



17 Biogeochemical Effects of Rising Atmospheric Carbon Dioxide

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KEY FINDINGS

1. Rising carbon dioxide (CO₂) has decreased seawater pH at long-term observing stations around the world, including in the open ocean north of Oahu, Hawai'i; near Alaska's Aleutian Islands; on the Gulf of Maine shore; and on Gray's Reef in the southeastern United States. This ocean acidification process has already affected some marine species and altered fundamental ecosystem processes, and further effects are likely (*high confidence, likely*).
2. While atmospheric CO₂ rises at approximately the same rate all over the globe, its non-climate effects on land vary depending on climate and dominant species. In terrestrial ecosystems, rising atmospheric CO₂ concentrations are expected to increase plant photosynthesis, growth, and water-use efficiency, though these effects are reduced when nutrients, drought, or other factors limit plant growth (*very high confidence, very likely*). Rising CO₂ would likely change carbon storage and influence terrestrial hydrology and biogeochemical cycling, but concomitant effects on vegetation composition and nutrient feedbacks are challenging to predict, making decadal forecasts uncertain.
3. Consequences of rising atmospheric CO₂ are expected to include difficult-to-predict changes in the ecosystem services that terrestrial and oceanic systems provide to humans. For instance, ocean acidification resulting from rising CO₂ has decreased the supply of larvae that sustains commercial shellfish production in the northwestern United States. In addition, CO₂ fertilization (increases) plus warming (decreases) are changing terrestrial crop yields (*high confidence, likely*).
4. Continued persistence of uptake of carbon by the land and ocean is uncertain. Climate and environmental changes create complex feedbacks to the carbon cycle; how these feedbacks modulate future effects of rising CO₂ on carbon sinks is unclear. There are several mechanisms that would reduce the ability of land and ocean sinks to continue taking up a large proportion of rising CO₂ (*very high confidence*).

Note: Confidence levels are provided as appropriate for quantitative, but not qualitative, Key Findings and statements.

17.1 Introduction

The most central planetary outcome of rising atmospheric carbon dioxide (CO₂), methane (CH₄), and black carbon is their warming effect on Earth's atmosphere, which influences weather and climate (IPCC 2013). The *Climate Science Special Report* (CSSR; USGCRP 2017) concludes with high confidence that Earth's observed temperature increase in the last century results from human influence, especially from emissions of greenhouse gases including CO₂ and CH₄ and particulates such as black carbon. Furthermore, CSSR (USGCRP 2017) demonstrates that the consequences of atmospheric warming are profound and diverse, significantly altering planetary surface temperatures and overall climate and thus also directly or indirectly altering countless oceanic and terrestrial processes.

Increased global temperatures lead to extremes in temperature and precipitation (IPCC 2013), causing

heatwaves, droughts, floods, and changing storm system patterns (Melillo et al., 2014), with additional consequences for the carbon cycle. For instance, warming and changing weather melt polar ice cover and thaw Arctic permafrost, releasing CH₄ and CO₂ as stored organic matter is microbially respired (see Ch. 11: Arctic and Boreal Carbon, p. 428). Melting glaciers and seawater expansion will raise sea levels, changing ecosystem boundaries and affecting net carbon fluxes (IPCC 2013; USGCRP 2017). Heating and ice melt will stratify the ocean, dampening the ability of vertical mixing to refresh surface waters with nutrients that support primary production (IPCC 2013). A warmer ocean will hold less carbon, because warmer ocean temperatures decrease the solubility of CO₂ in seawater (Zeebe and Wolf-Gladrow 2001). Both long-term increases in ocean temperature and short-term marine heatwaves may affect stocks of organic and inorganic carbon



contained in marine ecosystems and sediments (see Ch. 16: Coastal Ocean and Continental Shelves, p. 649). Changing snowpack dynamics will affect water availability significantly in riverine ecosystems. In midlatitudes, fire frequency and severity will change as a result of changes in temperature and precipitation. These shifts and feedbacks are very likely to have widespread, interacting effects on human and natural systems that elicit a variety of responses.

Upon this backdrop of accumulating, thermally driven planetary climate change that impacts the carbon cycle, rising atmospheric CO₂ is also affecting oceanic and terrestrial systems in nonthermal ways that have only begun to be understood since the *First State of the Carbon Cycle Report* (SOCCR1; CCSP 2007). The observed rise in atmospheric CO₂ since the 1950s is lower than the contributions from estimated emissions because both the ocean and land continue to take up a portion of the atmospheric CO₂ from anthropogenic (i.e., human) activities, indicating both systems are carbon sinks (Ballantyne et al., 2012). Ocean uptake prevents some degree of atmospheric warming but results in ocean acidification (see Ch. 16: Coastal Ocean and Continental Shelves), which drives a host of chemical and biological impacts, as reviewed below. The terrestrial “CO₂ fertilization effect” is the increased uptake of CO₂ per unit land area caused by rising CO₂, which is greater than could be expected from plant regrowth after land-use change and stimulation by increased nutrient availability. Global analysis suggests that CO₂ fertilization is responsible for up to 60% of the overall land sink (Schimel et al., 2015), but persistence of these benefits into the future is highly uncertain (Müller et al., 2014; Smith et al., 2016). Moreover, the thermal impacts of climate change will interact with, enhance, or in some cases overwhelm the nonthermal effects of rising atmospheric CO₂ on ecosystems; these different future scenarios are explored elsewhere in this report (see Ch. 19: Future of the North American Carbon Cycle, p. 760). These findings have important implications; the current partitioning of anthropogenic CO₂ sinks among the ocean, atmosphere, and terrestrial biosphere, therefore, also will

change in the future. Because CO₂ is involved in all aspects of growth in biological systems there also are important non-climate effects of increased atmospheric CO₂ concentration.

To better explain the non-climate effects of rising CO₂ on ecological systems, this chapter first reviews the historical context of rising CO₂ and then examines its impact on ocean and terrestrial systems (see Figure 17.1, p. 693), including ocean acidification, productivity and ecosystem changes, interactions with other environmental changes, and carbon cycle feedbacks. Also examined are changes in ecosystem services (or benefits to humans) resulting from chemical changes in Earth system processes and how those intersect with thermally driven changes. This examination is followed by a review of outstanding research needs for gaining greater clarity on the effects of rising CO₂ on oceanic and terrestrial systems.

Such a comprehensive, collected examination of the effects of carbon cycle changes is new in the *Second State of the Carbon Cycle Report* (SOCCR2) and responds to the requirement in the Global Change Research Act that “analyzes the effect of global change on the natural environment, agriculture, energy production and use, land and water resources, transportation, human health and welfare, human social systems, and biological diversity” (Global Change Research Act 1990, Section 106). Since publication of SOCCR1 (CCSP 2007), many highly influential reports have assessed the consequences of carbon cycle changes on Earth systems, including the *Third National Climate Assessment* (Melillo et al., 2014), the *Intergovernmental Panel on Climate Change Fifth Assessment Report* (IPCC AR5; IPCC 2013), and the *CSSR* (USGCRP 2017). This chapter updates the conclusions of the reports cited above, with the most recent literature and with particular attention to North America. Those reports treat the direct and indirect effects of increasing CO₂ in greater detail than does this chapter, which focuses to a greater extent on the direct and non-climatic effects of increased atmospheric CO₂ concentrations.

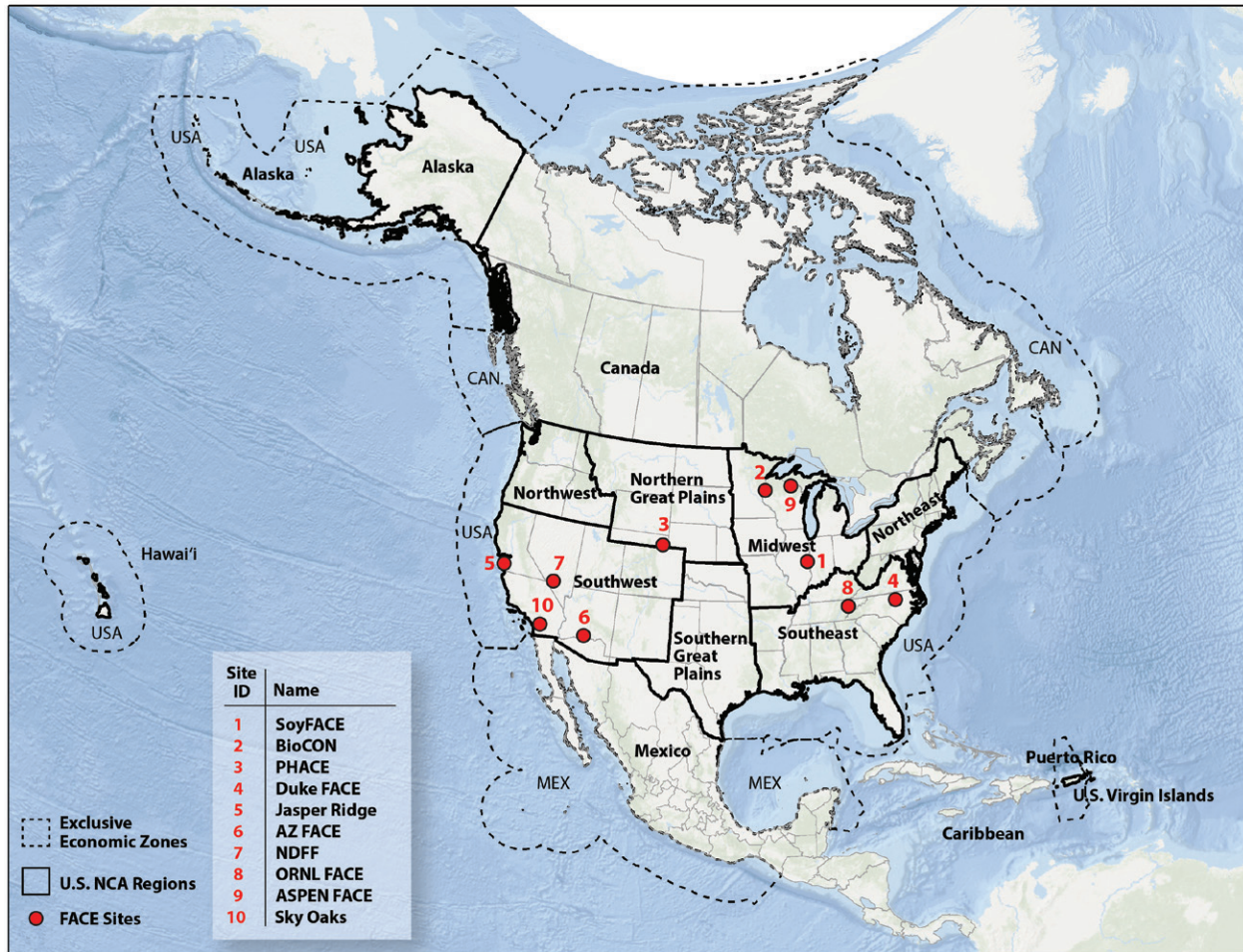


Figure 17.1. Study Sites Examining Terrestrial Ecosystem Responses to Elevated Carbon Dioxide (CO₂). Projects include 1) Soybean Free Air Concentration Enrichment (SoyFACE); 2) Biodiversity, CO₂, and Nitrogen (BioCON); 3) Prairie Heating and CO₂ Enrichment (PHACE); 4) Duke Forest Free-Air CO₂ Enrichment (FACE) Experiment; 5) Jasper Ridge Global Change Experiment; 6) Maricopa, Ariz., FACE experiments; 7) Nevada Desert FACE Facility (NDDFF); 8) Oak Ridge National Laboratory (ORNL) FACE; 9) Aspen FACE Experiment; and 10) Sky Oaks Long-term Carbon Flux Measurements. [Figure source: Christopher DeRolph, Oak Ridge National Laboratory.]

17.2 Atmospheric CO₂ in Prior Geological Ages

Over geological time (i.e., the last 500 million years), atmospheric CO₂ levels have at times been well in excess of current CO₂ concentrations (see Figure 17.2, p. 694). However, human civilization developed during the last 10,000 years, a time when atmospheric CO₂ was never higher than it is today (Augustin et al., 2004). Once humans began extensively altering the landscape and burning fossil fuels,

atmospheric CO₂ and CH₄ began to rise rapidly and drive changes in atmospheric, terrestrial, and oceanic systems and processes (Olofsson and Hickler 2007).

Changes in atmospheric CO₂ changed Earth's climate and ocean pH and altered the course of plant evolution. Atmospheric CO₂ was likely higher than 5,000 parts per million (ppm) at times during the last 540 million years (Phanerozoic Eon) and declined to current levels during the last 25 million years (Doney and Schimel 2007; Royer 2006; see

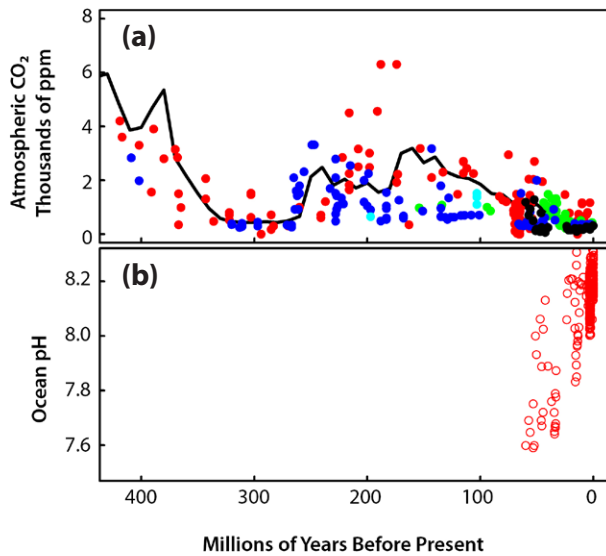


Figure 17.2. Geological Context of Carbon Dioxide (CO₂). (a) Paleoreconstruction of atmospheric CO₂ in parts per million (ppm) versus time over the past 400 million years. The Geologic Carbon Cycle (GEOCARB) Model simulation is depicted by the black line; also shown (as dots) are publicly archived proxy data for paleosol carbon isotopes (red), phytoplankton carbon isotopes (green), stomatal indices (blue), marine boron isotopes (black), and liverwort carbon isotopes (cyan). (b) Ocean surface pH, shown in red, has increased over the last 50 million years as atmospheric CO₂ declined. [Data sources: Panel (a) from Royer 2006. Data are publicly available at www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/climate-forcing. Panel (b) proxy data from Hönisch et al., 2012.]

Figure 17.2, this page). During this eon, periods of frequent glaciation events in Earth's history are associated with CO₂ concentrations below 1,000 ppm (Royer 2006). A strong decline of atmospheric CO₂ during the Carboniferous Period (359 million years ago) is associated with the proliferation of land plants. Extensive burial of plants from this period resulted in the massive deposits of fossil fuels now being mined. Declining atmospheric CO₂ concentrations at the Eocene-Oligocene boundary (34 million years ago) induced dynamic ice sheet formation over Antarctica and ultimately led to substantial cooling of global climate over the subsequent 10 million years (DeConto and Pollard 2003). During the Quaternary Period (last 1 million years), ice core records

show that temperature increases of ~3°C were associated with CO₂ increases of ~100 ppm (Petit et al., 1999). Recent analyses show that during the last deglaciation (from ~21,500 to ~11,500 years ago), observed increases in global temperature lagged behind observed increases in atmospheric CO₂ (Shakun et al., 2012). The glacial-interglacial cycle in Earth's climate during the Quaternary period is caused by a combination of changes in Earth's orbit, atmospheric greenhouse gases, and ocean circulation (Rohling et al., 2018).

The evolution of different ways of performing photosynthesis has a strong influence on the non-climate consequences of rising CO₂ on land. Fundamental to plant life on Earth, atmospheric CO₂ concentrations and their dynamics over geological time have played an important role in the evolution of photosynthesis and the distribution of different vegetation types (Beerling et al., 2001; Monson and Collatz 2011). RUBISCO (ribulose-1, 5-bisphosphate carboxylase-oxygenase), the enzyme that catalyzes the transfer of atmospheric CO₂ into plant sugars and biomass, evolved in early algae during a time of high CO₂ at least 2.8 billion years ago (Doney and Schimel 2007), though perhaps much earlier (Allwood et al., 2006; Raven et al., 2012). Plants evolved different photosynthetic mechanisms and anatomies in response to the relatively low CO₂ concentrations that persisted from about 300 million years ago, an environment which enabled C₄ grasses (e.g., ancestors of maize, sugarcane, and sorghum) and the cactus family to dominate arid portions of the Earth because of their greater water-use efficiency and drought tolerance (Berner 1997; Osborne and Sack 2012; Pagani et al., 2005).

Prior geological eras also provide information about potential impacts of high atmospheric CO₂ on ocean chemistry (Hönisch et al., 2012). Atmospheric CO₂ dissolves in seawater and creates carbonic acid, which lowers pH and decreases the concentration of carbonate ions present in solution. The closest analogs to present conditions may be the Paleocene-Eocene Thermal Maximum



(56 million years ago), Triassic-Jurassic mass extinction (~200 million years ago), and Permo-Triassic mass extinction (252.3 million years ago; Hönisch et al., 2012). All these events are associated with evidence of detrimental impacts on calcifying organisms including, in some instances, their extinction. However, definitively attributing negative effects on calcifiers to acidification is not possible because of other factors (e.g., ocean circulation, warming, oxygenation, and asteroid impacts) that may have co-occurred or contributed to the decline or demise of these organisms. Moreover, geochemical proxies indicating pH or ocean carbonate chemistry conditions, particularly for times before the Cretaceous Period (>65 million years ago), are limited and have large uncertainties.

Since the start of the Industrial Revolution, anthropogenic emissions have resulted in increased atmospheric CO₂ concentrations detectable by changes in the ratio of ¹³C and ¹²C isotopes in the biosphere (Keeling 1979; Suess 1955). Fossil fuels have less of the ¹³C isotope because they are composed of dead plants and animals, and burning them changes the isotope ratio in the atmosphere. Isotopic studies indicate some of the carbon released from fossil sources becomes incorporated into all organisms, including those as diverse as trees (Suess 1955), marine fish (Fraile et al., 2016), and penguins (Hilton et al., 2006). The decrease in ocean pH since the start of the Industrial Revolution matches or exceeds the pH levels observed for the Quaternary glacial-interglacial period (Pelejero et al., 2010; Turley et al., 2006). Moreover, projected changes in ocean pH by 2100 well exceed those that occurred during the preindustrial period (Bijma et al., 2013; Turley et al., 2006). Recent global changes in upper ocean chemistry likely are occurring more rapidly than at any time over the past 300 million years (Doney et al., 2014; Hönisch et al., 2012). The rates and magnitude of change may soon move the ocean ecosystem into “uncharted territory,” with conditions unlike any that contemporary marine life have faced during their recent evolutionary history (Gattuso et al., 2015; Turley et al., 2006).

17.3 Aquatic Consequences of Rising CO₂

17.3.1 Ocean Acidification

Increased uptake of CO₂ by the ocean from the beginning of the Industrial Revolution has led to decreased seawater pH and a lower calcium carbonate (CaCO₃) mineral saturation state (see Ch. 16: Coastal Ocean and Continental Shelves, Section 16.4.2, p. 670). Average pH values for open-ocean surface water have decreased by approximately 0.11 units from a preindustrial mean value of 8.17, equivalent to an increase of about 28% in hydrogen ion concentration (Feely et al., 2004, 2009; Gattuso et al., 2015; Orr et al., 2005). As a result of ocean acidification, the oceanic average concentration of carbonate ion (CO₃²⁻) has declined about 16% from preindustrial values (Bopp et al., 2013; Doney et al., 2009; Gattuso et al., 2015). These changes in carbonate chemistry caused by rising atmospheric CO₂ have a variety of effects on aquatic life (e.g., Orr et al., 2005 and Kroeker et al., 2013), which is now an area of active research. Thirty-year ocean time-series datasets (e.g., Bates et al., 2014; Dore et al., 2009) provide direct evidence of this phenomenon worldwide (see Figure 17.3, p. 696). By the end of this century, surface ocean pH is expected to decline by another 0.1 to 0.4 units, and CO₃²⁻ concentration is expected to decline by as much as 50% compared to preindustrial conditions (see Figure 17.4, p. 697).

Significant changes in ocean acidity are readily apparent in the subtropical open ocean (see Figure 17.3, p. 696) and in several coastal locations (Sutton et al., 2016). High-quality, long-term datasets in extremely nearshore locations are limited, but ocean acidification has been documented year-round at time-series observatories near Alaska’s Aleutian Islands and Oahu, Hawai’i (both open-ocean sites), and the Gulf of Maine and Gray’s Reef off Georgia (both coastal ocean sites; Sutton et al., 2016). Conditions are more variable at coastal and nearshore time-series sites in the California Current and off Washington state (see Ch. 16: Coastal Ocean and Continental Shelves, Section 16.4.2), but they still confirm the presence of significantly

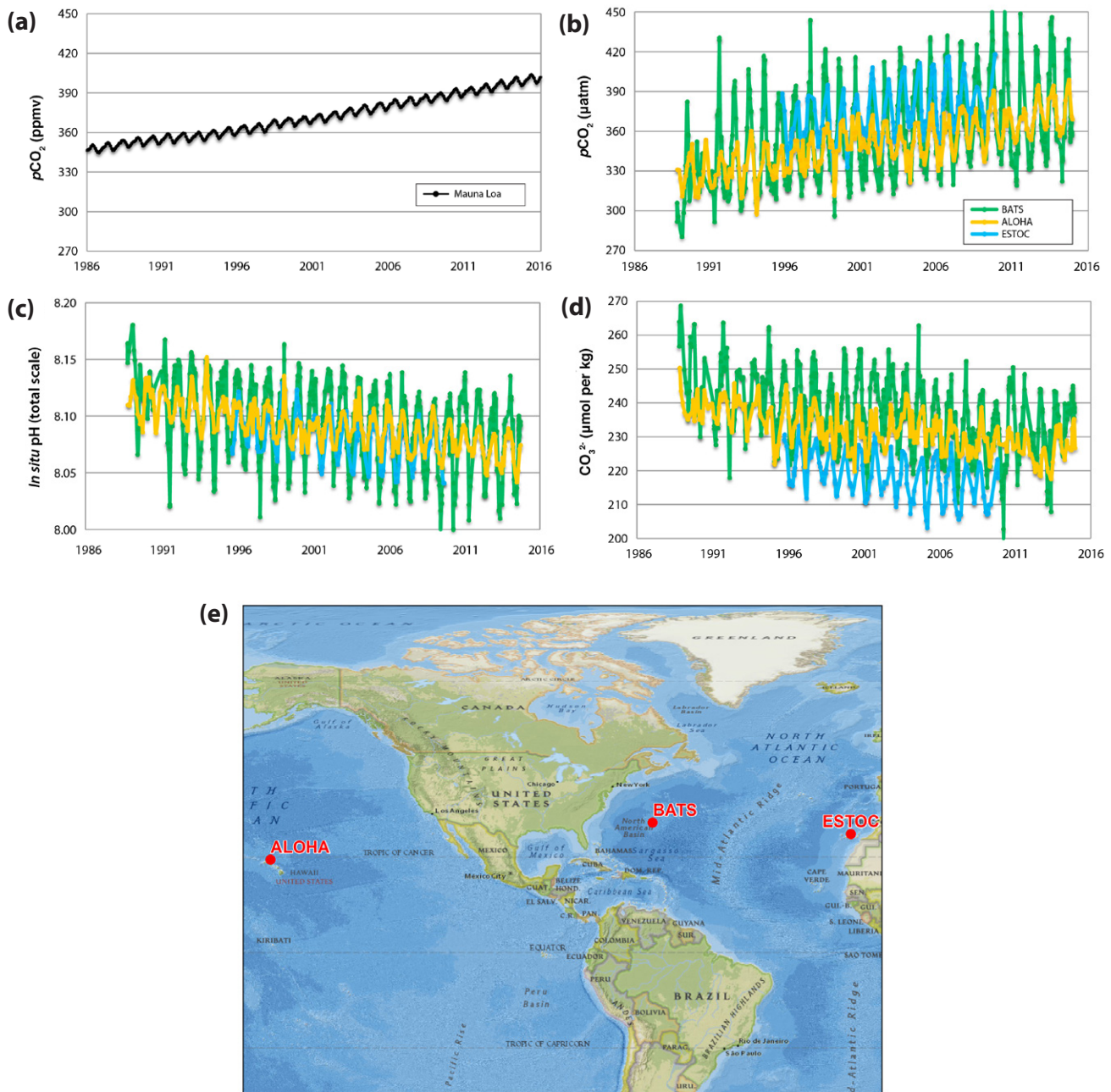


Figure 17.3. Evidence for Ocean Acidification from Ocean Time-Series Stations. (a) Mauna Loa, Hawai'i; atmospheric carbon dioxide (CO_2) in parts per million by volume (ppmv) versus time. (b) Surface ocean partial pressure of CO_2 ($p\text{CO}_2$) in microatmospheres (μatm) versus time for three ocean time-series monitoring stations: Bermuda Atlantic Time-series Study (BATS), A Long-Term Oligotrophic Habitat Assessment (ALOHA), and European Station for Time series in the Ocean at the Canary Islands (ESTOC). (c) Surface ocean pH versus time for BATS, ALOHA, and ESTOC. (d) Carbonate ion (CO_3^{2-}) versus time for BATS, ALOHA, and ESTOC. (e) Map of BATS, ALOHA, and ESTOC monitoring station locations. [Figure sources: Panel (a) from Scripps Institution of Oceanography, NOAA Earth System Research Laboratory. Panels (b–d) adapted from Fig. 3.18 (updated with new time-series data) from Rhein et al., 2013; Copyright IPCC, used with permission. Panel (e) from Christopher DeRolph, Oak Ridge National Laboratory.]

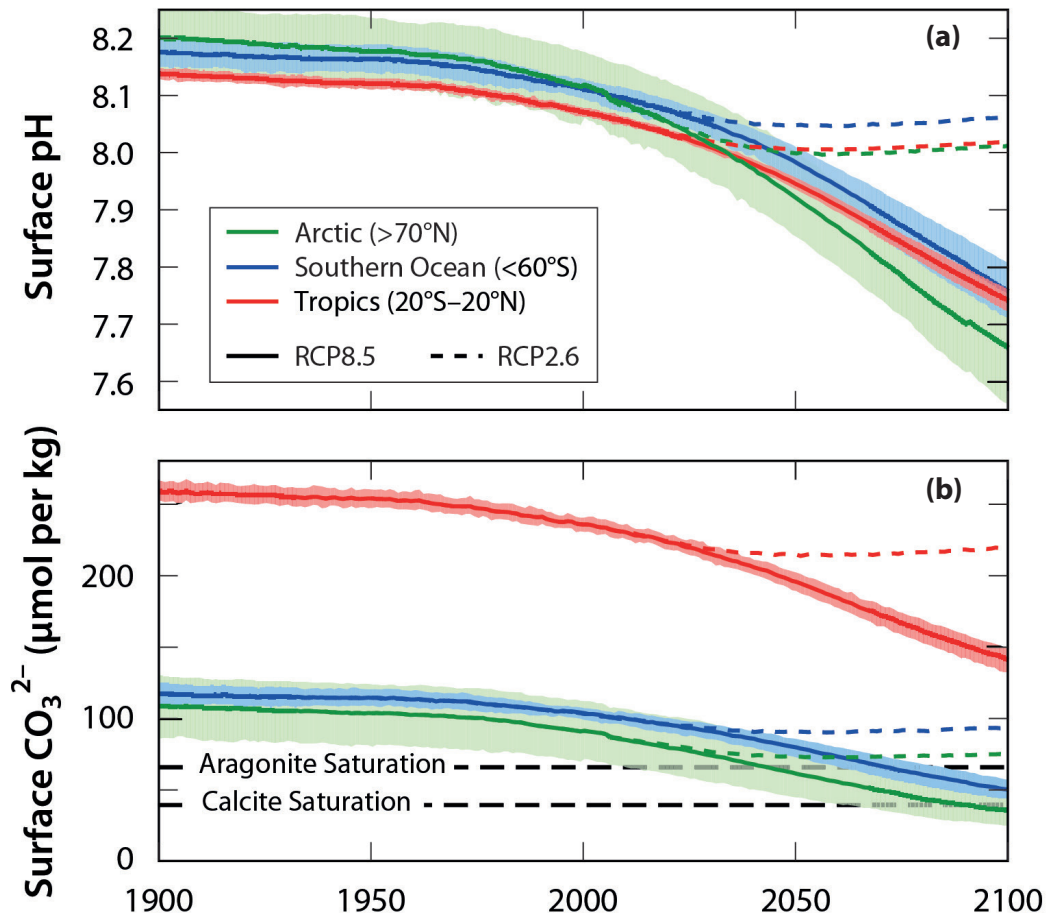


Figure 17.4. Regional Differences in Acidification Projections. Changes in (a) surface ocean pH and (b) surface carbonate ion (CO_3^{2-}) concentration (in micromoles per kg) through time for three ocean locations for the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway (RCP)8.5 and 2.6 scenarios based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) analysis. See Ch. 19: Future of the North American Carbon Cycle, p. 760, for RCP explanations. [Figure source: Adapted from Figs. 6.28(a) and 6.29(a) from Ciais et al., 2013; Copyright IPCC, used with permission.]

acidified conditions during some portions of every year (Sutton et al., 2016). The pH values in coastal waters are much more variable than those in the open ocean (Friedrich et al., 2012; Hofmann et al., 2010; Johnson et al., 2013; Sutton et al., 2016) because of natural processes such as upwelling, biological consumption and release of CO_2 , temperature- and salinity-driven solubility changes in CO_2 , or local human inputs of acid-producing substances (see Ch. 16: Coastal Ocean and Continental Shelves, Section 16.4.2, p. 670). Variable coastal processes make long-term pH trends somewhat harder

to discern (Sutton et al., 2016), but these processes can enhance acidification (Doney 2010; Feely et al., 2008; Kelly et al., 2011) far beyond global average projections. The projected long-term average global increase in acidity (decreasing pH values) in the next 20 to 40 years due to atmospheric CO_2 (see Figure 17.4, this page) is much greater than the natural variability of pH values observed since monitoring began, underscoring the idea that marine life will face unfamiliar seawater chemistry conditions in the near future.



Many coastal margins also suffer from excess anthropogenic nitrogen and phosphorus inputs, which cause algal overgrowth (eutrophication) and, in some cases, increased microbial digestion (remineralization) of organic matter in bottom waters (see Ch. 16: Coastal Ocean and Continental Shelves, p. 649). These processes further increase CO₂ in water, reduce oxygen (i.e., deoxygenation) and pH, and decrease CaCO₃ mineral saturation (Cai et al., 2011; Diaz and Rosenberg 2008; Feely et al., 2016; Rabalais et al., 2002). Multiple stresses to coastal zones (e.g., warming, ocean acidification, and deoxygenation) can cause compounding harm to marine ecosystem health (Bijma et al., 2013; Wallace et al., 2014), complicating detection of individual organism impacts and ecosystem trends from acidification (Duarte et al., 2013; Harvey et al., 2013). Future research about how to manage aquatic ecosystems under global change needs to account for the complexity of climate and non-climate drivers and responses in both coastal and ocean environments (Blackford 2010; Riebesell and Gattuso 2015).

17.3.2 Acidification of Freshwater

Inland freshwater can dissolve excess atmospheric CO₂ just as seawater does. However, the dearth of long-term, high-precision, high-accuracy carbonate chemistry datasets for even major freshwater bodies like the Laurentian Great Lakes precludes attributing a discernible acidification trend in freshwater bodies to atmospheric CO₂ (Phillips et al., 2015). As in coastal waters, local processes also can significantly alter freshwater pH, complicating detection and attribution of changes driven by atmospheric CO₂ in lakes and rivers. The effects of acidification-driven changes due to increasing atmospheric CO₂ on lake ecosystems have not been determined (Hasler et al., 2015), but species-level studies suggest that, just as in ocean environments, impacts to freshwater organisms could be widespread and yet difficult to forecast (Weiss et al., 2018).

17.3.3 Changes in Ocean Biology and Ocean Biological Processes

Investigations of ocean acidification's effect on marine life show evidence of a wide range of

sensitivities within and across diverse groups of organisms. Calcifying phytoplankton like coccolithophorids as well as multicellular organisms like scleractinian corals, pteropods, foraminifera, bivalves, crustaceans, and gastropods generally show negative but complex responses to ocean acidification, including altered biological processes such as growth, photosynthesis, calcification, and reproductive success (Bednaršek et al., 2016; Hofmann et al., 2010; Kroeker et al., 2013; Riebesell and Tortell 2011; Meyer and Riebesell 2015). Several finfish and shark species display altered risk-taking and hunting behaviors (Hamilton et al., 2014; Munday et al., 2014; Dixon et al., 2014), responses which have been related to changes in olfaction and neurotransmitter levels that result from ocean acidification (Munday et al., 2009; Dixon et al., 2010). Developmental changes in some harvested species such as summer flounder and tuna have also been noted (Chambers et al., 2014; Frommel et al., 2016). Conversely, photosynthesis of phytoplankton (algae), seagrasses, and kelp generally increases (Fu et al., 2007; Hutchins et al., 2013; Riebesell et al., 2007; Mackey et al., 2015), although net responses are highly species-specific and limited by several cellular processes, including species' carbon capture mechanisms (Mackey et al., 2015). Species responsible for harmful algal blooms are stimulated by changing ocean temperatures, carbonate chemistry, and nutrient ratios, displaying higher growth rates and greater toxin production (Fu et al., 2012). Theory suggests that acidification also may affect bioavailability of nutrients and trace minerals and stoichiometry of biogeochemical processes (Millero et al., 2009), but experimental results are mixed (Breitbarth et al., 2010; Shi et al., 2010). Co-occurrence of elevated temperatures, excessive nutrient inputs, changes in light availability, and increased hypoxia are likely to exacerbate and complicate the effects of ocean acidification on marine organisms or ecosystems (Bijma et al., 2013; Kroeker et al., 2013).

Ocean acidification impacts at the ecosystem level are difficult to predict because of the complexity of species- and population-level responses, but that research is beginning. Population-scale projections



of ocean acidification's effects have been developed for a few high-value, intensively managed single-species fisheries, including Tanner crab (Punt et al., 2016) and sea scallop (Cooley et al., 2015). More broadly, physiological and behavioral changes could alter predator-prey relationships and other species interactions, driving changes in species abundance and composition of ecological communities. Ocean acidification contributes to net loss of corals, and this loss destroys reef habitats and displaces associated marine communities (Hoegh-Guldberg et al., 2007). Ecosystem-scale projections incorporating ocean acidification and other environmental changes are only now being developed for select locations (e.g., California Current, Puget Sound, and northeastern United States; Busch et al., 2013; Fay et al., 2017; Kaplan et al., 2010). Much of the complexity in observed responses lies in 1) different timescales of response relative to the change in ocean acidification, 2) organisms' abilities to acclimate or genetically adapt, and 3) linkages between ocean acidification and other environmental stressors. Observational (Pespeni et al., 2013; Wootton et al., 2008), integrative (Boyd et al., 2014), and modeling (e.g., Dutkiewicz et al., 2015) studies emphasize the complexity of observed and predicted changes and suggest that future community and functional responses are likely to be more profound than the changes already observed.

17.3.4 Limits in Ocean CO₂ Uptake Capacity

Acidification varies with latitude because CO₂ solubility depends on temperature, with lower-temperature waters capable of holding more CO₂ and thus becoming more readily acidified. Models show that the suite of ocean changes (e.g., circulation, biological productivity, and ventilation) associated with atmospheric CO₂ absorption and the thermal effects of CO₂ and other greenhouse gases on the ocean are likely to decrease the ocean's future ability to take up atmospheric CO₂ (see Ch. 19: Future of the North American Carbon Cycle, Section 19.6, p. 779). In the near future, polar ecosystems may change enough to

become *undersaturated* with respect to CaCO₃ minerals (Feely et al., 2009; Orr et al., 2005; Steinacher et al., 2010), owing to the large amount of CO₂ already dissolved in high-latitude ocean areas. When waters are undersaturated, CaCO₃ minerals will not precipitate. Even though low-latitude ocean areas will not become undersaturated with CaCO₃ minerals in the future, pH conditions will exceed or have already exceeded the bounds of observed natural variability (see Figure 17.4, p. 697; Sutton et al., 2016), exposing low-latitude organisms such as warm-swath coral reefs to chemical conditions suboptimal for growth and calcification (Fabricius et al., 2011).

17.4 Terrestrial Consequences of Rising CO₂

The CO₂ fertilization effect is defined in SOCCR1 as the “phenomenon in which plant growth increases (and agricultural crop yields increase) due to the increased rates of photosynthesis of plant species in response to elevated concentrations of CO₂ in the atmosphere.” SOCCR1 concluded that the CO₂ fertilization effect was widespread, but whether enhanced photosynthesis would translate into a persistent land carbon sink was unclear (CCSP 2007). The global land carbon sink, calculated as the difference between human emissions and carbon accumulating in the atmosphere and ocean, has grown from 0.2 ± 0.5 petagrams of carbon (Pg C) per year in the 1960s to 3.0 ± 0.7 Pg C per year in 2014 (Le Quéré et al., 2015). This change consists of the effects of land-use change and the residual land sink (Le Quéré et al., 2016). The residual carbon sink is carbon that is stored on land but is calculated as the remainder of other observed carbon sinks rather than observed itself. Growth in the residual sink is attributed to global changes in CO₂, nitrogen deposition, and climate in both observational studies and modeling efforts (Ballantyne et al., 2012; Le Quéré et al., 2016; Schimel et al., 2015). However, predicting how the land carbon sink will respond to changing atmospheric CO₂ is challenging because the land sink is inferred by accounting rather than experimental testing. The research community has evaluated the CO₂ fertilization effect through experimental



Box 17.1 Short-Term Physiological Effects of CO₂ on Plants

Studies lasting from weeks up to more than a decade show that the response of vegetation to rising carbon dioxide (CO₂) is influenced by climate and environmental changes, which create complex feedbacks to the carbon cycle. Carbon gains from CO₂ fertilization lead to faster cycling or more carbon storage. The balance of the effects of climate and CO₂ fertilization on terrestrial carbon storage is uncertain.

Physiological Adjustment to Rising CO₂

Increased Photosynthesis per Leaf Area

- More efficient plants lead to increased biomass or increased rate of biomass cycling.
- Faster plant growth leads to limitation by nutrients or greater investment in roots (or both).
- Larger or faster-growing plants lead to greater carbon inputs into soil.

Decreased Water Conductance per Leaf Area

- Increased photosynthesis and decreased water use increase plant water-use efficiency.
- Reduced investment in photosynthetic enzymes increases plant nitrogen-use efficiency.
- Reduced investment in photosynthetic enzymes may result in total or partial loss of the fertilization effect.

Plant Species Responses

- Plants with CO₂-concentrating mechanisms (i.e., C₄ or crassulacean acid metabolism [CAM] plants) experience higher water-use efficiency but no direct effect on photosynthesis.
- Changing competition may result in new plant communities.
- Young, actively growing forests may represent an upper bound to increased productivity; there is little demonstrated enhancement of mature, slow-growing forests.
- Fast-growing species (e.g., weeds) may see more enhancement than slow-growing species.

Food and Crop Responses

- Decreased plant enzymes mean that herbivores need to harvest more leaf area to eat the same amount of protein.
- For the same input, crop yields likely will increase, while the protein content of crops probably will decrease.
- Pollen production may increase.

manipulations such as Free-Air CO₂ Enrichment (FACE) projects (see Figure 17.1, p. 693), tree rings, observational networks, and modeling experiments.

Plants take up carbon through the process of photosynthesis and synthesize biomass (e.g., leaves, wood, and roots) from simple, carbon-rich sugars derived from CO₂. As CO₂ increases in the atmosphere, plants can photosynthesize more quickly. Plants take up CO₂ through the same pores (stomata) from which they lose water, leading to a balance between CO₂ uptake and water loss. Rising CO₂ increases carbon uptake per unit of water lost, allowing plants

to close their stomata and therefore become more efficient in water usage (see Box 17.1, Short-Term Physiological Effects of CO₂ on Plants, this page). These physiological effects play out differently in different types of plants and under different environmental conditions. Twenty years of CO₂-enrichment experiments have shown that elevated CO₂ enhances photosynthetic carbon gain over the long term for certain ecosystem types but only over the short term for others (Leakey et al., 2009; Leuzinger et al., 2011; Norby and Zak 2011). Plant communities dominated by trees and grasses generally show greater stimulation of photosynthetic carbon uptake compared to



that of legumes, shrubs, and nonleguminous crops (Ainsworth and Rogers 2007).

Net primary production (NPP) is calculated as either the balance between carbon gained through photosynthesis and lost through respiration or the sum of all growth over a year. With increased CO_2 , NPP is enhanced by ~23% across a broad range of early successional forests (Norby et al., 2005). These results probably are not indicative of all forests, and smaller responses have been observed in the limited number of studies carried out in old-growth temperate, boreal, and tropical forests (Hickler et al., 2008; Körner et al., 2005). Also clear is that the temporal pattern of NPP responses to elevated CO_2 differs among forests (e.g., McCarthy et al., 2010; Norby et al., 2010).

Plants balance carbon gain and water loss. Stomatal conductance is depressed at elevated CO_2 , so plants may reduce water loss without reducing carbon gain, an observation which has been noted at the leaf and canopy scales (Keenan et al., 2013; Leakey et al., 2009; Peñuelas et al., 2011). Observations of decreased canopy evapotranspiration at elevated CO_2 are therefore coupled with those of increased soil moisture. Crop carbon accumulation and water-use efficiency can be enhanced under drought conditions (Blum 2009; Morison et al., 2008), but extreme droughts may reduce or eliminate these enhancements (Gray et al., 2016).

Plant growth over years is not limited by CO_2 alone (Körner 2015). If another environmental factor limits growth, then experimentally increasing CO_2 causes diminished enhancement of photosynthesis and plant production (Ainsworth and Long 2005; Ainsworth and Rogers 2007). For example, nitrogen is sequestered in long-lived biomass and soil pools and may not always be readily available to plants. In this case, nitrogen limitation inhibits increases in plant production associated with elevated CO_2 , a process which is referred to as a negative feedback. In systems where nitrogen cycling did not reduce sink strength, the effects of CO_2 fertilization on increasing NPP persisted (Drake

et al., 2011; Finzi et al., 2006). The effects of rising CO_2 on tree biomass may be inferred from tree-ring records, but results are mixed; some studies show no effect from changing CO_2 , and others show increased growth or water-use efficiency (Andreu-Hayles et al., 2011; Cole et al., 2009; Knapp and Soulé 2011; Koutavas 2013).

Because of these complications, whether rising CO_2 will lead to larger standing biomass and carbon storage is unclear, in part because of the enormous complexity of the entire system (Norby and Zak 2011; Leuzinger and Hattenschwiler 2013). While instantaneous and annual fluxes of carbon are well studied in the FACE literature, the allocation of carbon to stems, roots, and leaves, for example, varies among experiments (DeLucia et al., 2005), and enhancement of multidecadal carbon stocks (e.g., woody biomass and soil organic matter) is not well studied (Leuzinger and Hattenschwiler 2013; Norby and Zak 2011). Increased carbon supply from plants can lead to heightened activity of soil fauna and more rapid cycling of carbon rather than increased carbon storage in soils (Phillips et al., 2012; van Groenigen et al., 2011, 2014). Because observed changes in soil carbon were small over the timescale of the FACE studies (3 to 16 years), firm conclusions about the impact of elevated CO_2 on soil carbon remain elusive (Luo et al., 2011). In general, research suggests that large effects of rising CO_2 on carbon storage in soils are limited (Schlesinger and Lichter 2001), although the combined effects of CO_2 and nitrogen deposition and rising temperatures may significantly affect soil carbon loss (Zhou et al., 2016).

17.5 Carbon Cycle Feedbacks of Rising CO_2

Climate and rising atmospheric CO_2 can alter the amount of carbon taken up or released by ecosystems and the ocean. Rising temperatures influence the response of the carbon cycle to rising CO_2 in diverse and complicated ways, yielding both positive and negative feedbacks (Deryng et al., 2016; Dieleman et al., 2012; Holding et al., 2015). Positive feedbacks tend to be additive of the original effect,



negative feedbacks tend to counteract the original effect. Overall, rising temperatures tend to release more land and ocean carbon into the atmosphere, while rising CO₂ is projected to increase land and ocean uptake (Friedlingstein et al., 2006). However, the importance of this positive feedback is variable according to different locations and time frames. Earth System Model assessments that incorporate carbon cycle feedbacks to projected climate change show that the combined effects of climate change result in an overall larger increase in CO₂ concentrations, thus contributing to additional climate warming (a positive feedback). However, this feedback is highly uncertain due to its dependence on various factors, so different studies may report large ranges in predicted CO₂ concentrations (Blok et al., 2010; Elberling et al., 2013; Hodgkins et al., 2014; McCalley et al., 2014; Schneider von Deimling et al., 2012; Schuur et al., 2009). Temperature also indirectly influences radiative CO₂ effects. For example, increased evaporation from the ocean in a warmer world yields higher atmospheric water vapor concentrations that further amplify the impact of CO₂ on climate warming (Myhre et al., 2013). Another chapter in this report presents a broader discussion of the impacts of multiple environmental changes (see Ch. 19: Future of the North American Carbon Cycle, p. 760).

On land, the direct effect of rising CO₂ on plant photosynthesis and growth interacts with rising temperature (Gray et al., 2016; Zhu et al., 2016). Rising CO₂ increases the photosynthetic temperature optimum (Long 1991) because of the decreasing relative solubility of CO₂ versus oxygen at higher temperatures (Jordan and Ogren 1984). While photosynthesis, respiration, and decomposition sensitivities to temperature act on short timescales of decades, chemical weathering sensitivities act over several hundred thousand years and are largely responsible for moderating CO₂ levels throughout the geological record. Rising temperatures affect biogeochemical processes through enhanced NPP, faster microbial decomposition of organic matter and increased emissions of CO₂ from microbial respiration in soils, and increased rates of chemical

weathering (Galloway et al., 2014). However, interactions between rising CO₂ and temperature are complicated by nonuniform warming patterns, and research shows that climate warming can either stimulate or suppress plant productivity depending on the season and region (Xia et al., 2014). In the cryosphere, higher temperatures thaw permafrost and melt ice, processes which release stored CO₂ and CH₄ back into the atmosphere (Schneider von Deimling et al., 2012).

Chemical weathering of minerals, which consumes CO₂ from the atmosphere, provides an important feedback mechanism for CO₂ in the carbon cycle (Berner 1992; Colbourn et al., 2015; Kump et al., 2000; see Ch. 12: Soils, p. 469). Carbon dioxide is found in soils and surficial deposits because of plant and microbial respiration as well as chemical weathering of minerals. Carbonic acid, which is formed naturally when CO₂ becomes dissolved into infiltrating rainwater, can dissolve primary minerals, a process that consumes CO₂. Also, CaCO₃ may precipitate in soils and surficial deposits if concentrations are high enough, a process that may be enhanced by low soil moisture and in semiarid and arid climates (Berner 1992). The rates of mineral reactions depend on several factors, including temperature, pressure, and mineral saturation state, all of which are influenced by climate. As temperatures rise, weathering rates of most minerals increase, leading to greater CO₂ consumption (Brady and Carroll 1994; Velbel 1993). Precipitation (e.g., rain and snowmelt) flushes solutes away, lowering the saturation state for primary minerals in solution, thereby promoting higher mineral weathering rates (Clow and Mast 2010; Kump et al., 2000). Thus, greater precipitation would lead to lower mineral saturation states, higher weathering rates, and greater CO₂ consumption (Clow and Mast 2010). These feedback mechanisms have the potential to help mitigate the effects of rising atmospheric CO₂ concentrations, but their effects will vary spatially and temporally in concert with changes in temperature and precipitation. For example, while the northeastern United States may see relatively strong increases in weathering rates because of increasing



temperature and precipitation (IPCC 2013), the Southwest might experience more mixed impacts because of increasing temperature but decreasing precipitation (IPCC 2013).

17.6 Consequences for Ecosystem Services

Oceanic ecosystem services critical for human survival, such as the provision of fish and seafood, carbon storage, coastal protection by reefs, and climate modulation, face significant risks from the combined effects of ocean acidification, warming, and sea level rise (Gattuso et al., 2015). Under the current rate of CO₂ emissions, most marine organisms evaluated to date will face a very high risk of impacts by 2100, and some, including coral reefs (Hughes et al., 2017; Ainsworth et al., 2016; Hughes et al., 2018) and bivalve shellfish (Kroeker et al., 2013), already face moderate to high risk today (Gattuso et al., 2015; see Figure 17.5, p. 704). For future scenarios without significant mitigation of CO₂ emissions, predicted impacts to ocean ecosystem services are moderate for the early decades of this century but put all ecosystem services at high or very high risk by 2100 (Gattuso et al., 2015).

17.6.1 Biodiversity

Rising CO₂ will affect species differentially. Described here are the direct effects of rising CO₂ rather than the impacts of warming, which are discussed comprehensively in CSSR (USGCRP 2017). Acidification by CO₂ has been associated with a decline in shell-bearing benthic organisms (Hall-Spencer et al., 2008; Kroeker et al., 2011). Declines in oyster spat survival at a commercial hatchery in the U.S. Pacific Northwest that temporarily jeopardized the region's oyster aquaculture industry have been definitively attributed to ocean acidification (Barton et al., 2015). Laboratory studies and meta-analyses have provided evidence for and against detrimental effects on marine biodiversity (Bijma et al., 2013; Dupont et al., 2010; Hendriks and Duarte 2010; Hendriks et al., 2010). Foundational organisms such as microbial populations, while not deeply studied, also demonstrate a range of positive

to negative responses to ocean acidification (Bunse et al., 2016). The effects of ocean acidification on marine ecosystem structure are only now being identified. Models simulating ocean acidification's impacts on bivalve shellfish have shown a restructuring of the entire California Current ecosystem by a combination of indirect predator-prey effects (Busch et al., 2013; Kaplan et al., 2010). Another model showed substantial restructuring of phytoplankton communities under ocean acidification and warming (Dutkiewicz et al., 2015), but studies still have not determined whether this restructuring would have significant effects on phytoplankton community function or food-web relationships.

On land, elevated atmospheric CO₂ studies have demonstrated that seed yield can be increased (LaDeau and Clark 2001, 2006). In some crop species, increased seed production was accompanied by reduced quality (Ainsworth et al., 2002) but not in tree species (Way et al., 2010). Species show different growth responses to rising CO₂ (Dawes et al., 2011), possibly giving dominant plants an advantage (McDonald et al., 2002; Moore et al., 2006) and leading to changes in forest structure. However, the impact on biodiversity will depend on ecological responses that will remain uncertain without long-term study of ecological responses to rising CO₂ (Alin et al., 2015; Carey and Cottingham 2016; Elmendorf et al., 2016; Schimel et al., 2011).

17.6.2 Food and Fiber Provision

Ocean acidification is likely to have long-term effects on the population and diversity of fish and invertebrates, including economically and ecologically important shellfish (Pörtner et al., 2004). Although difficult to untangle, the combined effects of resource competition, pollution, overfishing, habitat modification, acidification, water temperature increases, and climate-driven changes on small-scale fisheries and aquaculture are likely to result in widespread changes in ocean ecosystems and in the fisheries themselves (HLPE 2014).

The impacts of ocean acidification on the food value, quality, and market value of marine species

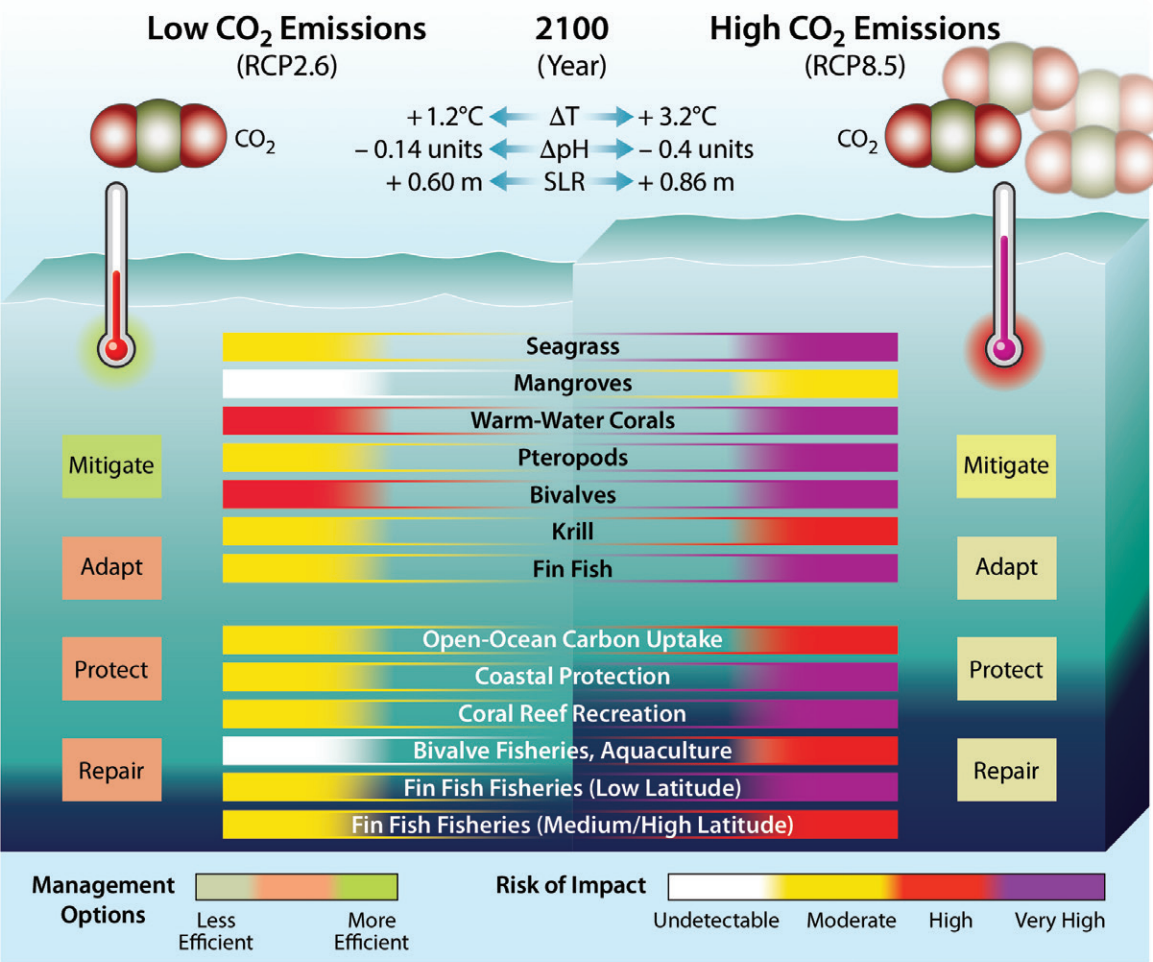


Figure 17.5. Ocean Impacts Projected by High and Low Carbon Dioxide (CO₂) Emissions Scenarios. Impacts on organisms and ecosystem services are shown—along with effects of acidification, warming, and sea level rise on ocean physics and chemistry—for both a low CO₂ emissions scenario (Representative Concentration Pathway [RCP]2.6), and for a high CO₂ scenario (RCP8.5). (See Ch. 19: Future of the North American Carbon Cycle for RCP explanations, p. 760.) Physical impacts on the ocean due to higher atmospheric CO₂ levels are largely related to the climatic effects of CO₂ and other radiatively active, anthropogenically released gases. These impacts include higher sea levels and shallower oceanic mixing (right-side water column, shown by a taller water level and shallower light aqua mixed layer). More severe risks of impacts from higher oceanic CO₂ levels on ocean taxa (top group, black text) in higher CO₂ emissions scenarios (center right) correspond to higher risks of impacts on ecosystem services (bottom group, white text, center right). Management options (i.e., activities that will mitigate, adapt, protect, or repair marine systems) are more numerous and more effective in lower CO₂ scenarios (far left) compared with those in a higher CO₂ world (far right). [Figure source: Adapted from Gattuso et al., 2015.]

have yet to be conclusively determined. One preliminary study (Dupont et al., 2014) notes that the taste and texture of pink shrimp (*Pandalus borealis*) were poorer when the shrimp had been raised under more acidified conditions. Assuming that ocean

acidification slows the growth of bivalve shellfish in the wild as it does in laboratory studies (Kroeker et al., 2013), harvest of the largest size class of sea scallop meat, which fetches a market price premium, is projected to decline under acidification (Cooley



et al., 2015). The growth-retarding effects of acidification on king and Tanner crab as reported by Long et al. (2013a, 2013b) are projected to harm fishery revenues (Punt et al., 2016), but the implications of acidification for the market quality of Alaskan crabs (e.g., taste and texture) are not yet known. If the laboratory and model results reviewed above hold true in natural ecosystems, ocean acidification is likely to decrease the volume or quality of marine harvests beyond simply the impacts on oyster aquaculture observed to date. The larval production shortage in the mid-2000s experienced by the Pacific Northwest oyster aquaculture industry that was conclusively attributed to ocean acidification remains the bellwether example of impacts to fisheries from rising CO₂ (Barton et al., 2015).

Terrestrial provisioning services (e.g., crops and livestock) also are responding to rising CO₂. For example, crop production increased in response to experimentally elevated CO₂ (Leakey et al., 2009), but increases in crop yield were accompanied by decreases in seed quality (Myers et al., 2014). Physiological changes also led to increased herbivory in some crops (DeLucia et al., 2012; Dermody et al., 2008). The effects of rising CO₂ on crop yield are tempered by other global changes. Corresponding increases in ground ozone decreases productivity (Morgan et al., 2006), and increased drought may remove the positive effects of rising CO₂ entirely (Gray et al., 2016). Carbon dioxide fertilization can have either direct or indirect consequences on agriculture. At higher levels of atmospheric warming and at low latitudes, model simulations show significant reductions in yields for all major crops, even with the positive benefits of CO₂ fertilization (Challinor et al., 2014). Indirect effects of rising CO₂ include the reduction in nutrient content and digestibility of pasture for livestock (Tubiello et al., 2007) and reductions in protein content by 10% to 14% in the edible portions of wheat, rice, barley, and potato and by 1.5% in soybeans (Müller et al., 2014; Taub et al., 2008).

Terrestrial food and fiber production over the next century may be more profoundly influenced by

climate change than by rising CO₂ itself. Climate changes could include heatwaves during growing seasons, droughts and lengthening of dry spells, and rising sea levels (Melillo et al., 2014; Nelson et al., 2014; Wiebe et al., 2015). The greater the greenhouse gas concentrations, the greater the change in the climate and climate-associated risks for agriculture and food security (Brown et al., 2015).

17.6.3 Carbon Storage in Vegetation and Soils

Vegetated coastal ecosystems store CO₂ in seagrasses, marshes, kelp, and mangroves at rates comparable with those of forest ecosystems (McLeod et al., 2011). This “blue carbon” is believed to be an important sink for atmospheric CO₂, but coastal habitats are under strong human-driven pressures worldwide including habitat destruction, rising ocean temperatures, sea level rise, and sediment starvation (see Ch. 15: Tidal Wetlands and Estuaries, p. 596). For example, erosion of coastal wetlands or thawing of coastal Arctic permafrost exposes buried organic carbon, which can either be respired *in situ* to release CH₄ or CO₂, exacerbating atmospheric warming, or be released to nearshore waters and respired there, contributing to local acidification (Aufdenkampe et al., 2011; see Ch. 11: Arctic and Boreal Carbon, p. 428). Seagrasses may help mitigate ocean acidification locally (Hendriks et al., 2014), underscoring the double benefit of protecting blue carbon habitats.

Carbon on land is stored in vegetation and soils. Forests account for approximately 66% of the land carbon sink (see Ch. 2: North American Carbon Budget, p. 71, and Ch. 9: Forests, p. 365), a percentage which could increase if strategies were applied to minimize forest losses from deforestation. However, carbon sinks change with the age of forest regrowth—the rate of carbon accumulation is rapid in young forests but typically quite low in old-growth forests. Restoring the organic content of agricultural and natural soils also can increase soil carbon storage (Lal 2003). Historically, soils have lost vast amounts of carbon when transitioning from natural to human-modified landscapes (e.g.,



through urbanization and forest and agricultural management; see also Ch. 5: Agriculture, p. 229, and Ch. 12: Soils, p. 469), but gauging the effect of land management on carbon storage is challenging. The land carbon sink is calculated using bookkeeping methods that sum together carbon into different respective ecosystem compartments (e.g., land, ocean, and atmosphere) at a variety of scales. The carbon sink is typically inferred by the existence of a residual (i.e., unaccounted) sink in the global carbon budget. Therefore, the effects of land management can be difficult to detect and attribute using carbon balance accounting methods (Erb et al., 2013).

17.6.4 Coastal Protection by Corals

In low-latitude areas around the world, coral reefs are particularly important for protecting coastlines, but the combined effects of rising temperature and ocean acidification slow the growth of stony coral reefs (Muehllehner et al., 2016; Wong et al., 2014), hindering their ability to grow or recover from damage (Hughes et al., 2017; Ainsworth et al., 2016; Hughes et al., 2018). Carbonate sediments also are being dissolved by ocean acidification, while sea level also rises; the net effect has accelerated the relative rate of sea level rise near Florida, Hawai'i, and the U.S. Virgin Islands, exposing those coastal communities to heightened risk of flooding (Yates et al., 2017). Globally, the loss of the three-dimensional structure of the reef could expose 200 million people to greater effects of storms and tsunamis (Ferrario et al., 2014). People living in the low-elevation coastal zone (LECZ), below 10 m in elevation (Vafeidis et al., 2011), face a higher risk of coastal hazards such as flooding and sea level rise due to climate change (Lichter and Felsenstein 2012). In the United States, population in the LECZ is forecast to increase by 188% from 23 million in 2000 to 44 million in 2060 (Neumann et al., 2015), so losses of coral reefs that protect coastlines heighten overall coastal community risk.

17.6.5 Water Availability

Reduced transpiration due to increased plant water-use efficiency (Leakey et al., 2009; Norby and Zak

2011) may allow more water to pass through soils and enter freshwater ecosystems. As discussed in Ch. 13: Terrestrial Wetlands, p. 507, and Ch. 14: Inland Waters, p. 568, inland waters act as hotspots for the degradation and outgassing of carbon originating from both terrestrial and aquatic sources. Increases in precipitation events, along with reductions in transpiration (Charney et al., 2016; van der Sleen et al., 2014), may facilitate the movement of materials from the landscape into water systems, altering ecosystem structure and function as seen extensively on Lake Erie (Smith et al., 2015). Conversely, the drying of systems that receive less precipitation will dramatically influence the timing of rainfed and snowmelt-driven ecosystems and municipalities reliant on surface waters for agriculture, fisheries, industry, and drinking water (Clow et al., 2010; Rao et al., 2004).

17.7 Synthesis, Knowledge Gaps, and Outlook

17.7.1 Current State of Knowledge

The rise of atmospheric CO₂—attributable primarily to human-caused fossil fuel emissions and land-use change—has been dampened by carbon uptake by the ocean and terrestrial biosphere. Nevertheless, today's atmospheric CO₂ levels are higher than at any time in at least the past 800,000 years (Hönisch et al., 2012). Uptake of this fossil fuel CO₂ has caused documented direct and indirect effects on terrestrial and oceanic systems and processes in different regions of North America and the rest of the planet. The capacity of these systems to continue to act as carbon sinks is not certain because the systems are dynamic and influenced by feedbacks related to CO₂ levels (see Section 17.3, p. 695). Another major set of consequences stems from the atmospheric warming caused by rising CO₂; weather and climate changes affect nearly every terrestrial and oceanic process (see Section 17.3–17.5) and often lead to additional feedbacks. Although reviewed in detail in other reports, including the IPCC AR5 (IPCC 2013) and CSSR (USGCRP 2017), these consequences deserve mention here because of their combined effects



with CO₂ on systems and processes throughout the land and ocean domains.

17.7.2 Key Knowledge Gaps and Opportunities

Research has uncovered many of the direct and indirect responses of natural systems to rising CO₂, but mechanisms often remain unclear. Since the SOCCR1 report, increasing computational power has enabled the development of complex models to examine the consequences of rising CO₂ and a changing carbon cycle. Observational and modeling studies, such as the new generation of FACE experiments now underway, are being planned in concert to enable strategic data collection. Some of these approaches allow for limitations of multiple resources (e.g., nitrogen and phosphorus), which could lead to more realistic projections of the terrestrial carbon sink's response to rising CO₂. As Figure 17.1, p. 693, illustrates, there are current FACE experiments in the Northwest, Northeast, Southern Plains, or any tropical ecosystem within the U.S. territories. While most experiments are in mesic (wet) or temperate ecosystems (see Figure 17.6, p. 708), understanding the response of tropical forests or coniferous boreal forests is critical to account for carbon cycle feedbacks. Oceanic models are providing insight into ecosystem relationships and dynamics under global change and into the biophysical underpinnings of ocean-atmosphere interactions. Despite these insights, knowledge of how multiple global change factors affect modeled processes would greatly improve model forecast ability. In contrast, most experimental manipulations are single-factor experiments in which only one variable is manipulated.

Disentangling the impacts of rising CO₂ and other concurrent changes in climate, land use, nutrient cycles, and atmospheric chemistry across all ecosystems likely requires long-term, sustained carbon cycle observations and monitoring of ecosystem and socioeconomic consequences. Long-term observing networks are critical to managing ecosystems sustainably and adaptively (e.g., Schindler and Hilborn 2015), and a focus on data management and interoperability across data platforms would improve understanding of long-term responses to rising CO₂ (Ciais et al., 2014). Few experiments on land or in the ocean extend to a decade in length, and therefore the long-term ecosystem responses are not clear.

Pörtner et al. (2014) conclude that there is medium to high agreement that ecosystem services will change. However, the effects of rising CO₂ on biodiversity and vegetation changes after disturbance remain poorly understood and could result in altered ecosystem function and different ecosystem services. This lack of understanding also limits the ability to anticipate recovery from acute disturbances such as storms, fires, disease, or insect outbreaks.

As forecasts of future conditions improve, investigating past conditions on Earth is still important. Over short timescales, historical terrestrial work is limited to studies that involve reconstructions of plant growth (e.g., tree rings). Exploring historical conditions decades or centuries before via ice core analysis, seafloor sediment core studies, and geological research will continue to uncover aspects of prior ages that are analogous to today, aiding the anticipation of potential changes in the Earth system as global change continues.

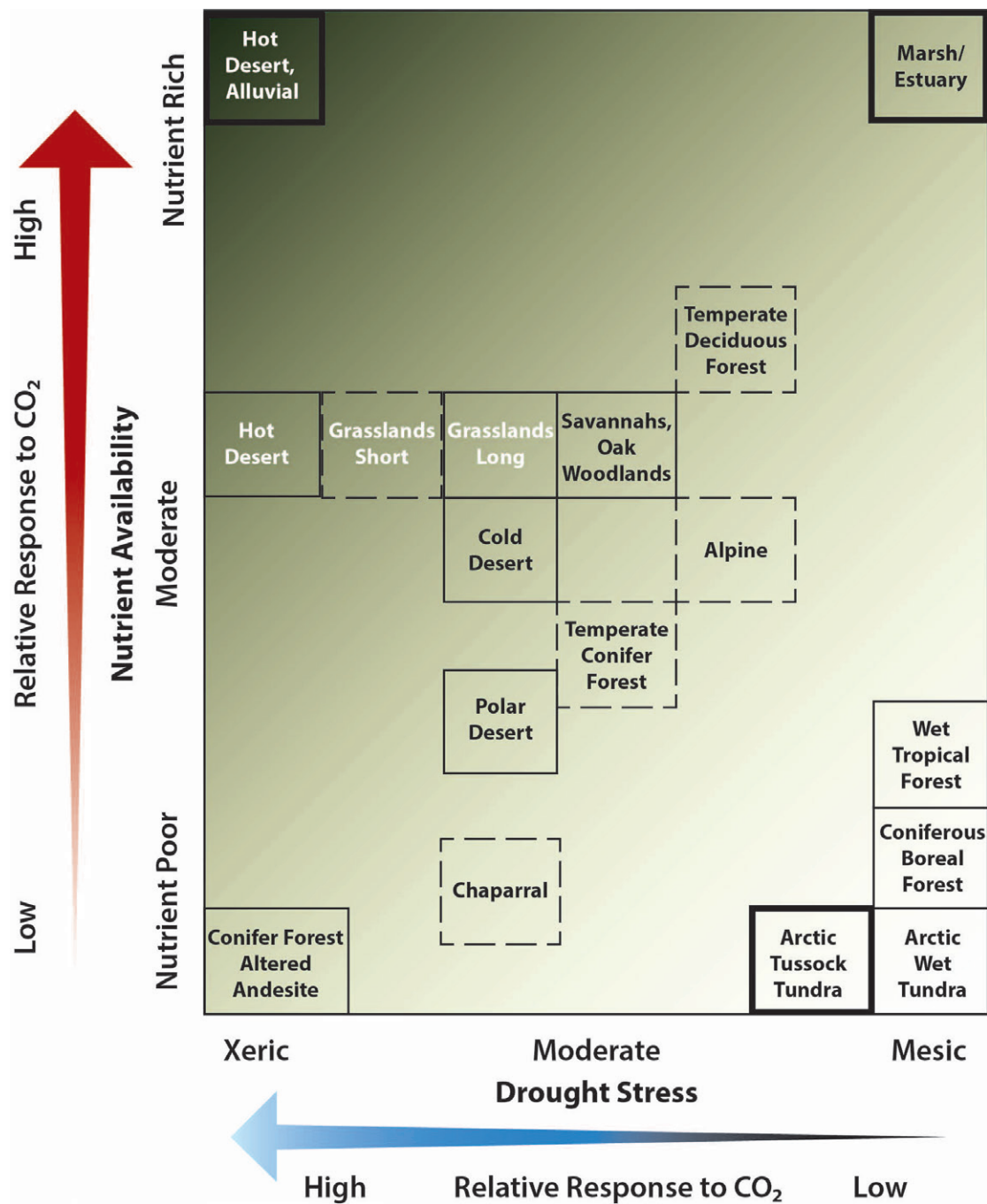


Figure 17.6. Hypothesized Ecosystem Responses to Elevated Carbon Dioxide (CO₂) Relative to Nutrient and Water Availability. Field studies, including Free-Air CO₂ Enrichment (FACE) experiments, have been conducted in desert, grasslands, chaparral, alpine, and temperate deciduous forests but not in tropical forests or coniferous boreal forests. Increasingly darker green indicates greater relative response to CO₂, based on the assumptions that response increases with drought stress and with nutrient availability. [Figure source: Reprinted from Norby et al., 2016 (originally adapted from Mooney et al., 1991).]



SUPPORTING EVIDENCE

KEY FINDING 1

Rising carbon dioxide (CO₂) has decreased seawater pH at long-term observing stations around the world, including in the open ocean north of Oahu, Hawai‘i; near Alaska’s Aleutian Islands; on the Gulf of Maine shore; and on Gray’s Reef in the southeastern United States. This ocean acidification process has already affected some marine species and altered fundamental ecosystem processes, and further effects are likely (*high confidence, likely*).

Description of evidence base

The atmospheric record indicates that both the ocean and land carbon sinks have increased as CO₂ has risen (Le Quéré et al., 2016). Modern-day ocean observations have confirmed that seawater pH is decreasing because of atmospheric CO₂ uptake (Feely et al., 2004, 2009; Gattuso et al., 2015; Orr et al., 2005). Time-series stations around North America (near Hawai‘i, Alaska, Washington, California, Georgia, and Maine) have documented decreased pH below preindustrial levels for some or all of the annual cycle (Sutton et al., 2016). Effects on marine life and fundamental ecosystem processes or characteristics, including calcification, biodiversity, growth rates, and nitrogen fixation, are reviewed in this chapter; they are documented in detail in Bijma et al. (2013), Bunse et al. (2016), Dupont et al. (2010), Fu et al. (2007, 2012), Hendriks and Duarte (2010), Hendriks et al. (2010), Hofmann et al. (2010), Hutchins et al. (2013), Kroeker et al. (2013), Meyer and Riebesell (2015), Riebesell and Tortell (2011), and Riebesell et al. (2007), among others. Future effects are projected by observational (Pespeni et al., 2013; Wootton et al., 2008), integrative (Boyd et al., 2014), and modeling (Dutkiewicz et al., 2015) studies.

Major uncertainties

In most cases, observed biological effects have not been mechanistically attributed to pH or carbonate and bicarbonate ion concentration changes. Laboratory studies may not perfectly reproduce the responses of organisms in nature, where environments and drivers are more complex and numerous. Genetic, behavioral, and phenotypic plasticity (flexibility) have not been evaluated for most of the species investigated in laboratory studies.

Estimated likelihood of impact or consequence, including short description of basis of estimate

Variation within populations (plasticity) and the existence of many competing environmental drivers could offset the effects of ocean acidification on some marine populations, but to an uncertain extent. Research has demonstrated effects on large groups of marine organisms (e.g., bivalve shellfish and stony corals) unambiguously enough to ascertain that continuing negative impacts to these communities are likely.

Summary sentence or paragraph that integrates the above information

Rising CO₂ has decreased seawater pH (*very high confidence*). This process of ocean acidification has affected some marine species (*very high confidence*) and altered fundamental ecosystem processes (*high confidence*), with further effects likely (*high confidence*). Continuing impacts are probable, but plasticity and the existence of other environmental drivers could offset the effects of ocean acidification on some marine populations to an uncertain extent.



KEY FINDING 2

While atmospheric CO₂ rises at approximately the same rate all over the globe, its non-climate effects on land vary depending on climate and dominant species. In terrestrial ecosystems, rising atmospheric CO₂ concentrations are expected to increase plant photosynthesis, growth, and water-use efficiency, though these effects are reduced when nutrients, drought, or other factors limit plant growth (*very high confidence, very likely*). Rising CO₂ would likely change carbon storage and influence terrestrial hydrology and biogeochemical cycling, but concomitant effects on vegetation composition and nutrient feedbacks are challenging to predict, making decadal forecasts uncertain.

Description of evidence base

Research definitively shows that the bodies of marine and terrestrial organisms have incorporated CO₂ released from the burning of fossil fuels, based on the change in isotope ratios within their biological material (Fraile et al., 2016; Hilton et al., 2006; Suess 1955).

On land, the historical record of the impact of rising CO₂ is more complex. Physiological theory suggests that, as CO₂ rises, photosynthesis should increase. Using preserved plant specimens, isotopomer analysis appears to support this physiological prediction (Ehlers et al., 2015), though this is a novel technique. The effects of rising CO₂ on tree biomass over multiple decades may be inferred from tree-ring records, but they provide mixed results (Andreu-Hayles et al., 2011; Cole et al., 2009; Knapp and Soule 2011; Koutavas 2013). Studies from a wide range of forest types across broad geographic regions have observed changes in the ratio of the ¹³C isotope to the ¹²C isotope ($\delta^{13}\text{C}$), observations which imply trees have experienced increased water-use efficiency as CO₂ has risen over the last two centuries, but growth was not clearly stimulated by rising CO₂ (Peñuelas et al., 2011).

Rising CO₂ tends to make plants close their stomata and thus use water more efficiently. The primary enzyme responsible for CO₂ uptake, ribulose-1,5-bisphosphate carboxylase-oxygenase (RUBISCO), accounts for a substantial portion of every plant's nitrogen requirement. As CO₂ rises, less RUBISCO is required for the same carbon gain, so plants become more efficient in nutrient use. These physiological effects play out differently in various types of plants and under diverse environmental conditions. Plants that lack a CO₂ concentration mechanism and pass a 3-carbon sugar molecule into the Benson-Calvin cycle (C₃ plants) are more likely to show an instantaneous photosynthetic response than plants with a CO₂ concentration mechanism like C₄ plants (that pass a 4-carbon sugar molecule to the Benson-Calvin cycle) or those that use crassulacean acid metabolism (CAM).

Twenty years of CO₂ enrichment experiments have shown that elevated CO₂ enhances photosynthetic carbon gain over the long term for certain ecosystem types but only over the short term for others (Leakey et al., 2009; Leuzinger et al., 2011; Norby and Zak 2011). Plant communities dominated by trees and grasses generally have shown greater stimulation of photosynthetic carbon uptake compared to that of legumes, shrubs, and nonleguminous C₃ crops (Ainsworth and Rogers 2007).

Net primary production (NPP) is calculated as either the balance between carbon gained through photosynthesis and lost through respiration or the sum of all growth over a year. NPP is



enhanced by ~23% across a broad range of early successional forests in response to elevated CO₂ (Norby et al., 2005). These results are likely not indicative of all forests, and smaller responses have been observed in the limited number of studies carried out in old-growth temperate, boreal, and tropical forests (Hickler et al., 2008; Körner et al., 2005). Also clear is that the temporal pattern of NPP responses to elevated CO₂ differs among forests. For example, McCarthy et al. (2010) reported that NPP in coniferous forests was enhanced by 22% to 30% and sustained over 10 years of exposure to 550 parts per million (ppm) of CO₂. In contrast, Norby et al. (2010) found that NPP was significantly enhanced for 6 years in hardwood forest plots exposed to 550 ppm CO₂ (compared with plots under current ambient CO₂), after which time the enhancement of NPP under elevated CO₂ declined from 24% to 9%.

Plants balance carbon gain and water loss. Stomatal conductance is depressed at elevated CO₂, so plants may reduce water loss without reducing carbon gain. This physiological effect has been observed at the leaf and canopy scales (Keenan et al., 2013; Leakey et al., 2009; Peñuelas et al., 2011) and represents the major mechanism leading to observations of decreased canopy evapotranspiration under elevated CO₂. For the hydrological cycle, this mechanism results in increased soil moisture. Even plants with CO₂ concentration mechanisms (i.e., C₄ and CAM plants) may experience increased water-use efficiency without any direct stimulation in photosynthesis (Leakey et al., 2009). Under drought conditions, elevated CO₂ may not directly stimulate photosynthesis in C₄ plants but can indirectly increase carbon gain by increasing water-use efficiency.

Physiological theory and experimental evidence indicate that rising CO₂ increases the photosynthetic temperature optimum (Long 1991) because of the decreasing relative solubility of CO₂ versus oxygen at higher temperatures (Jordan and Ogren 1984). These results imply that biomes that experience high temperatures may experience disproportionately enhanced photosynthesis and growth. Interannual variation in the increased growth of Loblolly pine trees was disproportionately enhanced by experimentally elevated CO₂ in warmer years (Moore et al., 2006).

Plant growth is not limited by CO₂ alone (Körner 2015). If, for example, another environmental factor limits growth, then experimentally increasing CO₂ has reduced effects on photosynthesis and growth (Ainsworth and Rogers 2007). This outcome is called “sink limitation.” Research suggests that nitrogen limitation may be one mechanism leading to declining NPP responses to elevated CO₂ in some ecosystems (Norby et al., 2010).

Nitrogen is sequestered in long-lived biomass and soil pools and may not be readily available to plants under some conditions. In this case, nitrogen limitation inhibits increases in plant production associated with elevated CO₂, an effect which is referred to as a negative feedback. In systems where nitrogen supply was sufficient, CO₂ fertilization effects on NPP persisted (Drake et al., 2011; Finzi et al., 2006). Nevertheless, elevated CO₂ also increases photosynthetic nitrogen-use efficiency, defined as the net amount of CO₂ assimilated per unit of leaf nitrogen (Ainsworth and Rogers 2007; Bader et al., 2010; Leakey et al., 2009).

Elevated atmospheric CO₂ experiments have demonstrated that seed yield can be increased (LaDeau and Clark 2001, 2006). In some crop species, increased seed production was accompanied by reduced quality (Ainsworth et al., 2002), but this was not observed in tree species (Way et al., 2010). Species show different growth responses to rising CO₂ (Dawes et al., 2011), and



dominant plants may have an advantage with rising CO₂ (McDonald et al., 2002; Moore et al., 2006), leading to changes in forest structure.

Major uncertainties

Unclear is whether rising CO₂ will lead to larger standing biomass and carbon storage or simply faster cycling of carbon (Norby and Zak 2011). While instantaneous and annual fluxes of carbon are well studied in the Free-Air CO₂ Enrichment (FACE) literature, the allocation of carbon to different pools varies between experiments (DeLucia et al., 2005), and enhancement of multidecadal carbon stocks (e.g., woody biomass and soil organic matter) is not well studied (Leuzinger and Hattenschwiler 2013; Norby and Zak 2011). Plant growth is increased by CO₂, but gross plant respiration is also stimulated (Leakey et al., 2009). Root growth and the incorporation of organic material below ground are observed in response to elevated CO₂ but so too is enhanced soil respiration fueled by releases of carbon from root systems (Drake et al., 2011; Hoosbeek et al., 2007; Jackson et al., 2009; Lagomarsino et al., 2013; Selsted et al., 2012). Increased carbon supply from plants can lead to enhanced activity of soil fauna and more rapid cycling of carbon, rather than increased carbon storage in soils (Phillips et al., 2012; van Groenigen et al., 2011, 2014). Observed changes in soil carbon were small over the timescale of the FACE studies (3 to 16 years), and thus firm conclusions remain elusive (Luo et al., 2011). In general, large effects of rising CO₂ on carbon storage in soils are not expected (Schlesinger and Lichter 2001).

The long-term effects of rising CO₂ are uncertain because there is only one whole-ecosystem study (i.e., of a salt marsh) that extends to 20 years. Instantaneous physiological responses to CO₂ (Farquhar et al., 1980) typically are modified by feedbacks in system-level studies (Leakey et al., 2009; Norby and Zak 2011). Long-term records from tree-ring analyses are limited to reconstructions of aboveground growth. These studies rarely account for changes in carbon allocation strategies (DeLucia et al., 2005; Norby et al., 2010) caused by rising CO₂ or changes in nutrient limitation (Finzi et al., 2006; McCarthy et al., 2010; Zhu et al., 2016) or belowground carbon storage (Drake et al., 2011; Phillips et al., 2012; van Groenigen et al., 2014).

Summary sentence or paragraph that integrates the above information

While CO₂ is rising globally, there is high confidence that its effects on terrestrial ecosystems will vary across spatial scales because the effects of CO₂ on plants vary by species and may be altered by nutrient and water availability. The long-term impacts of rising CO₂ on carbon storage in terrestrial ecosystems are uncertain.

KEY FINDING 3

Consequences of rising atmospheric CO₂ are expected to include difficult-to-predict changes in the ecosystem services that terrestrial and oceanic systems provide to humans. For instance, ocean acidification resulting from rising CO₂ has decreased the supply of larvae that sustains commercial shellfish production in the northwestern United States. In addition, CO₂ fertilization (increases) plus warming (decreases) are changing terrestrial crop yields (*high confidence, likely*).

Description of evidence base

Commercial oyster larvae in the U.S. Pacific Northwest were significantly damaged by ocean acidification, which caused much higher than usual larval mortality for several years in the



mid-2000s (Barton et al., 2015). Harmful impacts on oysters by ocean acidification were well documented (e.g., Kroeker et al., 2013, and references therein). Crop production increased in response to experimentally elevated CO₂ (Leakey et al., 2009), accompanied by decreases in seed quality. Decreased protein content has been documented in wheat, barley, rice, potatoes, and soybeans grown at high CO₂ (Myers et al., 2014; Taub et al., 2008). Physiological changes also led to increased herbivory in some crops (DeLucia et al., 2012; Dermody et al., 2008). Additional effects are expected for human populations via changes in ocean services, as reviewed in Pörtner et al. (2014). Gattuso et al. (2015) completed a literature review, plus expert judgement assessment, to determine the risk that ocean ecosystem services face from the combined effects of ocean acidification and warming.

Major uncertainties

Uncertainty is related to how rising CO₂ may have affected an array of marine and terrestrial harvests and how they may be affected in the future. Evaluating ecosystem services is difficult, and forecasting changes to these services is even more challenging.

Assessment of confidence based on evidence and agreement, including short description of nature of evidence and level of agreement

Very high confidence in the existence and attribution of impacts to increased atmospheric CO₂; medium confidence about future projected impacts on ecosystem services.

Estimated likelihood of impact or consequence, including short description of basis of estimate

Studies have already documented impacts to marine and terrestrial harvests. Whether rising CO₂ will affect all marine and terrestrial harvests is uncertain.

Summary sentence or paragraph that integrates the above information

Rising CO₂ has affected commercial shellfish stocks (very high confidence) and changed crop production yields (very high confidence). Additional consequences expected for human populations include more changes to ecosystem services or changes to benefits that terrestrial and oceanic systems provide to humans (medium confidence). Uncertainty centers around the difficulty of evaluating all exploited species and all ecosystem services and projecting potential future impacts on all of them.

KEY FINDING 4

Continued persistence of uptake of carbon by the land and ocean is uncertain. Climate and environmental changes create complex feedbacks to the carbon cycle; how these feedbacks modulate future effects of rising CO₂ on carbon sinks is unclear. There are several mechanisms that would reduce the ability of land and ocean sinks to continue taking up a large proportion of rising CO₂ (*very high confidence*).

Description of evidence base

Acidification varies depending on latitude because CO₂ solubility depends on temperature, with lower-temperature waters holding more CO₂. Polar ecosystems may become undersaturated with calcium carbonate (Ca₃O²⁻) minerals in the near future (Orr et al., 2005; Steinacher et al., 2010) because of the large amount of CO₂ already dissolved in cold high-latitude ocean areas. Even though low-latitude ocean areas will not become corrosive to Ca₃O²⁻ minerals in the future,



conditions will soon surpass the bounds of natural variability (see Figure 17.4, p. 697). In some places, conditions have already done so (Sutton et al., 2016), exposing low-latitude organisms, such as warm-water coral reefs, to chemical conditions that are considered suboptimal in regard to growth and calcification (Fabricius et al., 2011).

On land, the direct effect of rising CO₂ on plant photosynthesis and growth interacts with rising temperature (Gray et al., 2016; Zhu et al., 2016). Rising CO₂ increases the photosynthetic temperature optimum (Long 1991) because of the decreasing relative solubility of CO₂ versus oxygen at higher temperatures (Jordan and Ogren 1984). Although the sensitivities of photosynthesis, respiration, and decomposition to temperature act on short timescales of decades, chemical weathering sensitivities act over several hundred thousand years and are largely responsible for moderating CO₂ levels throughout the geological record. Higher temperatures affect biogeochemical processes through 1) enhanced NPP; 2) faster microbial decomposition of organic matter involving increased emissions of CO₂ from microbial respiration in soils; and 3) increased rates of chemical weathering, which consumes CO₂ from the atmosphere (Galloway et al., 2014). However, interactions between rising CO₂ and temperatures are complicated by nonuniform climate warming patterns, and research shows that this warming can either stimulate or suppress productivity depending on the season and region (Xia et al., 2014). Higher temperatures and drought have been implicated in widespread tree mortality (Breshears et al., 2009; Allen et al., 2010, 2015), and increased aridity in recent years has had a substantially negative effect on forest growth (Allen et al., 2015); these effects are expected to continue (Ficklin and Novick 2017). While some amelioration of physiological stress might be caused by rising CO₂ (Ainsworth and Rogers 2007; Blum 2009; Morison et al., 2008), extreme droughts may reduce or eliminate these benefits (Gray et al., 2016). There are very few experiments on tree mortality, but no evidence was found that elevated CO₂ reduced drought mortality (Duan et al., 2014).

In the ocean, higher temperatures affect the carbon cycle by decreasing CO₂ solubility in seawater (Zeebe and Wolf-Gladrow 2001); a warmer ocean will hold less carbon. Also, increased surface ocean stratification from the warmer water will prevent CO₂ absorbed by the surface ocean from penetrating into deeper water masses by reducing deep mixing, thereby decreasing overall oceanic carbon uptake and storage (IPCC 2013). In the cryosphere, higher temperatures thaw permafrost and melt ice, processes which release CO₂ and methane (CH₄) from microbial respiration back into the atmosphere (Schneider von Deimling et al., 2012).

Rising temperatures thus influence the response of the carbon cycle to rising CO₂ in diverse and complicated ways, yielding both positive and negative feedbacks to atmospheric CO₂ (Deryng et al., 2016; Dieleman et al., 2012; Holding et al., 2015). Overall, higher temperatures tend to release land and ocean carbon into the atmosphere, while rising CO₂ is projected to increase land and ocean uptake (Friedlingstein et al., 2006), but magnitudes are variable and uncertain. Earth System Model assessments that include carbon cycle feedbacks to climate change show that the combined effects of environmental change yield an overall increase in CO₂ concentrations and thus would likely contribute to more climate warming. The multimodel average CO₂ concentration in 2100 is 985 ± 97 ppm, compared to a concentration of 936 ppm in models lacking carbon cycle feedbacks (Collins et al., 2013). This feedback is highly uncertain because of its dependence on a variety of factors, and thus studies arrive at large ranges in responses (Blok et al., 2010; Elberling et al., 2013; Hodgkins et al., 2014; McCalley et al., 2014; Schneider von Deimling et al., 2012;



Schuur et al., 2009). Temperature also indirectly influences CO₂ radiative effects. For example, enhanced evaporation from the ocean in a warmer world yields higher atmospheric water vapor concentrations that further amplify the impact of CO₂ on climate warming (Myhre et al., 2013).

Major uncertainties

The source or sink status of coastal zones has been difficult to determine, but evidence points to weakening CO₂ release from low-latitude coastal zones and strengthening CO₂ uptake from mid- and high-latitude systems, leading to greater release of dissolved inorganic carbon to the ocean (Cai 2011).

The effect of rising CO₂ on succession and biodiversity remains poorly understood and quantified and could result in changed ecosystem function and different ecosystem services. This lack of understanding also limits the ability to anticipate recovery from acute disturbances such as storms, fires, disease, or insect outbreaks.

Disentangling the impacts of rising CO₂ and other concurrent changes in climate, land use, nutrient cycles, and atmospheric chemistry across all ecosystems probably will require long-term, sustained carbon cycle observations and monitoring of ecosystem and socioeconomic consequences. Long-term observing networks are critical to managing ecosystems sustainably and adaptively (e.g., Schindler and Hilborn 2015), and a focus on data management and interoperability across data platforms would improve understanding of long-term responses to rising CO₂ (Ciais et al., 2014). Few experiments on land or in the ocean extend to a decade, and the balance of conclusions from observational studies is not settled.

Summary sentence or paragraph that integrates the above information

Both oceanic and terrestrial ecosystems are influenced by CO₂ and a variety of environmental controls, including temperature. The effects of climate and CO₂ are likely to interact with each other (i.e., the effect of changing CO₂ depends on the climatic conditions). These interactions likely will cause complex feedbacks to climate.



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