b–d and Supplementary

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Fig. 3). Although higher evapotranspiration rates in warmed ecosystems in early spring led to slightly lower SWC than in control ecosystems, significant decreases in SWC became apparent only in July 2003 (Fig. 1d). Daytime VPDs in warmed EcoCELLs reached levels high enough (more than 10 mbar) to decrease leaf stomatal conductance (g_s)[13–15] by late March 2003, more than two months earlier than in control EcoCELLs. VPDs in warmed EcoCELLs remained above 10 mbar twice as long as they did in control EcoCELLs.

Thus, the earlier decline in NEE observed in warmed ecosystems in 2003 seems to have resulted, at least initially, from higher daytime VPDs that substantially constrained canopy-level CO_2 uptake[16]. The importance of VPD as a regulator of canopy conductance (g_{canopy}) has been demonstrated in a wide range of graminoid-dominated ecosystems[8,17–19], and decreases in g_s caused by high VPDs[15] have been shown to decrease canopy[8] and leaf-level[14] CO_2 assimilation. Lower CO_2 uptake by the canopy may have led to decreased canopy development and duration (also see Supplementary Information) and thus to a lower NPP, which limited NEE even further in conjunction with a decrease in soil CO_2 efflux[8]. This VPD response may have been exacerbated by drier surface soils in warmed ecosystems beginning in May 2003 (Fig. 1d), potentially lowering the apparent g_s. Decreases in mean weekly NEE observed in warmed ecosystems in the treatment year (Fig. 1f) resulted mainly from large decreases in daytime NEE (Supplementary Fig. 4a) that may have been due partly to higher aboveground plant respiration immediately following the step increase in temperature (Supplementary Fig. 4b, inset, and Supplementary Information). Hence, immediate and ongoing plant physiological responses to increased temperatures and VPDs in 2003 seem to have contributed to overall declines in annual ecosystem CO_2 balance primarily by decreasing NPP. Canopy green index explained between 70% and 78% of the variability observed in mean weekly NEE (Supplementary Fig. 6), with canopy clipping in late August 2003 (and August 2004) eliminating nearly all CO_2 uptake in all ecosystems and eliminating differences in NEE between control and warmed ecosystems for the rest of the treatment year (Fig. 1f).

Persistence of lower SWC in warmed ecosystems into the first post-treatment year (2004) (Fig. 1d) may explain the two-week slower start in plant canopy green-up and growth in spring of 2004 than in the controls (Fig. 1e). Canopy green-up in these ecosystems seemed to start only after springtime rains restocked topsoil moisture to levels present in unwarmed ecosystems two weeks earlier. In 2004, VPD differences between previously warmed and unwarmed ecosystems disappeared when air temperatures in treated EcoCELLs were returned to pretreatment levels (Fig. 1b). In 2005 (the second post-treatment year), the start of canopy green-up in previously warmed ecosystems was once again delayed (Fig. 1e). In contrast to the return of normal plant canopy development in previously warmed ecosystems in 2004 after the delayed start, however, plant canopy development in 2005 in previously warmed ecosystems was decreased, but not as severely as the decrease observed in 2003. In 2005, decreased canopy size did not result in significant decreases in NEE, presumably because lower VPDs in 2005 did not constrain g_s and g_s-modulated

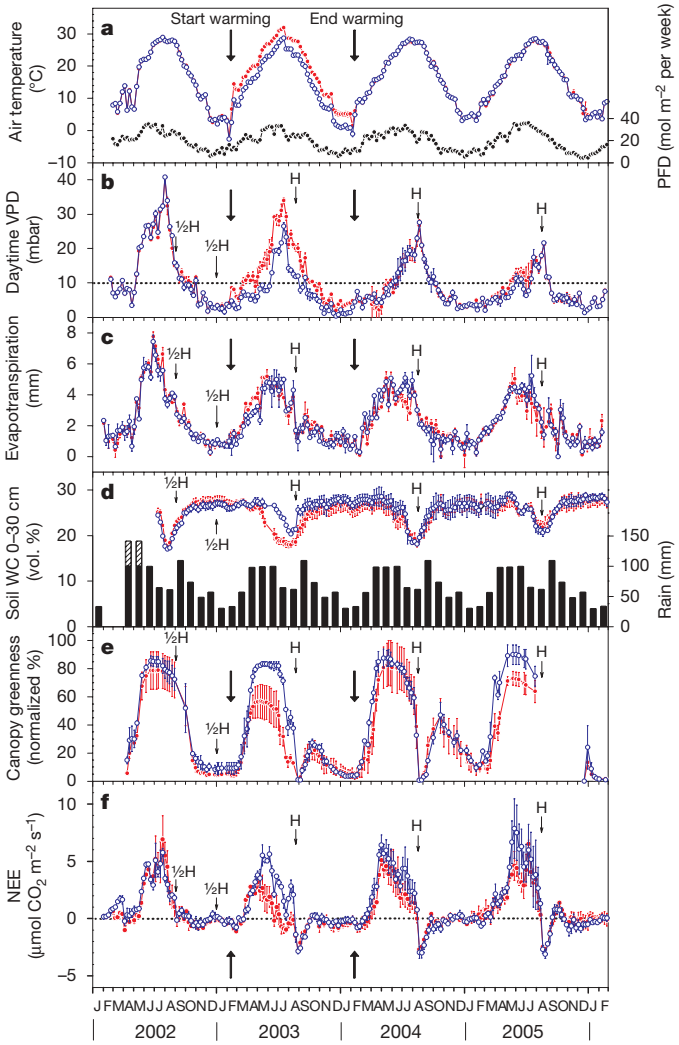

Figure 1 | Four-year time courses covering pretreatment (11 February 2002 to 10 February 2003), treatment and post-treatment years. Weekly means are shown. **a**, Air temperature and photon flux density (PFD). **b**, Daytime atmospheric VPD with line at 10 mbar denoting VPD above which g_s can be strongly decreased. **c**, Ecosystem evapotranspiration. **d**, SWC of the 0–30 cm layer; bars show applied monthly rainfall (lighter-shaded bar-tops in April and May 2002 denote additional rain applied to compensate for below-target rainfall in February and March 2002). **e**, Plant canopy greenness index. **f**, NEE based on 24 h means; positive values indicate net CO_2 uptake by the ecosystem, and negative values net CO_2 release. Aboveground plant biomass harvests are indicated by H, and half-plot harvests by ½H. Open blue circles, control ecosystems; filled red circles, treated ecosystems (warmed in 2003). Error bars indicate s.e.m. for $n = 2$ EcoCELLs.

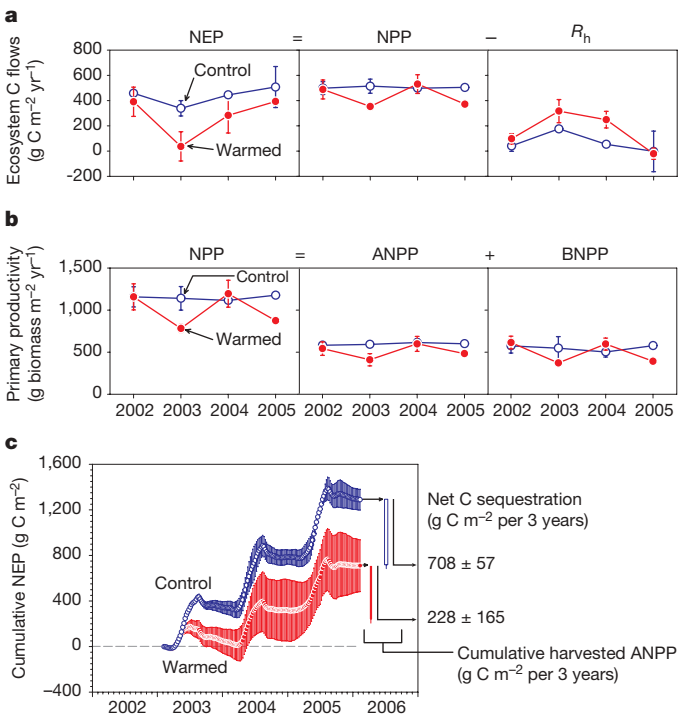

Figure 2 | Effects of an anomalously warm year on annual ecosystem C flows. a, NEP, NPP and R_h. **b**, Primary productivity: NPP, ANPP and belowground NPP (BNPP). Cumulative net ecosystem productivity—NEP (**c**). Error bars indicate s.e.m. for $n = 2$ EcoCELLs.

leaf photosynthesis as much as higher VPDs in 2003 seem to have done.

Aggregated effects of the warm year included a 63% decrease in NEP in 2003, relative to the controls, followed by only a partial recovery in NEP in the first post-treatment year (2004; Figs 2a and 3) and complete recovery in the second post-treatment year (2005). Large decreases in NPP in 2003 (Fig. 2a, b) clearly contributed to the decrease in NEP in that year (see also Supplementary Information). Full recovery of NPP in 2004 enabled a partial recovery of NEP in 2004. Full recovery of NEP in 2005 occurred despite a two-year lagged decrease in NPP. However, this decrease in NPP may, in turn, have resulted in decreased C supplies to soil heterotrophs, thus also decreasing heterotrophic respiration (R_h) and enabling recovery of NEP.

Our results indicate that a lack of complete NEP recovery in 2004 was caused by a lagged warming-induced stimulation of R_h (calculated as NPP minus NEP; Fig. 2a). Conversely, full recovery of NEP in 2005 in previously warmed ecosystems was possible only because R_h of these ecosystems returned to levels measured in the pretreatment year in ecosystems assigned to the warming treatment. The absence of significant stimulation of R_h in warmed ecosystems in 2003 may have been caused by large decreases in the SWC of the uppermost soil horizons (Fig. 1d), suppressing soil microbial activity. Stimulation of R_h in 2004 in previously warmed ecosystems may have resulted from a recovery of soil moisture levels (and possibly plant-available soil N levels) that enabled a breakdown of undecomposed rhizodeposits produced in 2003 along with a breakdown of fresh rhizodeposits produced in 2004 by fully recovered plant canopies (Fig. 1e), photosynthate supplies and NPP (Fig. 2a, b). Causes of the unexpected recurring decrease in NPP and in plant canopy development in the second post-treatment year in previously warmed ecosystems are unclear but may have included a decrease in labile N caused by the previous year's post-warming rebounding aboveground NPP (ANPP) that was harvested in the late summer of 2004. Regardless of the cause, the NPP response observed in 2005 and the response showing lower R_h in 2005 in previously warmed ecosystems demonstrate the potential for longer-term and unexpected lagged responses that may affect the CO_2 balance of an ecosystem.

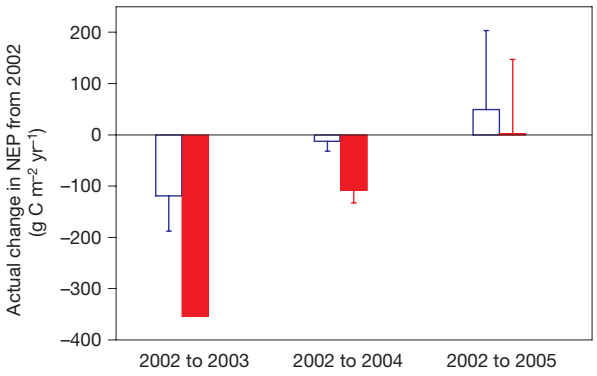

Figure 3 | Actual change in ecosystem annual NEP for control and warmed ecosystems from 2002 to 2003, 2002 to 2004, and 2002 to 2005. Results are means and s.e.m. ($n = 2$); the error bar for 'warmed 2002 to 2003' was ± 0.11 g C m^{-2} yr^{-1} and is not visible at the y-axis scale used in the figure. This figure also shows a strong warming-induced decrease in annual NEP in warmed ecosystems during the treatment year, only partial recovery in 2004, and complete recovery in 2005. Open blue columns, control ecosystems for 2002, 2004 and 2005; filled red columns, treated ecosystems (warmed in 2003) for 2002, 2004 and 2005. The graph shows that the lagged decrease in NEP that occurred in the year after the anomalously warm year was about one-third as large as the synchronous warming-induced decrease that occurred in the warm year (seen by comparing the first two red bars with each other). When accounting for changes in NEP in the control ecosystems in both years, however, the true effect was 40% of the immediate effect.

Data from this study and other field studies[20–23] suggest that warming affects NEE and thus NEP in the year of the temperature anomaly primarily through hydrological feedbacks on plant canopy physiology (g_s and CO_2 assimilation), development, size (greenness) and duration (Fig. 1b, e, f, and Supplementary Figs 6, 7 and 8; see also Supplementary Information). In fact, declines in ANPP observed in tallgrass prairie in the field in years with low precipitation[24] were similar to those that we observed in 2003 in response to the warm year. The responses we observed in subsequent years seem to have been due to more complex interacting feedbacks, which may include lagged decomposition of plant residues, carryover effects of the previous year's water deficits, and feedbacks through nutrient cycles. The collective result of synchronous and lagged declines in NEP observed during the four years of our study was a persistent decrease in annual net ecosystem C sequestration (NEP minus C removed in annual ANPP harvests that would decompose and release CO_2) that led to a threefold decrease by the end of the fourth year of the experiment (2005; Fig. 2c). CO_2 fluxes measured in our study were realistic and comparable to those measured in tallgrass prairie in the field[25].

Taken together, results from this multiyear experiment demonstrate, first, that the response of ecosystems to climate variability seems to be more complex than can easily be inferred from traditional experimental and observational approaches; second, that an increase in frequency and intensity of anomalously warm years may decrease the ability of terrestrial ecosystems to absorb CO_2 and store carbon[22,23]—more than would be expected on the basis of previous experimental approaches—and third, that the lagged effects of climate anomalies on NEP (less than observed during the year of the anomaly) provide a basis for validating timescales and mechanisms used in models[26], as well as projecting actual ecosystem C sequestration and calculating carbon credits across multiple years.

METHODS SUMMARY

We installed three large monoliths (2.44 m long, 1.22 m wide and 1.80 m deep) of intact soil and their actual plant communities excavated from a C_4-dominated tallgrass prairie in central Oklahoma, USA (Supplementary Fig. 1; also see Supplementary Information) into each of four 184-m^3 (7.5 m long, 5.5 m wide and 4.5 m high) daylight EcoCELLs[7,8] that served as both individual controlled-environment chambers and large differential open-flow whole-ecosystem gas exchange cuvettes enabling the continuous measurement of NEE. Air temperatures in the EcoCELLs in all four years of the experiment (2002–2005) were programmed to follow natural diel and seasonal oscillations based on data collected at the excavation site from 1993 to 2000 with the temperature in two of the EcoCELLs increased by 4 °C (Fig. 1a) in year 2 (the anomalously warm year) and then returned to the pretreatment regime in year 3. Annual rainfall was held constant in all four years (980 mm) and applied at the average monthly amount and natural mean frequency for each month (Fig. 1d). We monitored NEE continuously by measuring the difference between the [CO_2] in the air entering each EcoCELL and the [CO_2] of the mixed air inside each EcoCELL and multiplying this difference by the mass flow of air passing through the EcoCELL (20 mol s^{-1}; see Supplementary Methods). This value was then divided by the total land area of the three monoliths to yield NEE in units of μmol CO_2 m^{-2} s^{-1}. The annual NEP for each EcoCELL was calculated as the sum of all NEE values measured in an EcoCELL during the year. We measured annual NPP, ANPP and below-ground NPP (BNPP). We also continuously monitored evapotranspiration (daily), SWC (hourly) and plant canopy green index (weekly). Annual R_h was calculated for each EcoCELL as R_h = NPP minus NEP. Ecosystem C sequestration was calculated as NEP minus harvested ANPP-C. We analysed treatment effects on interannual and intra-annual data sets for all parameters primarily by using repeated-measures analysis of variance with each EcoCELL as a replicate ($n = 2$; Supplementary Table 1; also see Supplementary Methods).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions J.A.A. and P.S.J.V. headed up the study including leading proposal writing, project coordination, data interpretation and analysis, and manuscript preparation. P.S.J.V., R.L.J., J.D.L., D.E.S., J.A.A. and W.G.C. were directly involved in all aspects of the study on a day-to-day basis, with A.J.L., J.A.A., L.L.W. and R.A.S. focusing on plant community aspects; C.M.B. contributing to hydrological measurements; J.D.L. contributing to quantification of plant canopy dynamics; P.S.J.V. contributing particularly to measurements of soil CO_2 fluxes and soil C and N; and D.W.J. contributing to estimation of soil nutrients. D.S.S., Y.L., B.H.B., J.S.C., P.S.J.V. and J.A.A. developed the idea for the research. C.v.N. built and managed the database for the project and contributed to data analyses. P.E.B. coordinated outreach activities to local schools and brought research to the communities of Reno and Las Vegas. R.L.J., J.D.L. and P.S.J.V. worked closely with J.A.A. on data analysis and manuscript preparation. All authors discussed the results and commented on the manuscript.

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