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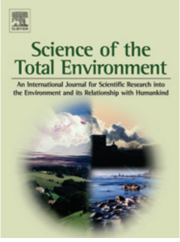

The response of terrestrial ecosystems to global climate change: Towards an integrated approach

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ABSTRACT

Accumulating evidence points to an anthropogenic 'fingerprint' on the global climate change that has occurred in the last century. Climate change has, and will continue to have, profound effects on the structure and function of terrestrial ecosystems. As such, there is a critical need to continue to develop a sound scientific basis for national and international policies regulating carbon sequestration and greenhouse gas emissions. This paper reflects on the nature of current global change experiments, and provides recommendations for a *unified multidisciplinary approach* to future research in this dynamic field. These recommendations include: (1) better integration between experiments and models, and amongst experimental, monitoring, and space-for-time studies; (2) stable and increased support for long-term studies and multi-factor experiments; (3) explicit inclusion of biodiversity, disturbance, and extreme events in experiments and models; (4) consideration of timing vs intensity of global change factors in experiments and models; (5) evaluation of potential thresholds or ecosystem 'tipping points'; and (6) increased support for model–model and model–experiment comparisons. These recommendations, which reflect discussions within the TERACC international network of global change scientists, will facilitate the unraveling of the complex direct and indirect effects of global climate change on terrestrial ecosystems and their components.

1. Introduction

Human-induced global climate change is rapidly emerging as the single most important environmental and policy concern of the 21st century. As such, the response of terrestrial ecosystems to this global phenomenon has been the subject of intense scientific scrutiny over the past several decades, and the focus of a growing number of single- and multi-factor ecosystem-scale manipulation experiments. Results from these experiments have greatly increased our understanding of the short-term responses of terrestrial ecosystems and their components to elevated atmospheric CO_2, warming, and changes in water availability, and have provided valuable input for dozens of ecosystem-, regional-, and global scale models that are allowing us to better synthesize current understanding and project future response patterns.

Despite these advances, urgent and immediate needs remain to continue to build a sound scientific basis for national and international policies regulating greenhouse gas emissions and carbon sequestration. In order to meet these complex needs in a timely fashion, a growing consensus exists within the scientific community that it will be necessary to better integrate observational, experimental, and modeling techniques into a *unified multidisciplinary approach* to understanding ecosystem response to global change (Norby and Luo, 2004; Classen and Langley, 2005; Midgley and Thuiller, 2005; Rustad, 2006; Heisler and Weltzin, 2006; Heimann and Reichstein, 2008).

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To this end, the international research coordination network "Terrestrial Ecosystem Response to Atmospheric and Climatic Change" (TERACC) was established in 2001. The goals of TERACC are to: (1) integrate and synthesize existing whole-ecosystem research on ecosystem responses to individual global change drivers, (2) foster new research on whole-ecosystem responses to the *combined* effects of elevated atmospheric CO_2, warming, and other aspects of global change, and (3) promote better communication and integration between experimentalists and modelers. In this paper, I summarize insights from the first 5 years of TERACC, and present a framework for future opportunities to better integrate observations, experiments and models.

2. Global climate change: past, present, and future

Accumulating evidence points to an anthropogenic 'fingerprint' on global climate change driven by fossil fuel combustion and changes in land use. Since the turn of the century to 2005, atmospheric greenhouse gas concentrations have increased by ~35%, 148%, and 14% for carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), respectively, and mean global temperature has increased by 0.75 °C (IPCC, 2007). Both 'recent' (past 1000 years) and geologic (past 650,000 years) reconstructions show that these increases in greenhouse gases and temperature are highly anomalous, and are currently higher than at any time in the past 650,000 years (Siegenthaler et al., 2005; National Academy of Sciences, 2006). Although more variable, changes have also been observed in patterns of precipitation, with global redistributions in precipitation amounts, and a general intensification of the hydrologic cycle leading to increases in the number of heavy rain events, and increases in the number and duration of droughts (Huntington, 2006; IPCC, 2007). Future projections indicate that these trends in greenhouse gases, temperature, and precipitation will continue, resulting in a warmer, wetter, yet drier world in the 21st century characterized by more numerous and more severe extreme events (Tebaldi et al., 2006; IPCC, 2007). These changes have already had, and will continue to have, dramatic effects on the productivity, biodiversity and biogeochemistry of terrestrial ecosystems.

3. How do we assess ecosystem response to global change?

Numerous approaches are being used to assess terrestrial ecosystem response to global change. These are discussed in broad terms here with the goal to evaluate opportunities for future synthesis and integration. Case studies highlight the need for and value in long-term experiments.

3.1. *Observations in time and space*

Observations in time and space can be made at single sites, networks of sites, and more recently, super-networks of sites. Although the accumulation of long-term records (or "long-term monitoring") is not always considered 'real science' (for a discussion, see Lovett et al., 2007), these studies provide invaluable insights and background information on ecosystem response to short-term changes in weather and long-term changes in climate. For example, Lauenroth and Sala (1992) measured precipitation inputs and aboveground net primary productivity (ANNP) at a short grass steppe site in Colorado, USA during the period 1939 to 1987. Their record shows 2 years of extreme drought (1954 and 1964) where precipitation deviated ~200 mm from the mean. Both years were also characterized by declines in ANPP. Although precipitation recovered to near normal levels in the ensuing years, ANPP showed a lag in recovery of 1–3 years, which they attribute to changes in vegetative structure. These results emphasize the value of long-term monitoring, the existence of 'lags' in response, and the importance of monitoring changes in vegetation dynamics.

At a larger scale, the National Science Foundation's (NSF) Long Term Ecological Research (LTER) network provides insights on ecosystem response to global change at broad spatial and temporal scales within the United States. This network currently consists of 26 study sites and involves the collaborative efforts of more than 1800 scientists and students (http://www.lternet.edu/). Precipitation varies from less than 100 mm/year for a tundra ecosystem at the Arctic LTER in Alaska, USA to ~2500 mm/year for a tropical rainforest at the Luquillo LTER in Puerto Rico. Temperature varies from ~−18 °C at The McMurdo Dry Valleys LTER in Antarctica to ~27 °C at the Luquillo tropical rainforest LTER in Puerto Rico. These conditions provide researcher's with a "natural" climate change laboratory. Knapp and Smith (2001), for example, used this natural gradient to demonstrate the significant, positive relationship between ANPP and precipitation for 9 of the 26 LTER sites ($r^2=0.83$, $P<0.001$).

International 'super' networks of sites and scientists have also been increasing in number, scope, and value over the past decade. Examples include:

International LTER (ILTER) — 34 country-based networks of scientists engaged in long-term, site-based research; http://www.ilternet.edu/networks/index.html;
Carbo Europe — 61 sites in 17 European countries focused on understanding and quantifying the terrestrial carbon balance of Europe; http://www.carboeurope.org/;
NitroEurope — 65 partners in 23 countries focused on understanding the nitrogen cycle and its influence on the European greenhouse gas balance; http://www.nitroeurope.eu/;
TERACC — 135 sites in 25 countries focused on using experimental manipulations and models to understand ecosystem response to single and multiple elements of global change; http://www.umaine.edu/teracc/.

These networks represent various levels of coordination, collaboration and communication and provide important frameworks for continental-or-greater-scale evaluations of global change effects on terrestrial ecosystems. The draw back is that these super-networks require increased financial and logistical resources for infra-structure and coordination, and therefore must require large and stable funding commitments.

3.2. *Climate gradient studies*

Although long-term observations in time and space provide the ultimate validation of ecosystem and global scale models,

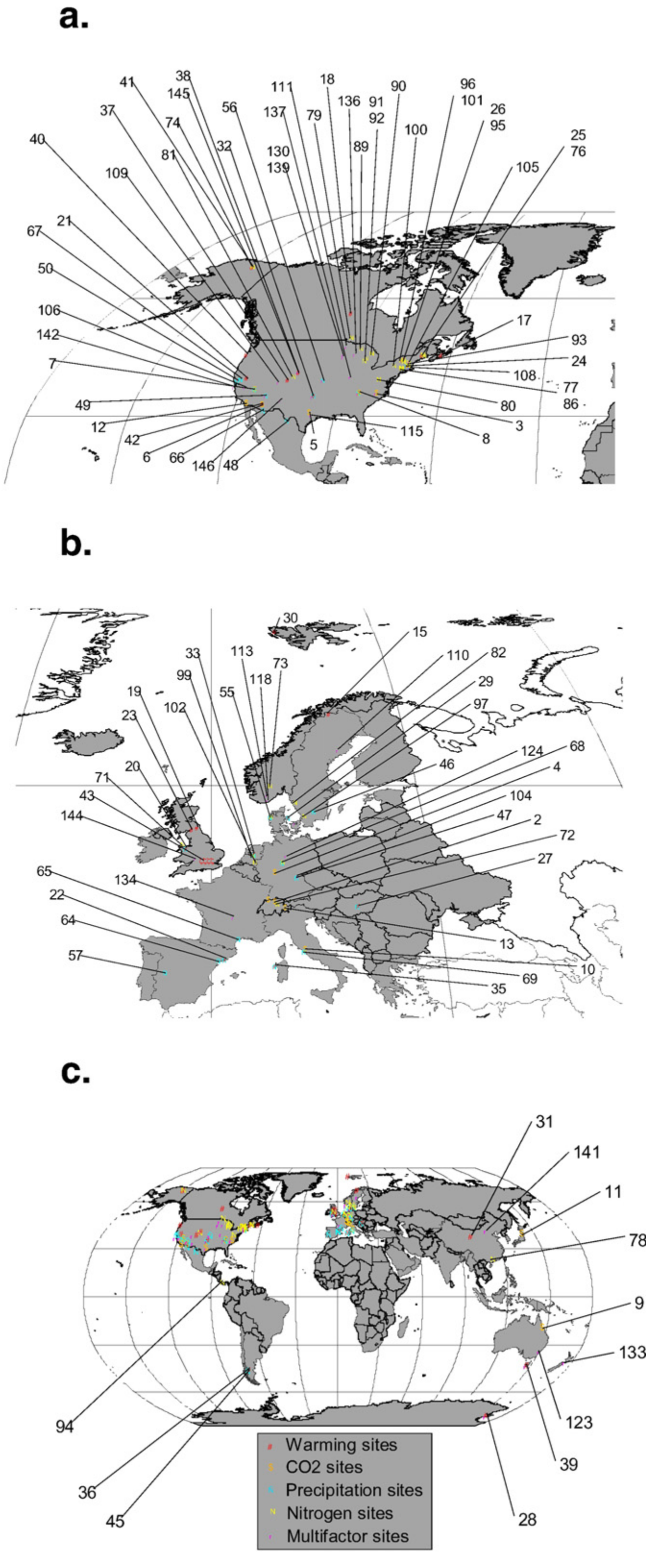

Fig. 1 – Location of single and multi-factor global climate change ecosystem-scale field manipulation sites identified in the TERACC network for (a) North America, (b) Europe, and (c) additional sites around the world. Numbers indicate sites listed in Table 1.

long-term records rarely go back more than 100 years and future responses remain unknown until they occur, making current validations of models of future conditions impossible. Climate gradient studies help fill this gap by exploiting “space-for-time” substitutions. These climatic “space-for-time” substitutions can be performed across geographical gradients, as discussed for ANPP and precipitation above, or elevational gradients. For example, Murphy et al. (1998) evaluated the influence of climate on litter decomposition across an elevational gradient in Arizona, USA. Surprisingly, results showed that decay rates were greater at higher elevations at colder temperatures. The authors concluded that litter decomposition was more sensitive to soil moisture than soil temperature in this semi-arid ecosystem.

3.3. *Experiments*

Experimental manipulations of whole ecosystems or ecosystem components are powerful tools that allow for the elucidation of cause-and-effect relationships and provide for a mechanistic understanding of short-term responses of ecosystems to single or multiple elements of global change (Rustad, 2006). Concern exists, however, that these results from short-term manipulation experiments may be transient, and that both the magnitude and direction of response may change over time. Examples from long-term ecosystem manipulation experiments validate this concern, and highlight the need to support longer-term studies in order to incorporate these findings into ecosystem, regional, and global scale models.

3.3.1. *Elevated CO_2 experiments*

The locations of elevated CO_2 experiments (emphasizing Free Air CO_2 Enrichment systems [FACE]) and/or multi-factor experiments, as identified in the TERACC network, are shown in Fig. 1 and Table 1. Results from these experiments have provided valuable insights on ecosystem response to elevated CO_2. For example, results from three TERACC-sponsored syntheses have shown that: (1) light-saturated C uptake, diurnal C assimilation, plant growth, and aboveground production increase with elevated CO_2, while specific leaf area and stomatal conductance decrease (Ainsworth and Long, 2005), (2) forest response to elevated CO_2 is conserved across a broad range of productivity (Norby et al., 2005), and (3) increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2 (Finzi et al., 2007).

Many of the FACE experiments have been ongoing for 8 years or longer. Of these, the elevated CO_2 experiment at the Duke Forest Face site in North Carolina, USA is one of the longest continuously running experimental CO_2 manipulations. Initiated in 1996 in a mature *Pinus taeda* forest ecosystem, atmospheric CO_2 is experimentally elevated at 200 ppm above ambient. Early results from 1998–2000 showed a significant increase in estimated annual rates of total soil respiration of ~0.30 kg C m^2/year in the elevated CO_2 plots compared to the controls (Bernhardt et al., 2006). However, this initial stimulation of soil respiration declined to ~0.12 kg C m^2/year in 2003 after 7 years of manipulations. Modeling analyses suggest that this decline over time may be attributed, in part, to

Table 1 – Single and multi-factor global change experiments identified within the TERACC network

Experiment type	Map location #	Site name	Location (City, State or Povence, Country)	Biome	Latitude	Longitude	Publications
Elevated CO_2 experiments	2	Basel	Switzerland	Deciduous forest	47.58	7.58	Asshoff et al. (2006)
	2	Eschikon	Eschikon, Switzerland	Grassland	47.37	8.53	Zanetti et al. (1996)
	3	FACTS-I	North Carolina, United States	Coniferous forest	35.97	−79.08	Hendrey et al. (1999)
	4	GiFACE (Linden)	Linden, Germany	Grassland	50.53	8.69	Jäger et al. (2003)
	5	LYCOG	Texas, United States	Grassland	31.03	−97.33	Polley et al. (in press)
	6	Maricopa	Arizona, United States	Agricultural crops	33.07	−111.98	Lewin et al. (1994)
	7	Nevada Desert	Nevada, United States	Desert	36.82	−115.92	Jordon et al. (1999)
	8	ORNL-FACE	Tennessee, United States	Deciduous forest	35.90	−84.33	Norby et al. (2001)
	9	OzFACE	Queensland, Australia	Grassland	−19.00	147.00	Stokes et al. (2005)
	10	POP-EUROFACE	Viterbo, Italy	Deciduous forest	42.42	12.10	Miglietta et al. (2001)
	11	Rice FACE	Shizukuishi, Japan	Agricultural crops	39.63	140.95	Okada et al. (2001)
	12	Sky Oaks	California, United States	Shrubland	33.37	−116.62	Cheng et al. (in review)
	13	Stillberg	Davos, Switzerland	Grassland	46.75	9.75	Hättenschwiler et al. (2002)
Warming experiments	15	Abisko	Abisko, Sweden	Tundra	68.35	18.82	Aerts et al. (2007)
	15	Abisko Bog	Abisko, Sweden	Wetland	68.35	18.82	Aerts et al. (2004)
	17	Abraham's Lake	Nova Scotia, Canada	Coniferous forest	45.10	−62.83	No publications to date
	18	BOREAS	Manitob, Canada	Coniferous forest	55.88	−98.33	Sellers et al. (1995)
	19	Buxton Climate Change Impacts Lab	Sheffield, United Kingdom	Grassland	55.30	−2.00	Thompson et al. (2000)
	20	Clocaenog (VULCAN)	Wales, United Kingdom	Coniferous forest	53.05	−3.47	Beier et al. (2004)
	21	Ecocells	Nevada, United States	Grassland	39.50	−119.78	Verburg et al. (2005)
	22	Garraf — SP (VULCAN)	Barcelona, Spain	Shrubland	41.30	1.82	Sardans et al. (2006)
	23	Great Dun Fell	Penrith, United Kingdom	Grassland	55.08	−2.75	Ineson et al. (1998)
	24	Harvard Forest	Massachusetts, United States	Deciduous forest	42.50	−72.17	Peterjohn et al. (1994)
	25	Howland Forest	Maine, United States	Coniferous forest	45.17	−68.80	Rustad and Fernandez (1998)
	26	Huntington Wildlife Forest	New York, United States	Deciduous forest	43.98	−74.23	McHale et al. (1998)
	27	Kiskun Sag (VULCAN)	Keshkemet, Hungary	Shrubland	46.88	19.38	Kovács-Láng et al. (2002)
	28	McMurdo Dry Valleys LTER	Antarctica	Desert	−77.63	162.88	Burkins et al. (2001)
	29	Mols (VULCAN)	Ebeltoft, Denmark	Shrubland	56.38	10.95	Beier et al. (2004)
	30	Ny Alesund	Norway	Tundra	79.13	11.77	Robinson et al. (1998)
	31	Oinghai–Tibet Plateau	Oinghai Province, China	Grassland	37.62	101.20	No publications to date
	32	Oklahoma Tall Grass Prairie	Oklahoma, United States	Grassland	34.98	−97.52	Wan et al. (2005)
	33	Oldebroek (VULCAN)	Zwolle, The Netherlands	Shrubland	52.40	5.92	Beier et al. (2004)
	8	Oak Ridge National Laboratory (ORNL)	Tennessee, United States	Deciduous forest	35.90	−84.35	Norby et al. (1997)
	35	Porto Conte Capo Caccia (VULCAN)	Sardinia, Italy	Shrubland	40.62	8.17	de Dato et al. (2006)
	36	Rio Mayo	Rio Mayo, Argentina	Grassland	−45.42	−70.27	Sala et al. (1989)
	37	Rocky Mountain Biological Laboratory	Colorado, United States	Grassland	38.88	−107.03	Cross and Harte (2007)
	38	Shortgrass Steppe	Colorado, United States	Grassland	40.82	−104.77	Alward et al. (1999)

(continued on next page)

Table 1 (*continued*)

Experiment type	Map location #	Site name	Location (City, State or Povence, Country)	Biome	Latitude	Longitude	Publications
	39	TasFACE	Tasmania, Australia	Grassland	−42.69	147.26	No publications to date
	40	TERA	Oregon, United States	Coniferous forest	45.33	−124.03	Lin et al. (1999)
	41	Toolik Lake	Alaska, United States	Tundra	68.64	−149.58	Marion et al. (1997)
	42	US Arid–Land Agricultural. Research Center	Arizona, United States	Desert	33.07	−111.97	Kimball (2005)
	43	Wytham	Wytham, United Kingdom	Grassland	51.77	−1.33	Thompson et al. (2000)
Precipitation change experiments	147	Amazon	Brazil	Tropical Forest	−2.90	−54.95	Nepstad et al. (2001)
	45	Argentina	Argentina	Grassland	−45.68	−70.27	Sala et al. (1989)
	46	ASA	Sweden	Coniferous forest	57.13	14.75	Linder (1987)
	47	Bayreuth	Bayreuth, Germany	Deciduous forest	49.95	11.57	No publications to date
	47	Bayreuth	Bayreuth, Germany	Wetland	49.95	11.57	No publications to date
	48	Big Bend National. Park	Texas, United States	Desert	29.00	−103.10	Huxman et al. (2004b)
	49	CAREER	Arizona, United States	Grassland	35.25	−111.66	Hungate et al. (2002)
	50	Central Valley	California, United States	Grassland	38.80	−122.25	Adair et al. (in press)
	20	Clocaenog (VULCAN)	Wales, United Kingdom	Grassland	53.05	−3.47	Beier et al. (2004)
	22	Garraf — SP (VULCAN)	Barcelona, Spain	Shrubland	41.30	1.82	Sardans et al. (2006)
	24	Harvard Forest	Massachusetts, United States	Deciduous forest	42.50	−72.17	Borken et al. (2006)
	27	Kiskun Sag (VULCAN)	Keshkemet, Hungary	Shrubland	46.88	19.38	Beier et al. (2004)
	55	Klosterhede	West Jutland, Denmark	Coniferous forest	56.48	8.40	Gundersdon et al. (1994)
	56	Konza Prairie LTER	Kansas, United States	Grassland	39.05	−96.35	Fay et al. (2000)
	57	Las Majadas del Tietar (MIND)	Caceres, Spain	Shrubland	39.93	−5.78	Mikkelsen et al. (2008)
	58	Mojave Global Change Experiment	Nevada, United States	Desert	36.70	−115.90	Barker et al. (2006)
	29	Mols (VULCAN)	Ebeltoft, Denmark	Shrubland	56.38	10.95	Beier et al. (2004)
	32	Oklahoma tallgrass prairie	Oklahoma, United States	Grassland	35.25	−97.50	Liu et al. (2002)
	33	Oldebroek (VULCAN)	Zwolle, The Netherlands	Shrubland	52.40	5.92	Beier et al. (2004)
	62	ORNL TDE	Tennessee, United States	Deciduous forest	35.97	−84.27	Hanson et al. (1995)
	35	Porto Conte Capo Caccia	Sardinia, Italy	Shrubland	40.62	8.17	De Angelis et al. (2005)
	64	Prades	Barcelona, Spain	Shrubland	41.22	1.03	Lloret et al. (2004)
	65	Puéchabon State Forest (MIND)	France	Deciduous forest	43.44	3.58	Hoff et al. (2002)
	66	Santa Rita Experimental Range	Arizona, United States	Desert	31.58	−111.00	Silver et al. (2005)
	67	Sierra Foothills Research and Extension Center	California, United States	Shrubland	39.25	−121.28	Loik et al. (2004)
	68	Solling Forest	Solling, Germany	Coniferous forest	51.52	9.76	Bredemeier et al. (1995)
	69	Tolfa-allumiere (MIND)	Italy	Deciduous forest	42.13	11.97	Mikkelsen et al. (2008)
Nitrogen addition experiments	71	Aber Forest	Gwynedd, United Kingdom	Coniferous forest	53.48	−4.00	Emmet et al. (1995)
	72	Alptal	Einsiedeln, Switzerland	Coniferous forest	47.05	8.72	Hagedorn et al. (2001)
	73	Amli	Norway	Coniferous forest	59.90	8.57	Abrahamsen et al. (1995)
	76	Bear Brook Watershed in Maine (BBWM)	Maine, United States	Deciduous and coniferous forests	44.86	−68.10	Fernandez et al. (1999)

	86	Cary Institute of Ecosystem Sudies	New York, United States	Deciduous forest	41.83	−73.75	Lovett et al. (2000)
	77	Catskills	New York, United States	Deciduous forest	42.00	−74.00	Lovett et al. (2000)
	78	Dinghushan	Guangdong, China	Coniferous forest	23.17	112.17	Fang et al. (2006)
	79	ELA	Ontario, Canada	Coniferous forest	49.50	−93.50	Lamontagne et al. (2000)
	80	Fernow	West Virginia, United States	Deciduous forest	39.08	−79.68	Adams et al. (1995)
	81	Fraser	Colorado, United States	Coniferous forest	39.87	−105.87	Baron et al. (1998)
	82	Gardsjon	Stenungsund, Sweden	Coniferous forest	58.07	12.02	Kjønaas et al. (1998)
	24	Harvard Forest	Massachusetts, United States	Deciduous and coniferous forests	42.50	−72.17	Aber et al. (1998)
	25	Howland Forest	Maine, United States	Coniferous forest	45.20	−68.73	Gaige et al. (2007)
	26	Huntington Wildlife Forest	New York, United States	Coniferous forest	43.98	−74.23	Christopher et al. (2007)
	55	Klosterhede	Lemvig, Denmark	Coniferous forest	56.48	8.40	Anderson and Gundersen (2000)
	81	Lochvale	Colorado, United States	Coniferous forest	39.87	−105.87	Walthall (1985)
	89	Michigan Gradient A	Michigan, United States	Coniferous forest	46.87	−88.88	Burton et al. (1996)
	90	Michigan Gradient B	Michigan, United States	Coniferous forest	45.55	−84.85	Burton et al. (1996)
	91	Michigan Gradient C	Michigan, United States	Coniferous forest	44.38	−85.83	Burton et al. (1996)
	92	Michigan Gradient D	Michigan, United States	Coniferous forest	43.67	−86.15	Burton et al. (1996)
	93	Mount Ascutney	Vermont, United States	Coniferous forest	43.43	−72.45	McNulty and Aber (1993)
	94	NITROF	Panama	Tropical montane	8.75	−82.25	No publications to date
	96	Pack Forest	New York, United States	Coniferous forest	43.55	−73.80	Mitchell et al. (2001)
	96	Pancake Hall Creek	New York, United States	Deciduous and coniferous forests	43.83	−74.85	Mitchell et al. (2001)
	97	Skogaby	Halmsted, Sweden	Coniferous forest	56.55	13.22	Majdi an Perrson (1995)
	68	Solling	Solling, Germany	Deciduous and coniferous forests	51.52	9.76	Beese et al. (1991)
	99	Speuld	Speuld, The Netherlands	Coniferous forest	52.22	5.65	Boxman et al. (1995)
	74	Toolik Lake	Alaska, United States	Tundra	68.63	−149.60	Shaver and Chapen (1995)
	100	Turkey Hill Plantation	New York, United States	Deciduous	42.45	−76.41	Philips and Fahey (2007)
	101	Woods Lake	New York, United States	Deciduous and coniferous forests	43.88	−74.95	Mitchell et al. (2001)
	102	Ysselstyn	Ysselsteyn, The Netherlands	Coniferous forest	51.50	5.92	Boxman et al. (1995)
Snow removal experiments	104	Coulissenhieb	Fichtelgebirge, Germany	Deciduous forest	50.13	11.87	Callesan et al. (2007)
	105	Hubbard Brook	New Hampshire, United States	Deciduous forest	43.82	−71.75	Campbell et al. (2005)
	106	Sierra Nevada Snow Climate Experiment	California, United States	Shrubland	37.50	−118.95	No publications to date
Warming and precipitation change experiments	108	BACE	Massachusetts, United States	Grassland	42.39	−71.22	No publications to date
	109	Canyonlands	Utah, United States	Shrubland	38.67	−109.42	Yeager et al. (2007)
	110	Flakaliden	Vindeln, Sweden	Coniferous forest	64.12	19.45	Kirschbaum (2004)
	111	Minnesota Peatlands	Minnesota, United States	Wetland	47.57	−93.58	Bridgham (1995)
	32	Oklahoma Tall Grass Prairie	Oklahoma, United States	Grassland	34.98	−97.52	Zhuo (2006)
	113	Storgama	Telemark, Norway	Heathland	59.02	8.30	Stuanes (2005)

(continued on next page)

Table 1 (*continued*)

Experiment type	Map location #	Site name	Location (City, State or Povence, Country)	Biome	Latitude	Longitude	Publications
	28	Taylor Valley	Antarctica	Desert	−77.63	162.88	No publications to date
	115	T-WaRM	Texas, United States	Shrubland	30.56	−96.35	Fuhlendorf (2001)
Warming and elevated CO_2 experiments	49	CAREER	Arizona, United States	Desert	35.16	−111.67	No publications to date
	118	CLIMEX	Grimstad, Norway	Coniferous forest	58.38	8.32	Beerling et al. (1997)
	110	Flakaliden	Vindeln, Sweden	Coniferous forest	64.12	19.45	Slaney et al. (2007)
	8	TACIT	Tennessee, United States	Deciduous forest	35.90	−84.35	Norby et al. (1997)
	39	TasFACE	Tasmania, Australia	Grassland	−42.69	147.26	Hovenden and Schimanski (2000)
Precipitation change and elevated CO_2 experiments	123	Hawkesbury Forest	North South Wales, Australia	Deciduous forest	−33.60	150.73	No publications to date
	124	High CO_2 on Maize	Braunschweig, Germany	Agricultural crops	52.30	10.43	No publications to date
Precipitation change and nitrogen addition experiments	56	RaMPS	Kansas, United States	Grassland	39.05	−96.35	No publications to date
	123	Hawkesbury Forest	Australia	Deciduous forest	−33.60	150.73	No publications to date
Elevated CO_2 and nitrogen addition experiments	124	Braunschweig	Braunschweig, Germany	Agricultural crops	52.30	10.43	Blagodatsky et al. (2006)
	130	Cedar Creek	Minnesota, United States	Grassland	45.40	−93.20	Reich et al. (2001)
	3	FACTS-I	North Carolina, United States	Coniferous forest	35.97	−79.08	Suwa et al. (2004)
Elevated CO_2 and clipping	133	Bulls	Bulls, New Zealand	Grassland	−40.23	175.27	Edwards et al. (2001)
	134	IMAGINE	Clermont-Ferrand, France	Grassland	45.77	3.07	No publications to date
CO_2 and ozone	136	FACTS-II (Rhinelander)	Wisconsin, United States	Deciduous forest	45.60	−89.70	Dickson et al. (2000)
	137	SoyFACE	Illinois, United States	Agricultural crops	40.03	−88.22	Ainsworth et al. (2006)
Multi-factor experiments (>2 factors)							
CO_2, N, Biodiversity	139	BIOCON	Minnesota, United States	Grassland	45.00	−93.00	Dijkstra (2005)
CO_2, Warm, Precipitation	140	CLIMAITE	Brandbjerg, Denmark	Shrubland	55.88	11.97	Mikkelsen et al. (2008)
Warm, Precipitation, N, Clipping	141	Duolun	Duolon, China	Grassland	42.03	116.26	Wang et al. (2000)
Warm, Precipitation, N, Clipping, CO_2	142	Jasper Ridge Global Change Experiment	California, United States	Grassland	37.40	−122.23	Field et al. (2007)
Warm, Precipitation, CO_2	8	OCCAM	Tennessee, United States	Deciduous forest	35.90	−84.35	Wan et al. (2007)
Warm, Precipitation, N, S	144	Peaknaze	Wales, United Kingdom	Grassland	52.00	−2.00	No publications to date
Warm, CO_2, Precipitation	145	PHACE	Wyoming, United States	Grassland	41.20	−104.89	No publications to date
Precipitation, N, creosote	146	Sevilleta LTER	New Mexico, United States	Grassland	34.36	−106.69	No publications to date

For citations, see Appendix A. Additional information on these sites can be found at: http://www.umaine.edu/teracc/.

declines in rates of N mineralization, providing some support for the hypothesis of progressive nutrient limitation (Bernhardt et al., 2006; Finzi et al., 2007). This phenomenon could not have been induced or observed in shorter-term experiments.

3.3.2. *Ecosystem warming experiments*

The locations of the ecosystem warming experiments identified in the TERACC network are shown in Fig. 1 and Table 1. Data from many of these experiments were synthesized in a meta-analysis of ecosystem response to warming (Rustad et al., 2001). Results showed that 2–9 years of experimental warming of whole ecosystems or ecosystem components (e.g. soils) in the range 0.3 to 6.0 °C significantly increased soil respiration rates by 20%, net N mineralization rates by 46%, and plant productivity by 19%.

Since 2001, several of these studies have been completed, new studies have been initiated, and several are ongoing. Of the ongoing studies, the soil warming experiment at the Harvard Forest in Petersham, MA, USA is one of the longest running. Initiated in 1991, electric heat resistance cables buried at 10 cm depth in the soil warm surface soils to 5 °C above ambient in a mixed northern hardwood forest. The much publicized results from the first 4 years of warming showed a dramatic 26–75% increase in soil respiration (Peterjohn et al., 1994; Melillo et al., 1995). However, by 2000, 10 years after the initiation of treatments, soil respiration in the warmed plots was no longer significantly different from the control, a trend that has continued through the latest period of record (2004, pers. comm. Jacqueline Mohan). Melillo et al. (2002) hypothesized that the reduced response in the warmed plots was due to a depletion of labile carbon stocks (e.g. consistently predominantly of simple sugars and amino acids), which may be more temperature sensitive than more recalcitrant carbon fractions (consisting of more complex aromatic compounds). For further discussion of the temperature sensitivity of soil organic matter, (see Liski et al., 1999, Giardina and Ryan, 2000, Melillo et al., 2002, Gu et al., 2004). Alternatively, the response could also be an experimental artifact, and may reflect a decoupling of the above- and belowground ecosystems, with soil warming stimulating a belowground mineralization response without the concomitant aboveground stimulation in productivity, which would provide the ‘fuel’ for a sustained increase in respiration. Whichever the explanation, it would have been misleading to extrapolate the results from the initial 5 years of the experiment to predict longer-term trends. Given these results from the Harvard Forest experiment, and the continuation of several of the early ecosystem warming experiments initiated in the mid-1990s, it is likely time for a re-evaluation of ecosystem response to experimental warming.

3.3.3. *Precipitation manipulation experiments*

The locations of the precipitation manipulation experiments identified in the TERACC network are shown in Fig. 1 and Table 1. Because confidence in both historic reconstructions and future global trends in precipitation has lagged behind that for atmospheric CO_2 and temperature, fewer precipitation manipulation experiments have been initiated over the past several decades, and to date, no global synthesis of existing results has been undertaken. Of the existing experiments, the Konza Praire irrigation study in Kansas, USA is one of the longest, continuously running precipitation manipulation experiments. Initiated in 1991, the treatment involves the addition of supplemental water to meet plant water demand in a tall grass prairie ecosystem. Results from the first 8 years of the study (1991–1998) showed that (1) water availability limited ANPP six of the 8 years, (2) supplemental water increased ANPP by ~25% in the irrigated plots compared to the controls, and (3) the response was due to physiological changes in the dominant plant species (Knapp et al., 2001). Results for the next 5 years (1999–2003), however, showed that (1) supplemental water increased ANPP by ~70% compared to the control, and (2) the response was due to an increased cover of *Panicum virgatum*, and thus a shift in community composition (Knapp et al., 2001; A. Knapp, pers comm). These results once again highlight the importance of decadal-scale responses in ecosystem manipulation experiments. Results from this and other precipitation manipulation experiments also underscore the importance of changes in both the amount and timing of precipitation, as well as the role of the plant community in mediating these responses as discussed in Heisler and Weltzin (2006).

3.3.3. *Multi-factor experiments*

The locations of the multi-factor global change experiments identified in the TERACC network are shown in Fig. 1 and Table 1. The smaller number of multi-factor experiments compared to single factor experiments (25 vs 124) and the observation that the majority are in grassland or low-stature ecosystems with short life spans (Table 1) reflects the fact that fully replicated multi-factor experiments are logistically and financially challenging. Despite these constraints, an increasing number of experimental and modeling results are showing interactive, and in some cases, non-additive responses to combinations of treatments (Henry et al., 2005; Norby et al., 2007; Luo et al., 2008), which underscores the need to continue to conduct multi-factor experiments at a wider range of ecosystems types to tease apart these intricate relationships.

One of the longest, continuously running and most complex multi-factor experiment is the Jasper Ridge Global Change Experiment in the Santa Cruz Mountains of California, USA. Initiated in 1998, the experiment includes a full factorial combination of warming, nitrogen deposition, elevated carbon dioxide, and increased precipitation, with 8 replicates of each experimental unit (until 2003 when a fire reduced the replication to 6 but added fire as an additional treatment). Important results from this experiment include the existence of nutrient constraints on NPP responses to global changes (Menge and Field, 2007), shifts in plant and microbial species composition and associated changes in productivity (Zavaleta et al., 2003a), changes in phenology (Cleland et al., 2006), and a surprising CO_2- and warming-induced *increase* in growing season soil moisture. Perhaps the most important contributions of this long-term, multi-factor experiment are, however, to highlight the inherent complexity of natural ecosystems (even one as ‘simple’ as an annual grassland in California, USA), the plethora of additive and non-additive responses to various global change factors, and the importance of inter-annual variations in climate drivers in determining overall ecosystem responses.

3.4. *Models*

Models provide tools for conceptually and empirically integrating existing knowledge, generating testable hypotheses, highlighting gaps in knowledge, scaling experimental results up in time and space, and investigating multiple, interacting elements of global change. Experiments, in turn, can be used to test models. Recent advances and major uncertainties in process and large-scale plant production, biogeochemistry, hydrological and plant competition models were evaluated at a TERACC workshop on "Modeling Ecosystem Responses to Global Change: Techniques and Recent Advances" held in January 2005. Recommendations from this workshop, as summarized by Classen and Langley (2005), include the need to (1) better incorporate concepts of landscape heterogeneity into models; (2) design experiments to fill theoretical gaps in models; (3) better match measurement and modeling time-scales; (4) better understand the influence of small or large-scale stochastic events, such as extreme climatic events or fire, and incorporate this understanding into models; and (5) better integrate models with experiments, from hypothesis generation to extrapolation of results in time, space, and complexity.

4. Towards an integrated approach

All the approaches discussed above have their unique pros and cons (Table 2). The TERACC research community of empiricists and modelers advocates an approach that integrates these approaches to build on their strengths and minimize their weaknesses. Themes of this approach are as follows:

1. *Better integrate experiments with observations* — Experiments should be conducted at long-term study sites to take advantage of rich information on site characteristics, and historical records of annual and inter-annual responses to climate or other perturbations. Data from these long-term study sites could be more efficiently 'mined' to better define the next generation of experiments.
2. *Combine experimental and gradient studies* — Superimposing experiments across gradients allows researchers to investigate ecosystem response to a broader range of environmental conditions. For example, the pan-European VULCAN project superimposed experimental manipulations of temperature and precipitation across a climatic gradient in Mediterranean shrubland communities from Italy to the United Kingdom (Beier et al., 2004). One set of results underscored how soil moisture influences the temperature sensitivity of N mineralization. Nitrogen mineralization generally increased with increasing temperature, but only when moisture was neither limiting or in excess (Emmett et al., 2004).

   Combining experiments with gradient studies also allows the policy-relevant mid-term response (i.e. decades to century) to be bracketed between short-term experimental responses (i.e. years to decades) and long-term responses across gradients (i.e. centuries to millennia). This is discussed in detail by Dunne et al. (2004) who integrated a warming experiment with an elevation gradient study at the Rocky Mountain Biological Laboratory in Colorado, USA. In one case, results from both the warming experiment and the gradient study reinforced each other by showing that the timing of flowering for 11 sub-alpine meadow plant species was determined by the timing of snowmelt, regardless of how the snowmelt was induced. However, in a second case, the relationship between soil organic carbon and soil temperature was of opposite sign, depending on whether the temperature variation was due to the experiment or the natural gradient. The short-term, experimental response was dominated by a decline in soil organic carbon due to a shift from the more productive forbs to the less productive shrubs. However, because the litter of the shrubs is less decomposable than that of the forbs, soil organic carbon increases with warming over longer time periods, as evidenced across the gradient,. This complex pattern was only observable because of the integration of approaches.
3. *Better integrate experiments and models* — As discussed previously, experiments and models could be better matched and integrated. Additional and more robust data–model and model–model comparisons would also be beneficial for identifying data needs, gaps in models, and experimental priorities.
4. *Nature of experiments* — Much has been learned from the current generation of ecosystem-scale manipulation experiments. However, the following needs and suggestions have been made by the TERACC community:
   - Long-term studies and experiments — The current generation of experiments has demonstrated time and again that the magnitude and even direction of

Table 2 – Pros and cons of different approaches to evaluating global change effects on terrestrial ecosystems

Approach	Pros	Cons
Observations	1. Ultimate validation of ecosystem and global scale models	1. Long-term records rarely go back >100 years
		2. Future responses are unknown
Gradients	1. Allow for evaluation of ecosystem response to different climates	1. Impossible to match sites perfectly
	2. Allow for evaluating long-term effects	2. Sites have evolved with local climate over the millennia
		3. No broad spatial gradients for CO_2
Experiments	1. Tool to evaluate cause-and-effect relationships	1. Step increases is not realistic
	2. Tool to validate models	2. Can only realistically alter 2–3 factors
	3. Provide opportunity for 'surprises'	3. Can only generate short-term data on short-term response
Models	1. Integrate existing knowledge	1. Need to incorporate heterogeneity, disturbance etc.
	2. Allow for projections in time and space	2. Not possible to validate longer-term effects
	3. Provide for testing of conceptual and process understanding	3. Do not yet adequately incorporate biodiversity and stochastic events.

response may change over time. It is imperative to provide long-term support for long-term global change experiments.

- Multi-factor experiments — The current generation of experiments has demonstrated that terrestrial ecosystem responses to multiple, interacting vectors of global change can be non-additive. It is imperative to continue to initiate and support multi-factor experiments to explore these interactions.
- Biodiversity — It is becoming increasingly apparent that ecosystem response to global change is dependent on species composition (Midgley and Thuiller, 2005). More experiments, such as BIOCON at the Cedar Creek natural History Area in Minnesota, USA (Table 1; http://biocon.fr.umn.edu/) should be designed to focus on biodiversity, and the direct and indirect effects of changes in biodiversity should be included in models of ecosystem structure and function.
- Disturbance — Concepts of fire, disease, extreme climatic events and other types of disturbance need to be explicitly incorporated into models and experiments.
- Location of experiments — As apparent in Fig. 1 and Table 1, the majority of global change experiments are in North America and Europe, and many are in grassland or other low-stature ecosystems. New experiments should be initiated across a broader geographic area and in a wider range of biomes, particularly under-represented biomes. These include tropical, desert, wetland, and *mature* temperate and boreal forest ecosystems. Experiments should be located in parts of the world where climatic and/or species composition change is projected to be largest such as high latitude or tropical ecosystems. Research should also focus on ecotones, or northern or southern range limits, again, where change is expected to be largest and most apparent.
- Timing vs intensity — Global change experiments need to consider changes in the timing and intensity of the experimental factor as well as the magnitude. Experiments on single extreme events should be considered.
- Thresholds — Global change experiments need to consider sensitive thresholds of response or ecosystem 'tipping' points.

5. Concluding remarks

With the improved reconstructions of past climate change, the increased sophistication of ecosystem, regional, and global scale models to predict future climate change, and the growing body of literature on ecosystem response to multiple, interacting elements of global change, the scientific community is coming to a consensus that human-induced climate is having, and will continue to have, a dramatic impact on the earth's physical, chemical, and biological systems. It is thus imperative to continue to unravel the complex response of terrestrial ecosystems to global change as rapidly as possible in order to continue to build the scientific basis for national and international policy and land management decisions. TERACC is committed to the concept that this can best be done by integrating observational, experimental, and modeling techniques into a *unified multidisciplinary approach* as described in this paper, and that this effort will take continued local, regional, national and international cooperation and collaboration.

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This paper summarizes several of the themes expressed at the workshops on "From Transient to Steady State Response of Ecosystems to Atmospheric CO_2 Enrichment and Global Climate Change", April 28 to May 1, 2002, Durham, New Hampshire; "Interactions Between Increasing CO_2 and Temperature in Terrestrial Ecosystems", April 27–30, 2003, Lake Tahoe, CA; "Modeling Ecosystem Responses to Global Change: Techniques and Recent Advances", January 9–13, 2005, Fort Myers, Fl; Global Environmental Change and Biodiversity", May 1–4, 2005, Dourdan, France; "Effects of PREcipitation Change On Terrestrial Ecosystems (EPRECOT), May 22–25, 2006, Helsinore, Denmark. These workshops were sponsored or co-sponsored by the Terrestrial Ecosystem Response to Atmospheric and Climatic Change (TERACC), a research coordination network supported by the National Science Foundation (DEB-0090238). Many thanks to Tracey Walls for website and data management and Ellen Denny for production of GIS maps. This paper was prepared with support from the USDA Forest Service.

Appendix A. Citations for Table 1

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