REVIEW

Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation

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Abstract

Global mean temperature is predicted to increase by 2–7 °C and precipitation to change across the globe by the end of this century. To quantify climate effects on ecosystem processes, a number of climate change experiments have been established around the world in various ecosystems. Despite these efforts, general responses of terrestrial ecosystems to changes in temperature and precipitation, and especially to their combined effects, remain unclear. We used meta-analysis to synthesize ecosystem-level responses to warming, altered precipitation, and their combination. We focused on plant growth and ecosystem carbon (C) balance, including biomass, net primary production (NPP), respiration, net ecosystem exchange (NEE), and ecosystem photosynthesis, synthesizing results from 85 studies. We found that experimental warming and increased precipitation generally stimulated plant growth and ecosystem C fluxes, whereas decreased precipitation had the opposite effects. For example, warming significantly stimulated total NPP, increased ecosystem photosynthesis, and ecosystem respiration. Experimentally reduced precipitation suppressed aboveground NPP (ANPP) and NEE, whereas supplemental precipitation enhanced ANPP and NEE. Plant productivity and ecosystem C fluxes generally showed higher sensitivities to increased precipitation than to decreased precipitation. Interactive effects of warming and altered precipitation tended to be smaller than expected from additive, single-factor effects, though low statistical power limits the strength of these conclusions. New experiments with combined temperature and precipitation manipulations are needed to conclusively determine the importance of temperature–precipitation interactions on the C balance of terrestrial ecosystems under future climate conditions.

Keywords: ecosystem photosynthesis, meta-analysis, net ecosystem exchange, plant biomass, plant productivity, precipitation, respiration, warming

Introduction

Increasing greenhouse gas emissions are expected to raise global mean temperature by 2–7 °C by the end of this century (Allison *et al.*, 2009). Precipitation is projected to increase at high latitudes and decrease in most subtropical regions (IPCC, 2007). Temperature and precipitation are key drivers of ecosystem processes, so projected climate changes will likely alter ecosystem carbon (C) balance. Understanding the sensitivity of terrestrial C balance to climate change is a high priority, because of the potential for changes in terrestrial C storage to affect the pace of ongoing climatic change (Cox *et al.*, 2000).

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While both ecosystem photosynthesis and respiration often increase with warming (Rustad *et al.*, 2001), responses of net C balance to warming are less clear. Some lines of evidence suggest that warming increases net C uptake (Welker *et al.*, 2004; Oberbauer *et al.*, 2007; Sullivan *et al.*, 2008). Also, part of the residual terrestrial C sink is attributed to recent warming and lengthening of the growing season (Peñuelas & Filella, 2001; Lucht *et al.*, 2002; Nemani *et al.*, 2003). Furthermore, global C cycle models project increased terrestrial CO_2 uptake in response to warming through the middle of this century (Cao & Woodward, 1998; Cox *et al.*, 2000; Cramer *et al.*, 2001; Fung *et al.*, 2005; Friedlingstein *et al.*, 2006; Canadell *et al.*, 2007; Sitch *et al.*, 2008). On the other hand, the strong sensitivity of respiration to warming provides a potential positive feedback to warming (Woodwell *et al.*, 1998; Knorr *et al.*, 2005; Heimann & Reichstein, 2008),

and suggests that the sensitivity of respiration to warming will eventually surpass that of ecosystem photosynthesis. This is consistent with projections of most global biogeochemical models that continued warming will cause declines in net C uptake by around mid-century (Cao & Woodward, 1998; Cox *et al.*, 2000; Cramer *et al.*, 2001; Fung *et al.*, 2005; Friedlingstein *et al.*, 2006; Canadell *et al.*, 2007). Results from field experiments can help shed light on the direction and magnitude of ecosystem C balance responses to warming. Our first goal in this work was to synthesize results from field experiments that have examined the responses of plant biomass, productivity, and C balance of terrestrial ecosystems to experimental warming.

Water availability is critical to all life, so altered precipitation is virtually certain to affect terrestrial ecosystem processes. Yet, most inferences about the effects of altered precipitation on ecosystem processes rely on correlations between interannual and intersite variation in precipitation and processes of interest (Lieth, 1973; Churkina *et al.*, 1999; Knapp & Smith, 2001; Scurlock *et al.*, 2002; Huxman *et al.*, 2004; Garbulsky *et al.*, 2010). This approach takes advantage of the natural variation in precipitation between years, yet correlations have the potential drawback of confounding changes in other variables that covary with precipitation over space and time, such as temperature (e.g., Loik *et al.*, 2004; Breshears *et al.*, 2005; Ciais *et al.*, 2005). Experimental manipulations of precipitation can complement, and extend beyond, observational studies by causally linking precipitation change with ecosystem responses while keeping covarying climate variables constant. A number of field experiments examining responses of C cycling to altered precipitation now exist. Our second goal in this work was to synthesize results from these experiments using meta-analysis.

The combined effects of warming and altered precipitation are expected to have strong influences on C balance. For example, the combination of warming and decreased precipitation can cause large C losses (Loik *et al.*, 2004; Angert *et al.*, 2005; Breshears *et al.*, 2005; Ciais *et al.*, 2005). The expected shift from terrestrial C sink to source could be hastened if decreased precipitation occurs along with warming in the next few decades. Yet, warming-induced soil drying can also suppress soil respiration and thereby increase net C storage (Saleska *et al.*, 2003). A few field experiments have examined the interactive effects of warming and altered precipitation on C balance. Our third goal was to synthesize these interactive effects using meta-analysis.

Different terrestrial ecosystems are likely to vary in the magnitude and direction of their responses to warming and altered precipitation. For example, aboveground net primary production (ANPP) in cooler eco-systems has been found to exhibit stronger positive responses to warming than that of warmer ecosystems (Rustad *et al.*, 2001). Meanwhile, more C was lost in colder ecosystems due to a higher sensitivity of soil respiration to warming (Kirschbaum, 1995), which could potentially render such ecosystems as C sources. Reduced precipitation may have disproportionately large impacts on the C balance of semiarid ecosystems compared with ecosystems in more mesic environments. There have been a number of field experiments addressing effects of warming and altered precipitation on components of C balance, crossing a broad spectrum of climatic space. Our fourth goal was to test whether different ecosystem types and biomes, representing climatic space, vary systematically in their responses to warming and altered precipitation.

Meta-analysis provides a synthesis of individual studies and allows statistical testing whether responses are general across a variety of sites and conditions. For example, Arft *et al.* (1999) applied meta-analysis to examine the response of plant phenology, growth, and reproduction to experimental warming using 13 circumpolar experimental sites. Rustad *et al.* (2001) also used meta-analysis to synthesize findings on the responses of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental warming from 32 ecosystem warming experiments. In this paper, we applied meta-analysis to synthesize responses of plant biomass, productivity, and ecosystem C balance to warming and altered precipitation. We asked the following questions: (1) how do warming, increased and decreased precipitation, acting in isolation, affect plant growth and ecosystem C fluxes? (2) how do these responses vary across vegetation types and with climate?, and (3) is there evidence for interactive effects between warming and altered precipitation on plant growth and C cycling? We synthesized data from 85 studies where temperature, precipitation, or both were manipulated, covering tundra, boreal forests, temperate evergreen and deciduous forests, shrublands, grasslands, and deserts (Fig. 1 and Table 1).

Methods

Data compilation

Criteria for study selection influence the output of meta-analysis (Hungate *et al.*, 2009). Our criteria were: for multiple observations from a single site, we included the most recent result, because no significant temporal patterns were observed in the responses of soil respiration and plant productivity to warming in a previous meta-analysis (Rustad *et al.*, 2001); for multifactor experiments (e.g., warming and nutrient), we used data from temperature and/or precipitation treatments while
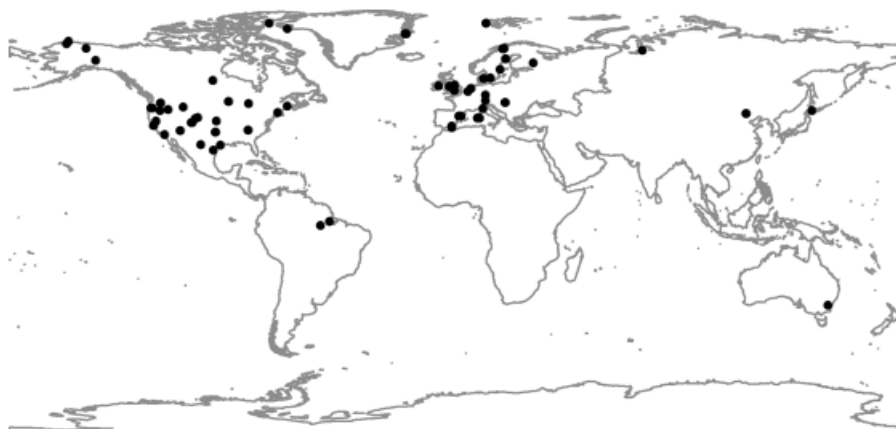
Fig. 1 Study sites included in this meta-analysis.

the other factors were kept at ambient levels (e.g., warming at ambient nutrient conditions), and interactive responses when warming and altered precipitation were combined factorially; we treated multiple levels of treatment as independent, even though they shared a common control. We used Google Scholar (Google Inc., Mountain View, CA, USA) for exhaustive search of peer-reviewed journal articles published before June 2009. Data collection was restricted to studies that were conducted in the field; no laboratory incubation or growth chamber experiments were included. For each selected study, we collected latitude, longitude, elevation, mean annual temperature (MAT) and precipitation (MAP), and biome type; we also collected information on experimental duration, soil moisture and temperature, experimental treatment type and size, treatment techniques, control and treatment means, sample size, and variance. These studies were located from 35.12 S to 78.56 N, with MAT of experimental sites ranging from -20 to $25\,°C$, and MAP from 200 to 2272 mm. We also grouped these studies into two broad vegetation types – woody and herbaceous – to test for differences in responses of functional groups. The experimental duration ranged from 1 to 11 years. Warming techniques included curtain covers, heating cables, open or closed top chambers, greenhouses, overhead infrared heat lamps, transplanting and passive nighttime warming; altered precipitation was achieved by hand sprinklers, metered hand sprayers, rain collectors, rainout shelters, sheeting, guttering, and pumping. Warming treatments caused an increase in soil temperature ranging from 0.1 to $10.2\,°C$; decreased precipitation treatments were between 41 and 1136 mm, and increased precipitation treatments ranged from 5 to 2148 mm.

We grouped the collected data into five categories of response variables (Table 2). (1) *Biomass*: For herbaceous plants, aboveground biomass was measured by clipping live biomass at the soil surface, oven-drying, and weighing. Allometric relationships were used for estimating woody plant aboveground biomass. Belowground biomass was measured by taking soil cores up to 30 cm in depth, removing plant tissues, oven-drying, and weighing. Total biomass was obtained from the sum of the aboveground and belowground biomass. (2) *Net primary productivity (NPP)*: ANPP was calculated by peak

aboveground biomass when there is no carryover of living biomass from previous years. Canopy biomass and shoot mass/shoot length relationships were also used for calculating ANPP of woody plants. Belowground NPP (BNPP) was estimated using root ingrowth cores, root distribution regression, and root biomass/root turnover rate relationships. Total NPP (TNPP) was calculated as the sum of ANPP and BNPP. (3) *Respiration*: Ecosystem respiration was obtained by measuring CO_2 exchange in the dark (either covering the gas-exchange chamber with shade cloth or measuring at night), using infrared gas analyzer (IRGA) or periodic headspace sampling and gas chromatography. Soil respiration was measured by IRGA or headspace sampling followed by gas chromatography. Aboveground respiration was calculated by subtracting soil respiration from ecosystem respiration. (4) *Net ecosystem exchange (NEE)*: NEE was measured using a transparent chamber with an IRGA. (5) *Ecosystem photosynthesis*: Ecosystem photosynthesis was calculated by the sum of NEE and ecosystem respiration.

Meta-analysis

Effect sizes. Effect size compares the treatment effects of all studies and expresses them on a common scale, aiming to highlight general responses over a broad range of ecosystems. A number of different metrics can be used for meta-analysis (Rosenberg *et al.*, 2000; Hungate *et al.*, 2009). For each response variable, we calculated three types of effect size metrics.

$$\text{Log response ratio}: X_{LR} = \ln(T/C), \quad (1)$$

where T and C are the means of treatment and control groups, respectively. The log ratio compares the relative difference between the treatments and controls.

$$\text{Absolute difference}: X_{AD} = T - C, \quad (2)$$

where T and C are defined as above. For biogeochemistry, this metric is effective in expressing ecological significance because it captures the magnitude of changes in mass or mass fluxes.

$$\text{Sensitivity}: X_S = (T - C)/(T_T - T_C)$$
$$\text{or } X_S = (T - C)/(PPT_T - PPT_C), \quad (3)$$

Table 1 Site characteristics for temperature and precipitation manipulation studies included in this meta-analysis

State/country	Site	Latitude	Longitude	Biome	Period	References
Temperature manipulation experiments						
Alaska, USA	Delta Junction	63.55	−145.44	Boreal forest	2000–2007	Bergner *et al.* (2004), Allison & Treseder (2008)
Alaska, USA	Toolik Lake	68.38	−149.34	Tundra	1989–2002	Hobbie & Chapin (1998), Jones *et al.* (1998), Grogan and Chapin III (2000), Welker *et al.* (1999), Oberbauer *et al.* (2007), La Puma *et al.* (2007)
Alaska, USA	Atqasuk	70.27	−157.24	Tundra	1996–2001	Oberbauer *et al.* (2007)
Alaska, USA	Barrow	71.18	−156.4	Tundra	1995–2001	Oberbauer *et al.* (2007)
Australia	Ginninderra Experiment Station	−35.12	149.06	Grassland	1995	Lilley *et al.* (2001)
Austria	Northern Limestone Alps	47.35	11.38	Forest	2004–2006	Schindlbacher *et al.* (2009)
Belgium	Drie Eiken Campus	51.09	4.24	Grassland	2003–2005	De Boeck *et al.* (2007, 2008)
California, USA	Jasper Ridge Biological Preserve	37.24	−122.14	Grassland	1997–2003	Zavaleta *et al.* (2003), Dukes *et al.* (2005)
Canada	Alexandra Fiord	78.53	−75.55	Tundra	1992–2001	Welker *et al.* (2004), Oberbauer *et al.* (2007)
Canada	Boreal Soil and Air Warming Experiment research site	55.53	−98.2	Black spruce forest	2004–2005	Bronson *et al.* (2008)
Oregon, USA	National Health and Environmental Effects Research Laboratory	44.34	−123.17	Douglas fir	1993–1997	Olszyk *et al.* (2003), Tingey *et al.* (2007)
China	Duolun County	42.02	116.17	Steppe	2005–2008	Niu *et al.* (2008), Liu *et al.* (2009), Xia *et al.* (2009)
Colorado, USA	Niwot Ridge	40.03	−105.36	Tundra	1994–1997	Welker *et al.* (1999)
Colorado, USA	Rocky Mountain Biological Laboratory	38.53	−107.02	Montane meadow	1991–1997	Harte & Shaw (1995), De Valpine & Harte (2001), Saleska *et al.* (2002)
Denmark	Mols CLIMOOR	56.23	10.57	Shrub	1999–2001	Emmett *et al.* (2004)
Finland	Mekrijarvi Research Station (University of Joensuu)	62.47	30.58	Scots pine forest	1996–2000	Niinistö *et al.* (2004)
Greenland	Pituffik	76.33	−68.3	High arctic fen	2003–2006	Sullivan *et al.* (2008)
Greenland	Zackenberg Research Station	74.28	−20.34	Grassland	1998–1999	Mertens *et al.* (2001), Marchand *et al.* (2004)
Hungary	VULCAN	46.53	19.23	Shrub	2002–2005	Peñuelas *et al.* (2007)
Hungary	Danube Tisza	46.52	19.25	Forest-steppe	2002–2006	Lellei-Kovács *et al.* (2008)
Italy	Sardinia VULCAN	40.36	8.9	Shrub	2004	Peñuelas *et al.* (2007)
Japan	Taisetsu Mountains	43.33	142.53	Shrub	1994–1999	Kudo & Suzuki (2003)
Maine, USA	Howland Integrated Forest Study	45.1	−68.4	Spruce-fir forest	1993–1995	Rustad & Fernandez (1998)
Massachusetts, USA	Harvard Forest	42.54	−72.18	Hardwood forest	1991–2000	Melillo *et al.* (2002)
Minnesota, USA	Glacial Lake Upham basin (Toivola and Alborn)	47	−92	Bog and sedge fen	1994–1997	Weltzin *et al.* (2000), Updegraff *et al.* (2001)
The Netherlands	Oldebroek CLIMOOR	52.24	5.55	Shrub	1999–2003	Emmett *et al.* (2004), Peñuelas *et al.* (2007)
Norway	Svalbard	78.56	11.5	Shrub	1991–1993	Wookey *et al.* (1995)
Russia	Tazovskiy Peninsula	67.56	74.52	Dwarf shrub tundra	2002–2003	Biasi *et al.* (2008)

Continued

Table 1 (*Contd.*)

State/country	Site	Latitude	Longitude	Biome	Period	References
Oklahoma, USA	Great Plain Apiaries (Kessler's Farm Field Laboratory)	34.59	−97.31	Grassland	1999–2003	Luo *et al.* (2001, 2009), Wan *et al.* (2005), Zhou *et al.* (2006, 2007)
Italy	Capo Caccia	40.37	8.1	Forest	2002–2004	De Dato *et al.* (2006)
Spain	Catalonia CLIMOOR	41.18	1.49	Shrub	1999–2005	Emmett *et al.* (2004), Peñuelas *et al.* (2007), Sardans *et al.* (2008)
Sweden	Abisko	68.19	18.51	Subarctic heath	1989–1999	Jonasson *et al.* (1999), Illeris *et al.* (2004)
Sweden	Abisko	68.21	18.49	Bog	2000–2002	Dorrepaal *et al.* (2004)
Sweden	Abisko Scientific Research Station	68.35	18.82	Subarctic dwarf shrub heath	1991–1997	Press *et al.* (1998), Hartley *et al.* (1999)
Sweden	Degero Stormyr	64.11	19.33	Fen	1995–1998	Gunnarsson *et al.* (2004)
Sweden	Latnjajaure field station	68.21	18.21	Mesic sedge meadow	1994–1998	Jónsdóttir *et al.* (2005)
Sweden	Lappmyran	64.09	19.35	Bog	2004–2005	Breeuwer *et al.* (2008)
Sweden	Åkerlänna Römosse	60.01	17.22	Bog	2004–2005	Breeuwer *et al.* (2008)
Sweden	Saxnäs Mosse	56.51	13.27	Bog	2004–2005	Breeuwer *et al.* (2008)
Tennessee, USA	Oak Ridge National Laboratory Global Change Field Research Facility	35.54	−84.2	Grassland	2002–2004	Wan *et al.* (2007)
Tennessee, USA	Oak Ridge National Laboratory Global Change Field Research Facility	35.54	−84.2	Red maple and sugar maple seedlings	1994–1997	Wan *et al.* (2004)
United Kingdom	Buxton	53.2	−2	Limestone grassland	1994–2004	Grime *et al.* (2000, 2008)
United Kingdom	University of York	53.58	−1.06	Wheat, maize	2004–2005	Hartley *et al.* (2007)
United Kingdom	Wytham	51.46	−1.2	Limestone grassland	1994–1998	Grime *et al.* (2000), Thompson *et al.* (2000)
United Kingdom	Clocaenog CLIMOOR	53.03	−3.28	Shrub	1999–2003	Emmett *et al.* (2004), Peñuelas *et al.* (2007)
Precipitation manipulation experiments						
Brazil	Amazon	−2.9	−54.95	Forest	2000–2004	Davidson *et al.* (2008)
Brazil	Caxiuana National Forest	−1.43	−51.27	Forest	2002–2003	Sotta *et al.* (2007)
California, USA	Sierra Foothill research and Extension Center	39.15	−121.17	Grassland	2003–2006	Silver *et al.* (2005), Chou *et al.* (2008)
California, USA	Jasper Ridge Biological Preserve	37.24	−122.14	Grassland	1997–2003	Zavaleta *et al.* (2003), Dukes *et al.* (2005)
California, USA	Irvine Ranch Land Reserve	33.62	−117.76	Grassland	2006	Harpole *et al.* (2007)
Spain	Catalonia CLIMOOR	41.18	1.49	Shrub	1999–2005	Emmett *et al.* (2004), Peñuelas *et al.* (2007)
China	Duolun County	42.02	116.16	Steppe	2005–2008	Xiao *et al.* (2007), Niu *et al.* (2008), Chen *et al.* (2009), Liu *et al.* (2009)
China	Xilingol	43.26–44.29	115.32–117.12	Grassland	2005	Chen *et al.* (2008)
Denmark	Mols CLIMOOR	56.23	10.57	Shrub	1999–2001	Emmett *et al.* (2004), Peñuelas *et al.* (2007)

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Table 1 (*Contd.*)

State/country	Site	Latitude	Longitude	Biome	Period	References
Germany	Ecological-botanical Garden of Bayreuth University	49.55	11.35	Grassland	2005	Mirzaei *et al.* (2008)
Greenland	Zackenberg Research Station	74.3	−21	High arctic semi desert	1997–1999	Illeris *et al.* (2003)
Hungary	DanubeTisza	46.52	19.25	Forest-steppe	2002–2006	Lellei-Kovács *et al.* (2008)
Hungary	CLIMOOR	46.53	19.23	Shrub	2002–2005	Peñuelas *et al.* (2007)
Ireland	Clara bog	53.19	−7.58	Bog	2007	Robroek *et al.* (2009)
Italy	Monte Rondinaio	44.08	10.35	Dwarf-shrub heath	1999–2003	Lisa *et al.* (2007)
Kansas, USA	Konza Prairie Biological Station	39.1	−96.9	Tallgrass prairie	2004	Fay *et al.* (2000, 2008), Harper *et al.* (2005)
The Netherlands	Oldebroek CLIMOOR	52.24	5.55	Shrub	1999–2003	Emmett *et al.* (2004), Peñuelas *et al.* (2007)
Norway	Svalbard	78.56	11.5	Shrub	1991–1993	Wookey *et al.* (1995)
United Kingdom	Clocaenog CLIMOOR	53.03	−3.28	Shrub	1999–2001	Emmett *et al.* (2004), Peñuelas *et al.* (2007)
Oklahoma, USA	Great Plain Apiaries (Kessler's Farm Field Laboratory)	34.59	−97.31	Grassland	2002–2003	Zhou *et al.* (2006), Sherry *et al.* (2008)
Oregon, USA	Northern Great Basin Experimental Range	43.29	−119.43	Grassland	1994–2000	Bates *et al.* (2006)
Italy	Capo Caccia	40.37	8.1	Forest	2002–2004	De Dato *et al.* (2006)
Italy	Sardinia VULCAN	40.36	8.9	Shrub	2004	Peñuelas *et al.* (2007)
Spain	Prades Mountains in Southern Catalonia	41.13	0.55	Holm oak forest	1999–2003	Ogaya & Peñuelas (2007)
Spain	Cabo de Gata	36.49	−2.15	Shortgrass prairie	2005–2006	Miranda *et al.* (2009)
Spain	El Cautivo	37	−2.26	Shortgrass prairie	2005–2006	Miranda *et al.* (2009)
Spain	Catalonia CLIMOOR	41.18	1.49	Shrub	1999–2005	Sardans *et al.* (2008)
Sweden	Abisko Scientific Research Station	68.21	18.49	Shrub	1991–1995	Press *et al.* (1998)
Texas, USA	The University of Houston Coastal Center	29.38	−95.04	Tallgrass prairie	2002–2004	Siemann *et al.* (2007)
Texas, USA	Big Bend National Park	29.5	−103.1	Grassland	2002–2004	Patrick *et al.* (2007)
Texas, USA	Texas Agricultural Experiment Station	27.4	−98.12	Grassland	1996–1997	McCulley *et al.* (2007)
United Kingdom	Buxton	53.2	−2	Limestone grassland	1994–1998	Grime *et al.* (2000, 2008)
United Kingdom	Wytham	51.46	−1.2	Limestone grassland	1994–1998	Grime *et al.* (2000, 2008)
Wyoming, USA	Yellowstone National Park	44.55–45.1	−110.1 to −110.5	Grassland	2005	Risch & Frank (2007)
Temperature × precipitation manipulation experiments						
California, USA	Jasper Ridge Biological Preserve	37.24	−122.14	Grassland	1998–2003	Dukes *et al.* (2005)

Table 1 (*Contd.*)

State/country	Site	Latitude	Longitude	Biome	Period	References
Arizona, USA	C. Hart Merriam elevation gradient	35.35–35.69	−111.43 to −111.73	Grassland	2002–2009	Z. Wu, P. Dijkstra, G. W. Koch, B. A. Hungate, unpublished results
China	Duolun County	42.02	116.17	Steppe	2005–2008	Niu *et al.* (2008), Liu *et al.* (2009)
Oklahoma, USA	Great Plain Apiaries (Kessler's Farm Field Laboratory)	34.59	−97.31	Tallgrass prairie	2002–2004	Zhou *et al.* (2006), Sherry *et al.* (2008)
United Kingdom	Buxton	53.2	−2	Limestone grassland	1994–2004	Grime *et al.* (2000, 2008), Thompson *et al.* (2000)
United Kingdom	Wytham	51.46	−1.2	Limestone grassland	1994–1998	Grime *et al.* (2000, 2008), Thompson *et al.* (2000)

Table 2 Response variables investigated in the meta-analysis

1. Biomass (g m^{-2})
   a. Total biomass
   b. Aboveground biomass
   c. Belowground biomass
2. Net primary productivity (NPP, g m^{-2} yr^{-1})
   a. Total NPP
   b. Aboveground NPP
   c. Belowground NPP
3. Respiration (μmol CO$_2$ m^{-2} s^{-1})
   a. Ecosystem respiration
   b. Aboveground respiration
   c. Soil respiration
4. Net ecosystem exchange (μmol CO$_2$ m^{-2} s^{-1})
5. Ecosystem photosynthesis (μmol CO$_2$ m^{-2} s^{-1})

where T and C are defined as above, T_T and T_C are the soil temperature in treatment and control plots, respectively, and PPT_T and PPT_C are the precipitation amounts received in treatment and control plots, respectively. This metric was used to quantify responses to climate change treatments, normalizing absolute responses to the magnitude of the treatment imposed. This metric yields positive values if the response is in the same direction as the climate change treatment. For example, in ecosystems where water is a limiting resource for plant growth, reduced biomass in response to decreased precipitation treatment and increased biomass in response to supplemental precipitation both yield positive values of sensitivity, facilitating the comparison of experiments where treatment size or direction of precipitation manipulation differed. We also used the sensitivity metrics to compare the magnitude of responses to decreased and increased precipitation treatments.

Weighting functions. We tested the sensitivity of the results to various weighting functions, using weights based on equal weights, variance, sample size, and experimental duration. We applied four different weighting functions:

(1) Weighting all the studies uniformly, where effect size metrics only depend on the means of control and treatment groups.
(2) Weighting by the inverse of the pooled variance (Hedges & Olkin, 1985), such that studies with lower variance have higher weight.
(3) Weighting by sample size as calculated from

$$weight_N = (N_C N_T)/(N_C + N_T),$$

where N_C and N_T are the sample sizes for control and treatment groups, respectively. More weights are given to well-replicated studies with larger sample sizes.
(4) Weighting by experimental duration as calculated from

$$weight_d = (d_C d_T)/(d_C + d_T),$$

where d_C and d_T are the experimental durations of the control and treatment groups, respectively. This approach gives higher weights to experiments that last longer.

We used METAWIN 2.1 (Rosenberg *et al.*, 2000) to conduct meta-analyses, generating mean effect sizes and 95% bootstrapped confidence intervals (95% CI). Treatment effects are considered significant when the 95% CI does not overlap with 0, and the direction and magnitude of the effect are determined by the sign and size of the 95% CI. We present summary results for log ratio effect sizes weighted by all weighting functions, but for absolute and sensitivity metrics we chose to present results weighted by sample size, because different weighing functions had little influence on the significance of results. In the text, we report mean responses to climate change treatments, and their 95% CIs, to capture the general pattern and magnitude of the influence of climate change treatments, as well as the range observed. For efficiency, we report mean responses and 95% CIs as: mean value (lower confidence limit to upper confidence limit) and appropriate units. This convention will be used throughout this article.

Statistical analysis

Tests of interactions. To evaluate the interactive effects of temperature and precipitation, for each experiment, we calculated the expected interactive response based on

observed single factor responses, assuming that effects were additive, and compared the expected against the observed interactive effect. Sufficient sample size for this analysis ($n > 2$) existed for aboveground biomass, ANPP, ecosystem respiration, NEE, and ecosystem photosynthesis, but not for belowground and total plant biomass and productivity, aboveground and soil respiration. We used R to test whether the slope differed from 1 and intercept from 0 in the linear regression (R 2.8.0, R Foundation for Statistical Computing, Vienna, Austria).

Relationships between response variables and climate. We investigated the relationships between the magnitudes of responses of plant growth and ecosystem C balance to climate change treatments and climate, using the sensitivity metric because it standardizes treatment effects to the magnitude of the treatment imposed, yielding effect sizes normalized for treatments across all ecosystems. We used linear regression to investigate the relationships between effect sizes and MAT and MAP in R (R 2.8.0, R Foundation for Statistical Computing, Vienna, Austria).

Results

Effects of climate change treatments on plant biomass

Warming enhanced aboveground biomass across the experiments surveyed, but did not significantly affect total or belowground biomass (Table 3). Warming significantly stimulated total biomass when weighted by duration of the experiment (Table 3), indicating that positive responses became more pronounced in long-term experiments. Warming increased aboveground biomass on average by 27% (41.9, 18.6–72.0 g m^{-2}). Total biomass and aboveground biomass showed significantly positive sensitivities of 242.4 (12.4–447.8) g m^{-2} °C^{-1} and 50.5 (17.7–112.3) g m^{-2} °C^{-1} to warming, respectively. The high values reflect large changes in total and aboveground biomass in response to <1 °C change in soil temperature, which occurred in a number of cases (Wookey *et al.*, 1995; Press *et al.*, 1998; Jonasson *et al.*, 1999; Saleska *et al.*, 2002; Kudo & Suzuki, 2003; Dukes *et al.*, 2005; Jónsdóttir *et al.*, 2005; Biasi *et al.*, 2008; Sardans *et al.*, 2008). Decreased precipitation suppressed aboveground biomass, whereas increased precipitation stimulated aboveground and belowground biomass (Table 3). Reduced precipitation suppressed aboveground biomass by 15% (19.6, 3.6–49.3 g m^{-2}). Increased precipitation stimulated aboveground biomass on average by 12% (12.1, −1.7 to 27.8 g m^{-2}) and belowground biomass by 11% (20.3, 7.5–45.0 g m^{-2}). Both aboveground and belowground biomass showed positive sensitivities to increased precipitation, and aboveground biomass showed positive sensitivity to decreased precipitation as well (Table 4). Aboveground biomass showed no difference in sensitivity to increased and reduced precipitation treatments (Table 4). There was no evidence for variation of responses of plant biomass to warming or altered precipitation as a function of climate (Table 5).

The combined effects of experimental warming and altered precipitation on plant biomass and productivity

Table 3 Log response ratio effect size metrics of biomass, net primary production (NPP), respiration, net ecosystem exchange and ecosystem photosynthesis under temperature and precipitation manipulation

	Warming	Decreased precipitation	Increased precipitation
Total biomass	0 0 0 + (7)	na	na
Aboveground biomass	+ + + + (32)	− − − − (10)	+ + + + (19)
Belowground biomass	−0 0 0 (6)	na	+ + + + (4)
TNPP	+ + + + (6)	na	+ + + + (2)
ANPP	0 0 0 0 (18)	− − − − (14)	+ + + + (14)
BNPP	+ + + + (5)	na	+ + + + (4)
Ecosystem respiration	+ + + + (28)	0 0 0 0 (4)	+ + + + (16)
Aboveground respiration	+ + + + (2)	na	0 0 0 0 (5)
Soil respiration	+ 0 + + (27)	− − − − (8)	+ 0 + + (16)
Net ecosystem exchange*	0 0 0 0 (26)	− − − − (4)	+ + + + (16)
Ecosystem photosynthesis	+ + + + (24)	− − − − (4)	+ + + + (17)

Treatments include warming, decreased precipitation and increased precipitation. Significance of effect size is shown by (+) 95% bootstrapped confidence interval is greater than zero; (0) 95% bootstrapped confidence interval overlapped zero; (−) 95% bootstrapped confidence interval is smaller than zero. Multiple symbols indicate respectively the significance of effect size calculated using equal weights, weighting by inverse of pooled variance, weighting by sample size, and weighting by experimental duration. The number of experiments included in the analysis for the response variables under climate change treatments are in parentheses.
*Positive effect sizes indicate increases in net C uptake, and negative effect size indicate decreases in net C uptake.
na, not available (sample size is not sufficient for the analysis); TNPP, total NPP; ANPP, Aboveground NPP; BNPP, Belowground NPP.

Table 4 Sensitivity of response variables to experimentally altered precipitation weighting by sample size

Variables	Decreased precipitation		Increased precipitation	
	Mean	95% Bootstrapped CI	Mean	95% Bootstrapped CI
Total biomass ($g\,m^{-2}\,mm^{-1}$)	–	–	–	–
Aboveground biomass ($g\,m^{-2}\,mm^{-1}$)	0.16	0.04–0.33	0.30	0.03–0.66
Belowground biomass ($g\,m^{-2}\,mm^{-1}$)	–	–	0.09	0.03–0.20
Total NPP (TNPP, $g\,m^{-2}\,yr^{-1}\,mm^{-1}$)	–	–	0.04	0.01–0.14
Aboveground NPP (ANPP, $g\,m^{-2}\,yr^{-1}\,mm^{-1}$)	0.19	0.08–0.32	0.67	0.34–1.16
Belowground NPP (BNPP, $g\,m^{-2}\,yr^{-1}\,mm^{-1}$)	–	–	0.12	0.02–0.28
Ecosystem respiration ($\mu mol\,CO_2\,m^{-2}\,s^{-1}\,mm^{-1}$)	0.001	0.0007–0.002	0.02	0.007–0.03
Aboveground respiration ($\mu mol\,CO_2\,m^{-2}\,s^{-1}\,mm^{-1}$)	–	–	−0.001	−0.003 to 0.002
Soil respiration ($\mu mol\,CO_2\,m^{-2}\,s^{-1}\,mm^{-1}$)	0.0005	0.0001–0.001	0.02	0.006–0.05
Net ecosystem exchange ($\mu mol\,CO_2\,m^{-2}\,s^{-1}\,mm^{-1}$)	0.001	0.0007–0.002	0.06	0.01–0.14
Ecosystem photosynthesis ($\mu mol\,CO_2\,m^{-2}\,s^{-1}\,mm^{-1}$)	0.001	0.0005–0.002	0.03	0.01–0.06

were not simply predicted by their effects measured in isolation (Fig. 2). Observed responses tended to be smaller in absolute value than the expected responses based on the additive combination of single factor effects (slope significantly <1, $P = 0.02$). When single-factor effect sizes were small, interactions were not apparent (intercept not significantly different from 0, $P = 0.10$). Thus, interactions between warming and altered precipitation, when they occurred, tended to be more muted than single-factor experiments might suggest.

Effects of climate change treatments on plant productivity

Warming enhanced TNPP and BNPP across all study sites, but showed no significant effects on ANPP (Table 3). TNPP was stimulated by warming by an average of 15% (58.9, 35.2–95.7 $g\,m^{-2}\,yr^{-1}$) and BNPP by 52% (58.4, 51.3–66.6 $g\,m^{-2}\,yr^{-1}$). TNPP and BNPP showed sensitivities to warming of 38.9 (26.5–50.5) $g\,m^{-2}\,yr^{-1}\,°C^{-1}$ and 26.7 (20.1–33.8) $g\,m^{-2}\,yr^{-1}\,°C^{-1}$, respectively. Decreased precipitation significantly reduced ANPP, whereas increased precipitation stimulated total, aboveground, and belowground plant productivity (Table 3). ANPP was suppressed by decreased precipitation on average by 37% (33.7, 13.8–60.5 $g\,m^{-2}\,yr^{-1}$), with a significantly positive sensitivity (Table 4). Increased precipitation stimulated ANPP by 28% (103.7, 44.0–194.6 $g\,m^{-2}\,yr^{-1}$), exhibiting stronger sensitivity to increased than to reduced precipitation (Table 4). Supplemental precipitation also stimulated TNPP by 4% (16.1, 0.1–59.0 $g\,m^{-2}\,yr^{-1}$), and BNPP by 6% (86.0, 12.3–157.3 $g\,m^{-2}\,yr^{-1}$). TNPP, ANPP, and BNPP all showed significantly positive sensitivities to increased precipitation (Table 4).

Responses of ANPP to warming decreased with MAP ($P = 0.001$, Table 5), suggesting dry ecosystem were

more responsive to warming; responses of ANPP to increased precipitation declined with MAT ($P = 0.003$, Table 5), indicating cold ecosystems were more responsive to supplemental precipitation. No other significant relationships were observed between effect sizes of plant productivity with climate (Table 5).

Combined effects of warming and altered precipitation on ANPP were similar to those observed for aboveground biomass (Fig. 2). The slope of the linear regression was significantly <1 ($P = 0.04$) and intercept not significantly different from 0 ($P = 0.99$), indicating that the observed responses of ANPP to the combined effects of warming and altered precipitation effects were smaller than expected based on single-factor manipulations.

Effects of climate change treatments on respiration

Warming increased ecosystem respiration, aboveground respiration, and soil respiration (Table 3). Decreased precipitation suppressed soil respiration, but did not significantly alter ecosystem respiration (Table 3). Increased precipitation enhanced ecosystem and soil respiration, but had no significant effects on aboveground respiration (Table 3). Warming increased ecosystem respiration on average by 27% (0.32, 0.06–0.58 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$), aboveground respiration by 15% (0.52, 0.33–0.62 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$), and soil respiration by 12% (0.37, 0.13–0.64 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$), respectively. In addition, aboveground respiration showed a significantly positive sensitivity to warming of 0.30 (0.13–0.39) $\mu mol\,CO_2\,m^{-2}\,s^{-1}\,°C^{-1}$. Decreased precipitation reduced soil respiration by 12% (0.28, 0.02–0.74 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$), whereas increased precipitation stimulated ecosystem respiration on average by 30% (0.57, 0.23–0.98 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$) and soil respiration by 45% (1.36, 0.50–2.58 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$). Both ecosys-

Table 5 Linear regression analyses for relationships between sensitivity effect sizes (weighting by sample size) and climate including mean annual temperature (MAT) and mean annual precipitation (MAP)

Variables	Climate change treatment	MAT				MAP			
		Intercept	Slope	R^2	P-value	Intercept	Slope	R^2	P-value
Total biomass	W	252.2	2.7	4.E-03	ns	423.3	−0.4	0.2	ns
Aboveground biomass	W	82.6	−6.3	7.E-02	ns	129.4	−0.1	0.1	ns
	DP	0.2	−4.E-03	1.E-02	ns	−0.1	1.E-03	0.7	ns
	IP	0.5	−1.E-02	1.E-02	ns	0.5	−2.E-04	1.E-02	ns
Belowground biomass	W	−13.5	1.3	0.2	ns	2.0	−1.E-02	2.E-02	ns
	IP	0.1	3.E-04	4.E-04	ns	0.1	2.E-05	1.E-03	ns
Total NPP (TNPP)	W	34.9	0.4	1.E-02	ns	28.5	1.E-02	1.E-02	ns
Aboveground NPP (ANPP)	W	−20.9	1.0	1.E-02	ns	98.2	−0.2	0.6	0.001*
	DP	0.7	−4.E-02	0.2	ns	−4.E-02	4.E-04	0.4	ns
	IP	2.0	−0.1	0.3	0.003*	1.1	−3.E-04	1.E-02	ns
Belowground NPP (BNPP)	W	25.6	0.1	1.E-02	ns	22.9	1.E-02	1.E-02	ns
Ecosystem respiration	W	0.2	−1.E-02	3.E-02	ns	0.2	7.E-05	2.E-03	ns
	DP	6.E-04	5.E-05	7.E-02	ns	2.E-03	−1.E-06	0.1	ns
	IP	3.E-02	−2.E-03	5.E-02	ns	1.E-02	3.E-05	1.E-02	ns
Aboveground respiration	IP	−2.E-03	4.E-04	0.1	ns	1.E-02	−2.E-05	0.1	ns
Soil respiration	W	0.1	−4.E-03	1.E-02	ns	0.2	−1.E-04	2.E-02	ns
	DP	1.E-03	−4.E-06	1.E-03	ns	1.E-03	−4.E-07	6.E-02	ns
	IP	4.E-02	−2.E-03	0.2	ns	8.E-02	−1.E-04	0.2	0.03*
Net ecosystem exchange (NEE)	W	−0.2	2.E-02	0.1	ns	0.1	−0.001	0.1	ns
	DP	−1.E-03	2.E-04	0.4	ns	2.E-03	−4.E-06	0.4	ns
	IP	3.E-02	−2.E-03	0.1	ns	−5.E-03	7.E-05	3.E-02	ns
Ecosystem photosynthesis	W	0.2	−1.E-02	2.E-02	ns	−4.E-02	1.E-03	0.1	ns
	DP	3.E-03	−2.E-04	0.3	ns	3.E-04	3.E-06	0.2	ns
	IP	0.1	−4.E-03	0.1	ns	5.E-02	−2.E-05	2.E-03	ns

*Significant ($P < 0.05$).
W, warming; DP, decreased precipitation; IP, increased precipitation; ns, nonsignificant.

tem and soil respiration showed significantly higher sensitivities to increased precipitation than to decreased precipitation (Table 4). Respiration in ecosystems dominated by herbaceous and woody vegetation responded equally to temperature and precipitation treatments.

The relative effects of increased precipitation on soil respiration declined with increasing MAP ($P = 0.03$, Table 5), suggesting that increased precipitation has a larger stimulating effect on soil respiration in dry ecosystems. No other significant relationship between effects of warming and altered precipitation on respiration and climate was observed (Table 5).

The combined effects of warming and altered precipitation on ecosystem respiration were smaller than expected based on combined additive responses, indicated by a slope of the linear regression significantly <1 ($P = 0.03$, Fig. 3). When single-factor effect sizes were small, a lack of interactive effects were suggested by an intercept not significantly different from 0 ($P = 0.75$).

Effects of climate change treatments on NEE

Warming showed no significant effects on NEE. Decreased precipitation suppressed NEE, while increased precipitation stimulated NEE (Table 3). Decreased precipitation reduced NEE on average by 45% (0.09, 0.06–0.13 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$) and increased precipitation stimulated NEE by 56% (0.40, 0.01–0.89 $\mu mol\, CO_2\, m^{-2}\, s^{-1}$). NEE was significantly more sensitive to increased precipitation than to decreased precipitation (Table 4). Similar to plant biomass and productivity, the effects of warming on net C uptake were similar for ecosystems dominated by herbaceous and woody vegetation. The response of NEE to warming and altered precipitation did not vary with climate (Table 5). The slope of interactive against additive effects of warming and altered precipitation did not differ significantly from 1 ($P = 0.68$, Fig. 3), and the intercept did not differ from 0 ($P = 0.10$). Therefore, responses of NEE to temperature and precipitation manipulations in isolation were sufficient to predict their combined effects.
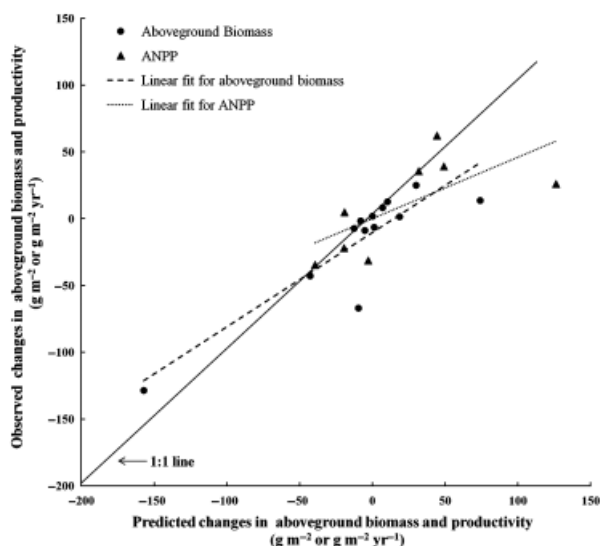
Fig. 2 Interactive effects of temperature and precipitation treatments on aboveground biomass (g m^{-2}) and aboveground net primary productivity (ANPP, g m^{-2} yr^{-1}). Predicted values are the sums of absolute effect sizes from single-factor manipulation, i.e., assuming effects of altered precipitation and warming are additive. The solid line is the 1 : 1 line, expected if interactions are absent. Linear regression for aboveground biomass (dashed line) is $y = -10.29 + 0.71x$ ($P < 0.001$); the slope is significantly <1 ($P = 0.02$) and the intercept is not significantly different from 0 ($P = 0.10$). Linear regression for ANPP (dotted line) is $y = 0.14 + 0.46x$ ($P = 0.07$); the slope is significantly <1 ($P = 0.04$) and the intercept is not significantly different from 0 ($P = 0.99$).

Fig. 3 Interactive effects of temperature and precipitation treatments on ecosystem respiration, ecosystem photosynthesis and net ecosystem exchange (NEE, µmol CO$_2$ m^{-2} s^{-1}). Predicted values are the sums of absolute effect sizes from single-factor manipulation, i.e., assuming effects of altered precipitation and warming are additive. The solid line is the 1 : 1 line, expected if interactions are absent. Linear regression for ecosystem respiration (dashed line) is $y = 0.02 + 0.75x$ ($P < 0.001$); the slope is significantly <1 ($P = 0.03$) and the intercept is not significantly different from 0 ($P = 0.75$). Linear regression for NEE (dotted line) is $y = -0.08 + 0.95x$ ($P < 0.001$); the slope is not significantly different from 1 ($P = 0.68$) and intercept is not significantly different from 0 ($P = 0.10$). Linear regression for ecosystem photosynthesis (dash-dotted line) is $y = 0.12 + 0.99x$ ($P < 0.001$); the slope is not significantly different from 1 ($P = 0.89$) and the intercept is not significantly different from 0 ($P = 0.08$).

Effects of climate change treatments on ecosystem photosynthesis

Warming and increased precipitation stimulated ecosystem photosynthesis, and decreased precipitation suppressed ecosystem photosynthesis (Table 3). Warming enhanced ecosystem photosynthesis on average by 20% (0.19, -0.05 to 0.47 µmol CO$_2$ m^{-2} s^{-1}) and increased precipitation stimulated ecosystem photosynthesis by 40% (1.13, 0.52–1.89 µmol CO$_2$ m^{-2} s^{-1}). Ecosystem photosynthesis was reduced by decreased precipitation by 9% (0.12, 0.03–0.26 µmol CO$_2$ m^{-2} s^{-1}). Ecosystem photosynthesis of herbaceous and woody vegetation responded similarly to experimental warming. Ecosystem photosynthesis showed a significantly positive sensitivity of 0.22 (0.04–0.42) µmol CO$_2$ m^{-2} s^{-1} °C^{-1} to warming, and a higher sensitivity to increased than decreased precipitation (Table 4). No significant relationship was observed between effects of experimental warming and altered precipitation on ecosystem photosynthesis and climate among different ecosystems (Table 5). Additive combinations of the responses of
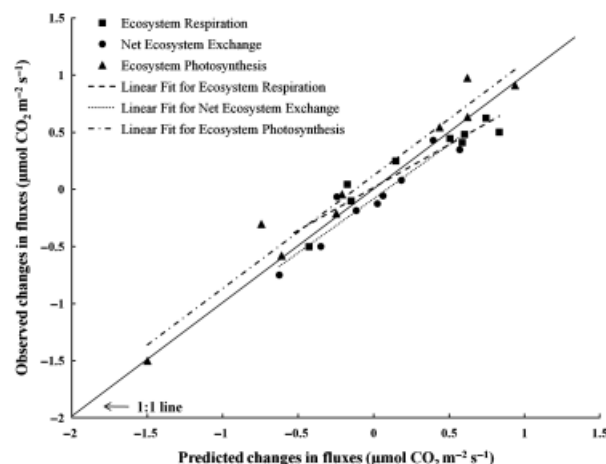
ecosystem photosynthesis to temperature and precipitation predicted well their combined effects (Fig. 3), as indicated by a slope not significantly different from 1 ($P = 0.89$) and an intercept not significantly different from 0 ($P = 0.08$).

Discussion

Effects of elevated temperature

We found that warming increased both respiration and ecosystem photosynthesis, but showed no significant effects on net C uptake. Meanwhile, warming also generally increased plant biomass and productivity. Another meta-analysis of ecosystem warming experiments (Rustad *et al.*, 2001) concluded that warming increased soil respiration and plant productivity, with a larger response in woody ecosystems. Our larger data set generally showed no difference in sensitivity to warming between ecosystems dominated by herbaceous and woody vegetation. Dormann & Woodin

(2002) reviewed 36 experiments from the arctic and also found that warming increased biomass. Warming stimulated plant productivity (Peñuelas *et al.*, 2007; Luo *et al.*, 2009), and also enhanced ecosystem photosynthesis because of increasing aboveground biomass (Sullivan *et al.*, 2008), due to enhanced soil nutrient mineralization (Hartley *et al.*, 1999; Grogan & Chapin, 2000; Melillo *et al.*, 2002), compensating for increased respiratory C losses (Melillo *et al.*, 2002). In one case, warming increased soil organic C content (Sardans *et al.*, 2008), perhaps because of suppressed microbial activity as a result of soil drying, as found in a mature black spruce forest (Allison & Treseder, 2008). Other studies have shown that experimental warming decreased plant biomass and photosynthesis due to warming-induced moisture stress (De Valpine & Harte, 2001; De Boeck *et al.*, 2007, 2008), suppressing both ecosystem photosynthesis and soil respiration, with the latter declining more (Liu *et al.*, 2009). In most experiments, warming increased soil respiration (Mertens *et al.*, 2001; Emmett *et al.*, 2004; Biasi *et al.*, 2008), due to higher activity of microbes and roots (Bergner *et al.*, 2004; Sardans *et al.*, 2008), and increased C input from plant production (Welker *et al.*, 2004; Luo *et al.*, 2009). Increasing respiratory C losses could transform a C sink into a C source, as responses of respiration can dominate effects on ecosystem net C balance (Illeris *et al.*, 2004; Oberbauer *et al.*, 2007). However, warming-induced respiratory CO_2 losses could decline because of lower litter quality from species composition shifts (Harte & Shaw, 1995; Biasi *et al.*, 2008).

Overall, we found little influence of experimental duration on the significance of results, except that warming-induced increases in total biomass only appeared in long-term experiments. Most studies included in this analysis were short term (<5 years), and warming-induced vegetative growth was not limited by nutrients due to increased litter decomposition and nutrient availability. Warming increased nitrogen (N) mineralization (Hartley *et al.*, 1999; Melillo *et al.*, 2002), and redistribution of N from soil to plants should eventually reach a point where labile N pools in soil cannot support increased aboveground growth, and respiratory C losses will dominate the overall C balance (Shaver *et al.*, 2000). For example, warming did not show any effect in the 5th year of treatment on a subarctic dwarf shrub heath (Hartley *et al.*, 1999). Arft *et al.* (1999) also found enhanced vegetative growth for the first 3 years, but no significant response for the fourth year. Initial increase of soil respiration is from the consumption of soil labile C (McHale *et al.*, 1998), and such responses can be transient because of the depletion of the labile soil C pool (Melillo *et al.*, 2002). Long-term soil warming can also cause microbial acclimation (Zogg *et al.*, 1997) and root acclimation (Atkin *et al.*, 2000), resulting in little or no response of ecosystem respiration to warming. Long-term warming could also induce soil drying that will suppress soil respiration (McHale *et al.*, 1998). Such long-term responses may be difficult to capture in warming experiments, yet it is important to distinguish transient patterns from long-term responses.

Rustad *et al.* (2001) used meta-analysis of warming experiments and found larger responses of plant productivity to warming in colder environments. However, no trend in our dataset was observed between responses of plant productivity to experimental warming and MAT. This difference between the two meta-analyses could result from sample size – our analysis included more studies covering a broader geographical range than was available to Rustad *et al.* (2001). Soil respiration has been long recognized as being temperature-dependent, often modeled with a Q_{10} function (Schleser, 1982; Chen & Tian, 2005). However, some lines of evidence suggest that sensitivity of soil respiration acclimates in response to warming (Luo *et al.*, 2001), such that increases in soil respiration are smaller than expected from the Q_{10} function. Kirschbaum (1995) found that soil respiration had higher sensitivity in colder environments, but this pattern was not apparent in our analysis.

Global mean temperature is predicted to increase 2–7 °C by the end of this century (Allison *et al.*, 2009). The sensitivity of ecosystem photosynthesis we found (0.22 μmol CO_2 m^{-2} s^{-1} °C^{-1}) in response to warming is nearly exactly balanced by sensitivity of ecosystem respiration (0.21 μmol CO_2 m^{-2} s^{-1} °C^{-1}), suggesting that short-term responses of both processes to projected warming are on the order of 0.4–1.5 μmol CO_2 m^{-2} s^{-1} (depending on the magnitude of the temperature increase). Whether these effects cancel or shift toward net carbon uptake or release will depend on processes that operate on longer time scales than accessible in manipulative experiments.

Effects of altered precipitation

We found that increased precipitation stimulated both respiration and ecosystem photosynthesis, and led to an overall increase in net C uptake, reflected in both increased plant biomass and productivity. Chen *et al.* (2009) showed that gross ecosystem productivity had a higher sensitivity to soil moisture than that of soil respiration, and therefore increased precipitation favors C sequestration. Our results contrast with a prior assessment of arctic experiments, which showed no significant effects of increased precipitation on plant biomass (Dormann & Woodin, 2002). We also synthe-

sized effects of decreased precipitation on ecosystem C balance and found that reduced precipitation suppressed both soil respiration and ecosystem photosynthesis, and resulted in an overall decrease in net C uptake, also reflected in decreased aboveground biomass and productivity. Decreased precipitation can also reduce nutrient availability because of water limitation of soil microbial processes (De Dato *et al.*, 2006; Sardans *et al.*, 2008). Decreased precipitation not only suppresses plant biomass and physiological processes, it can also cause mortality, as shown in a holm oak forest (Ogaya & Peñuelas, 2007). Ecosystem C cycling responded to both increased and decreased precipitation, with higher sensitivities to supplemental precipitation than to reduced precipitation. We also found ANPP had a significantly higher sensitivity to increased precipitation than that to decreased precipitation, similar to the prediction from long-term relationships between ANPP and annual precipitation (Knapp & Smith, 2001).

Our results showed the effects of altered total precipitation quantity on plant growth and ecosystem C fluxes, yet the timing and frequency of precipitation can also have large effects (Knapp *et al.*, 2008). Extension of the wet season increased microbial respiration and C uptake from enhanced plant productivity (Silver *et al.*, 2005). Alteration of precipitation timing in a sagebrush steppe caused plant productivity change and vegetation shifts (Bates *et al.*, 2006). Rainfall timing, such as the interval between rainfall events, influenced the productivity of grassland ecosystems (Fay *et al.*, 2000). Soil CO_2 flux declined more because of altered rainfall timing than reduced rainfall amount, with the combination of both causing the largest reduction (Harper *et al.*, 2005). Rain pulse sizes also affected soil respiration (Chen *et al.*, 2008), C sequestration and plant productivity (Heisler-White *et al.*, 2008; Chen *et al.*, 2009). Thus, the inferences from our results could be modified if changes in precipitation timing and frequency are considered.

The effect of moisture on soil respiration is complex, not well explained by simple linear relationships (Howard & Howard, 1979; Davidson *et al.*, 1998). Our finding that soil respiration was more responsive to increased precipitation in dry environments suggests that relative water limitation of these processes declines with increasing water availability. The global precipitation trends ranged from -7 to $+2$ mm per decade according to the IPCC (Solomon *et al.*, 2007). Based on our analysis of sensitivity to precipitation change, short-term responses of NEE to observed precipitation trends might range from a decrease of $0.007 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$ to an increase of $0.12 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$ (excluding influences of longer-term responses to precipitation, such as land-use changes and species composition shifts).

Temperature and precipitation interactions

Based on a small number of experiments that manipulated both temperature and precipitation, we found that ecosystem responses to the combination of warming and altered precipitation tended to be smaller than expected from the single-factor responses. Luo *et al.* (2008) modeled interactive effects of precipitation and temperature on ecosystem C dynamics, and showed that warming and doubled precipitation generally have positive effects on NPP, net ecosystem production, and respiration, whereas warming and reduced (halved) precipitation have negative effects on NPP. Similar to our results, the modeling study showed interactive effects were generally small (Luo *et al.*, 2008).

Conclusions

Meta-analysis supported some general conclusions about ecosystem responses to climate change: (1) Warming increased plant biomass and productivity, respiration and ecosystem photosynthesis, but did not affect net C uptake. (2) Increased precipitation stimulated plant biomass, productivity, respiration, ecosystem photosynthesis, and net C uptake. (3) Decreased precipitation suppressed aboveground biomass and productivity, soil respiration, ecosystem photosynthesis, and net C uptake. (4) Plant productivity and ecosystem C fluxes were more sensitive to increased precipitation than to reduced precipitation. (5) Herbaceous and woody plants showed similar responses to climate change treatments. (6) When interactions occurred between warming and altered precipitation, the combined responses tended to be smaller than expected from additive, single-factor effects. Finally, (7) the magnitude of responses of these ecosystem processes exhibited little systematic variation with climate, indicating general sensitivities across ecosystems to climate change treatments.

For future experiments on ecosystem-level responses to climate change treatments, we recommend:

(1) Measure total and belowground biomass and productivity in addition to aboveground biomass and productivity. Aboveground biomass and productivity are commonly used to estimate responses of plant growth to climate change. However, belowground biomass and productivity play an important role in such responses, with which total biomass and productivity can be calculated to quantify ecosystem level responses to climate change.

(2) Conduct more experiments manipulating precipitation. Because of the variability and unpredictability of future precipitation projections, more precipitation manipulation experiments are needed to eluci-

date the impacts of wide range of possible scenarios. These experiments should manipulate not only precipitation quantity, but also alter precipitation timing, frequency, intensity as well as seasonality.

(3) Design multifactorial experiments in a wide range of ecosystems. Temperature and precipitation effects could be additive, so single-factor experiments can be very informative and provide the basic mechanisms for ecosystem responses. However, complex interactions do exist and may not be consistent among ecosystems or treatments. In this sense, a single factor experiment is not adequate to illustrate the responses of ecosystem under interactive climate change effects.

(4) Establish experiments in underrepresented biomes and environments. Multiple-factor experiments have been limited to herbaceous ecosystems. Yet, given the greater biomass, soil microbial biomass, soil C pools, and high C fluxes in woody communities, it is crucial to include more woody systems in multifactor manipulation experiments. However, the technological and cost constrains make mature forest ecosystem warming experiments very difficult. In addition, most manipulation experiments have been in mid-to-high latitudes in northern hemisphere, and new experiments are needed in low latitude and tropical systems to identify a systematic variation of responses across ecosystems.

Acknowledgements

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