Terrestrial Plant Productivity and Carbon Allocation in a Changing Climate

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Abstract

Carbon dioxide from the atmosphere is assimilated into organic compounds via photosynthesis and subsequently allocated to different processes or pools within the plant. The contribution of plant material to the long-term storage of carbon in terrestrial ecosystems has important implications for our future climate. Plant production and allocation are expected to change in response to four prominent global change factors: elevated $[CO_2]$, warming, precipitation change, and nitrogen deposition. Our main focus in this chapter is on the responses and feedbacks among anthropogenic climate change and plant production and allocation in

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terrestrial ecosystems that span the globe. Many types of experimental manipulations have been used to examine plant responses to single and interacting environmental factors across a number of biomes. While plant growth often increased in response to elevated $[CO_2]$, warming, increased precipitation, and nitrogen deposition, limitation by nutrients (in the case of elevated $[CO_2]$) or interaction among factors (e.g., between warming and drought) can preclude or limit increases in plant growth. Also, allocation often changes in response to changing environmental conditions (e.g., increased root production under elevated $[CO_2]$), with implications for long-term ecosystem carbon storage. Furthermore, plant responses to atmospheric and climatic change occur against a complex background of biotic interactions, including changing plant community composition, competition, and interactions with insect herbivores. Unfortunately, dynamic plant community composition and other complex interactions are not well represented in large-scale land surface models projecting future climatic conditions. Large-scale and long-term experiments, in combination with technological improvements and model development, are needed to quantify plant production and allocation in response to single and interacting environmental factors in ecosystems that are critical to the global carbon budget and climate system.

Keywords

Net primary production • Carbon allocation • Elevated $[CO_2]$ • Warming • Changing precipitation regimes • Nitrogen deposition

Definitions

Feedback: A feedback occurs when the result of one process triggers changes in another process that in turn influence the initial process. Feedbacks can be positive, such that the initial event is amplified, or negative, such that the initial event is diminished.

Net primary production (NPP): The total amount of plant matter produced over time (usually 1 year).

CO_2 fertilization effect: The increased photosynthesis or growth of the terrestrial biosphere in response to rising atmospheric CO_2 concentration.

Carbon allocation: (1) the relative distribution of biomass in different ecosystem components (i.e., the amount of root biomass compared with the amount of aboveground, or "shoot," biomass), (2) the fluxes of carbon between different components of an ecosystem (i.e., NPP), and (3) the partitioning of gross primary production among different parts of the plant.

Gross primary production (GPP): The total amount of carbon fixed from the atmosphere via photosynthesis in a given amount of time (usually 1 year).

Intergovernmental Panel on Climate Change (IPCC): A scientific body established by the United Nations and the World Meteorological Organization to

assess the current state of knowledge on climate change and describe its potential global impacts.

Dynamic global vegetation models (DGVM): Models that represent the complex dynamics of plant community composition in response to environmental forcings and through time.

Plant functional types (PFT): Grouping of plant species based on similar characteristics such as life form (i.e., mosses, graminoids, shrubs, trees), stature, and physiology.

Meta-analysis: A statistical analysis of combined results from multiple independent experiments.

Litter quality: The physical and chemical characteristics of plant detritus that increase or decrease the rate at which the litter is decomposed by soil microbes and soil animals.

Soil respiration: CO_2 efflux from the soil that is the combined respiration of plant roots and soil organisms.

Acclimate: Gradual adjustment of an individual organism to a change in its environment that usually involves a change in physiology.

Throughfall: Rainfall in a forest that is not intercepted by tree canopies.

Reactive nitrogen compounds: Forms of nitrogen that interact with the biosphere and atmosphere, in contrast to relatively abundant, but inert, N_2 gas.

Introduction

Human activities are modifying the global climate in unprecedented ways. Atmospheric [CO_2] concentrations have been rising since the start of the Industrial Revolution and, depending on socioeconomic drivers, technological advances, and political decisions, may reach concentrations as high or higher than 1,000 ppm (more than double current concentrations) by 2100 (Meehl et al. 2007). In concert with rising CO_2, global temperatures have increased between 0.5 °C and 1 °C during the last ~150 years, and additional warming of between 1 °C and 6 °C is expected by the end of this century (Meehl et al. 2007) with the greatest increases in temperature expected in higher latitudes (McGuire et al. 2006). Rising global temperatures are projected to increase water vapor in the atmosphere, leading to larger and more intense precipitation events, more extreme precipitation regimes, and altered distribution of rainfall across latitudinal gradients. Observed patterns in the last part of the twentieth century included longer and more intense droughts as well as an increased frequency of heavy precipitation events with longer intervening dry periods (Trenberth 2011). In addition, a combination of fossil fuel combustion and emissions associated with the increased production and use of fertilizer and the planting of legumes have nearly doubled inputs of nitrogen to the living biosphere, and this trend is projected to continue throughout this century (Galloway et al. 2008). The combined effects of these unprecedented and rapid changes in the global atmosphere and climate will have impacts on plant
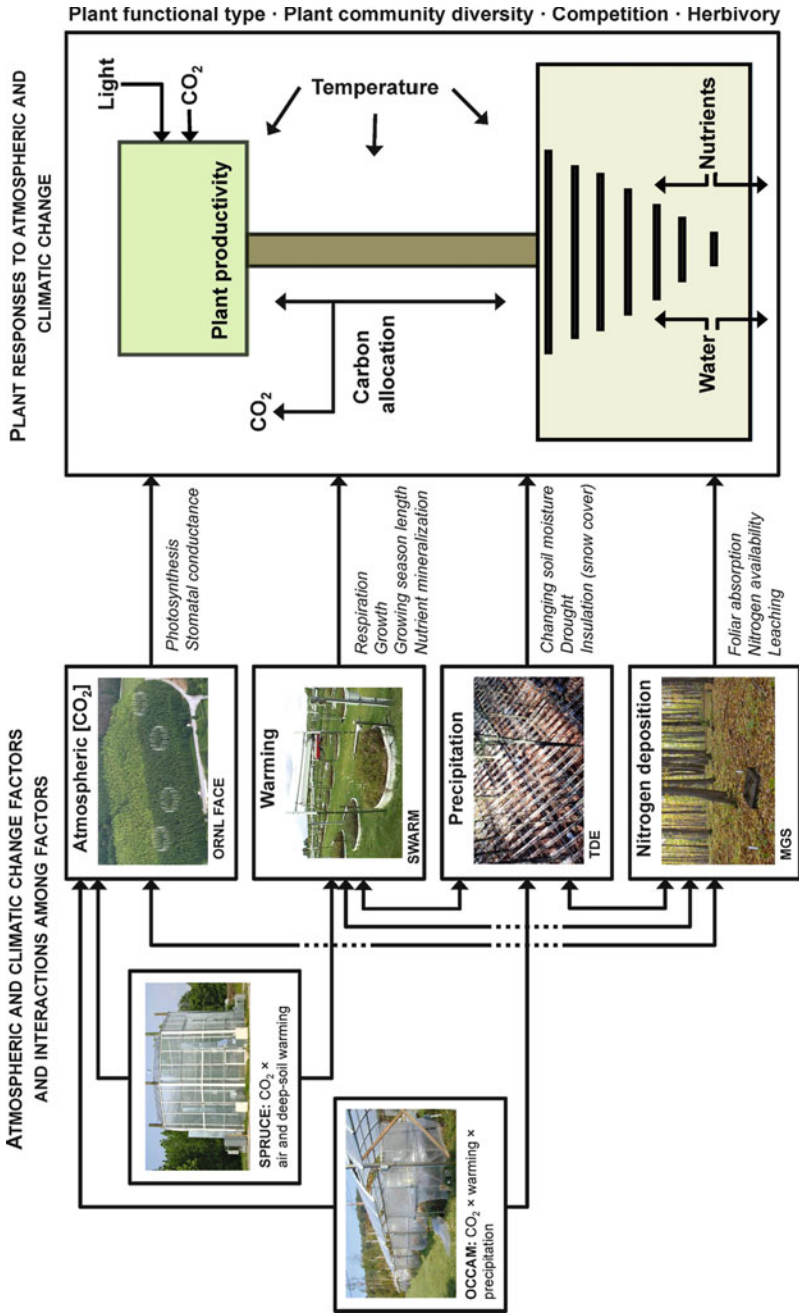
Fig. 36.1 (continued)

community production and allocation, thereby creating feedbacks to the global carbon cycle and the climate system.

Our goal in this chapter is to summarize the effects of prominent global change factors on plant production and allocation as measured in relatively large-scale, long-term experimental manipulations (i.e., Fig. 36.1). We first introduce readers to the processes by which carbon is fixed and incorporated into terrestrial ecosystems though plant photosynthesis and then allocated to different processes or pools within the plant. We then discuss plant production and allocation responses to four prominent global change factors: elevated $[CO_2]$, warming, precipitation change, and nitrogen deposition. We discuss each global change factor separately and describe the experimental manipulations used to examine plant responses to each individual factor. We also discuss the potential interaction of that factor with

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Fig. 36.1 Multiple interacting environmental factors, including elevated atmospheric $[CO_2]$, warming, precipitation, and nitrogen deposition, will affect important ecosystem properties, including plant production and carbon allocation, through changes in plant physiology as well as soil nutrient and water availability. Plant responses to atmospheric and climatic change will be modified by interactions among environmental factors and complex interactions within and among plant communities, including changes in plant community composition, competition among species, and interaction with insect herbivores. Plant community responses to atmospheric and climatic change factors, and the interactions among them, have been investigated in a number of large-scale, long-term experiments. The effects of elevated $[CO_2]$ on intact forested ecosystems have been investigated using free-air CO_2 enrichment (FACE) technology. For example, the response of a sweetgum (*Liquidambar styraciflua*) plantation to elevated $[CO_2]$ was investigated at the Oak Ridge National Laboratory (**ORNL**) **FACE** experiment in Tennessee, USA, for 12 growing seasons (Norby et al. 2010, photocredit: ORNL). The responses of plant communities to warming have been examined using overhead infrared lamps, as in the Soil Warming (**SWARM**) experiment conducted over a period of 9 years using intact peat mesocosms sampled from a bog and a fen in northern Minnesota, USA (water table was also manipulated in this experiment, Weltzin et al. 2000, photocredit: S. Bridgham). Open-top chambers have also been used to investigate plant community responses to warming, as in the Old-Field Community Climate and Atmosphere Manipulation (**OCCAM**) experiment that examined the responses of a constructed old-field community to a combination of elevated $[CO_2]$, warming, and drought over a period of 6 years in 4-m diameter chambers at ORNL (Kardol et al. 2010, photocredit: R. Norby). Forest responses to changing precipitation regimes have been investigated using throughfall displacement, as in the Throughfall Displacement Experiment (**TDE**) in a mature oak-dominated eastern deciduous forest at ORNL, where plastic troughs were used to redistribute throughfall among forested plots over a period of 14 years (Hanson et al. 2001, photocredit: P. Hanson). Plant community response to chronic nitrogen deposition has been investigated using small, frequent additions of nitrogen fertilizer, as in the Michigan Gradient Study (MGS). Beginning in 1994, the MGS examined forest responses to simulated nitrogen deposition across a geographic gradient of ambient nitrogen deposition in hardwood forests in northern Michigan, USA, that were dominated by sugar maple (*Acer saccharum*) (Pregitzer et al. 2008, photocredit: P. Micks). Improvements in technology will allow for larger-scale ecosystem manipulations. The Spruce and Peatland Responses Under Climatic and Environmental change (**SPRUCE**, http://mnspruce.ornl.gov) experiment will manipulate atmospheric $[CO_2]$ and both air and deep-soil temperatures to simulate extreme climate change in an intact forested bog in northern Minnesota, USA, over a period of 10 years using large (12-m diameter) open-top chambers combined with 3-m deep heating elements in the soil (e.g., Hanson et al. 2011)

other environmental factors (e.g., interactions between elevated [CO_2] and warming). We conclude with a discussion of responses of complex communities and future research needs. Our main focus is on the responses and feedbacks among anthropogenic climate change and plant production and allocation in terrestrial ecosystems. Although our goal was to maintain a global perspective, much of the experimental evidence comes from temperate ecosystems.

Plant Productivity

Put simply, plants are the interface between the atmosphere and the rest of the terrestrial biosphere. Plants take up carbon dioxide (CO_2) through photosynthesis, whereby the inorganic carbon (C) is converted into simple sugars – the fundamental building blocks for plant leaves, shoots, and roots, and the energy source to fuel the metabolism of cells throughout the plant. The *net primary production* (*NPP*) of plant material (i.e., the total amount of plant matter produced in 1 year) results in a supply of organic carbon in the terrestrial biosphere that provides energy for insect, animal, and human consumption in the form of green plant material and harvestable yield. Decaying plant litter also fuels soil food webs, including bacteria, fungi, nematodes, arthropods, and earthworms. Plant material that remains undecomposed by microbes and soil animals becomes incorporated into the soil system and stored for long periods of time; ancient plant detritus fuels our automobiles. Annual NPP differs among ecosystems; forests generally have the highest rates of production and arctic and alpine ecosystems the lowest, with deserts, grasslands, and old fields having intermediate levels of NPP (Knapp and Smith 2001). Each year, plants take up and respire one-sixth of atmospheric CO_2 (Denman et al. 2007). The gross fluxes of photosynthesis and plant respiration are 15 times the size of annual anthropogenic CO_2 emissions. Because of the importance of CO_2 in driving plant photosynthesis, it has long been hypothesized that rising atmospheric CO_2 concentrations ([CO_2]) would increase plant production (the so-called *CO_2 fertilization effect*). The strong link between atmospheric [CO_2] and global temperatures means that additional carbon uptake by the terrestrial biosphere can help to mitigate, or slow, the rise in atmospheric [CO_2] and therefore provide a negative feedback to rising global temperatures. Indeed, models that include enhanced CO_2 uptake by the biosphere as a response to rising [CO_2] predict much less warming than those that do not include the CO_2 fertilization effect (Matthews 2007). Much uncertainty exists regarding the strength of the negative feedback to rising atmospheric [CO_2], in part because plant carbon uptake is modified or limited by other environmental factors. For example, annual plant production is strongly, positively, related with annual precipitation amount (Knapp and Smith 2001). Drought is a particularly important climate factor, and declining precipitation may limit future carbon sequestration by the terrestrial biosphere (Sitch et al. 2008). Furthermore, plant production in most ecosystems, including terrestrial, freshwater, and marine, is limited by the availability of nitrogen, phosphorus, or both. Air and soil temperature also have important effects on plant

production, although the responses of plants to warming are more complicated than their responses to other environmental factors because warming can have differential (positive or negative) effects on different physiological processes, including photosynthesis, respiration, and plant phenology (Norby and Luo 2004). Feedbacks between plant production and global climate change are further complicated by complex interactions among multiple environmental factors, such as the exacerbation of drought by higher than average summer temperatures.

Plant Allocation

Once CO_2 is fixed into simple sugars, these carbon compounds are transported throughout the plant in the phloem for use in cellular metabolism (i.e., for respiration associated with the growth of new tissue or the maintenance of existing tissue) and to build new tissue, including leaves, wood, and roots. Carbon can also be released from plant roots to symbiotic mycorrhizal associations or via a process called root exudation, where labile carbon sources fuel microbial activity and associated nutrient mineralization in the rhizosphere. This sum total of all of these processes, which include both gains and losses of carbon from the plant, is *carbon allocation* (Poorter et al. 2012). The term "allocation" has been inconsistently used in the literature but has recently been defined as encompassing three important processes:

(1) the relative distribution of biomass in different ecosystem components (i.e., the amount of root biomass compared with the amount of aboveground, or "shoot," biomass)
(2) the fluxes of carbon between different components of an ecosystem (e.g., plant carbon uptake from the atmosphere)
(3) the partitioning of *gross primary production* (*GPP*, i.e., the total amount of carbon fixed from the atmosphere in a year) among different parts of the plant (Litton et al. 2007).

We discuss each of these three processes in more detail below.

Root/Shoot Ratios

The relative distribution of biomass in different ecosystem components is generally expressed as the ratio of total belowground plant biomass to total aboveground biomass (i.e., a root to shoot ratio, Mokany et al. 2006). Root/shoot ratios, which are the net consequence of annual fluxes of carbon among different plant components, do not allow quantification of annual carbon fluxes. However, root/shoot ratios are often used to characterize differences among plant species and communities in their response to changes in environmental conditions (Poorter et al. 2012), and they are relevant to discussions of global climate change because important climate assessments, such as the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), use prescribed root/shoot ratios of different vegetation

types to estimate belowground plant biomass or conduct greenhouse gas inventories (Mokany et al. 2006). Also, dynamic vegetation models (DVM) or *dynamic global vegetation models (DGVM)*, which represent the complex dynamics of plant community composition in response to environmental forcings and through time (Sitch et al. 2008), use root/shoot ratios to determine carbon allocation among *plant functional types* (*PFT*, a grouping of plant species based on similar characteristics).

Carbon Fluxes

The fluxes of carbon into and out of an ecosystem are important parameters in measurements of the consequences of global climate change for ecosystem carbon storage. The total amount of organic material fixed into plant biomass during a given time period (i.e., NPP), which includes organic matter lost in leaf fall or to herbivory, is an important first step in net ecosystem carbon storage. The NPP is often the main metric used to assess plant community response to atmospheric and climatic change.

Carbon Partitioning

Different plant tissues have a range of nutrient contents and turnover rates and perform a range of functions, including structural support, storage, transport, absorption, photosynthesis, or reproduction (Mokany et al. 2006). Therefore, the amount of carbon distributed to different plant compartments has important consequences for whole-plant function, for the amount of nutrients needed to support plant growth, and for the buildup of carbon in different compartments of an ecosystem, such as above- or belowground plant biomass or soil organic matter.

Carbon fluxes to different plant components tend to increase as gross primary production increases (Litton et al. 2007). However, changes in resource availability can change carbon partitioning above- or belowground. For example, increased belowground carbon partitioning, such as increased root proliferation, or deeper rooting distribution, can help to dampen the effect of variable precipitation regimes on plant water acquisition (Knapp et al. 2008), and hundreds of observations from across the globe indicate that decreasing mean annual precipitation tends to increase root/shoot ratios (Mokany et al. 2006). A recent **meta-analysis** (a statistical analysis of combined results from multiple independent experiments) of over 800 experiments indicated that plants grown at low levels of irradiance increase carbon allocation to leaves at the expense of fine roots; the converse was true of plants grown in nutrient-limited conditions, where large increases in allocation to roots at the expense of leaves and stems were observed (Poorter et al. 2012). However, relatively few data on plant carbon allocation exist from important ecosystems like the tundra, tropics, and desert, which cover

a large portion of global land surface (Mokany et al. 2006). Furthermore, the controls over carbon partitioning are still not well understood, which limits our capacity to model terrestrial ecosystems and predict effects of global change on carbon cycling (Litton et al. 2007).

Increases in the amount of carbon available for biosynthesis or increases in the rate of nutrient cycling within an ecosystem in response to atmospheric and climatic change are hypothesized to lead to changes in carbon allocation, which will affect long-term carbon storage in terrestrial ecosystems. For example, increases in the immediate return of carbon to the atmosphere via autotrophic (plant) or heterotrophic (e.g., microbial) respiration would provide a strong positive feedback to atmospheric CO_2 concentrations. In contrast, increased partitioning of carbon belowground to roots could increase carbon storage in long-lived soil pools, as plant roots may be more important than environmental factors in driving soil carbon accumulation. However, a major obstacle to quantifying the effects of atmospheric and climatic change on plant carbon allocation is the difficulty of quantifying the distribution of roots throughout the soil profile and the production of roots throughout the year. A large portion of annual NPP is partitioned belowground to "fine" roots with a narrow diameter that are used in the acquisition of water and nutrients (Jackson et al. 1997). Fine-root populations are particularly dynamic, with individual roots having lifespans on the order of a few days to a few years. Methods of sampling fine roots are necessarily destructive, and unlike aboveground tissues, root distributions in the soil are not visible during sample collections, leading to increased variability in estimates of root distribution. Methodology used to measure fine-root standing crop, production, and mortality ranges from the removal of soil cores or monoliths to intermittent standing crop assessment, in-growth cores, and imaging with minirhizotron cameras. Furthermore, it is difficult to separate roots of different species, making it difficult to determine species-specific belowground carbon partitioning. The technical and logistical constraints associated with the quantification of fine roots have discouraged many experimental manipulations from investigating the effect of atmospheric and climatic change on belowground carbon allocation.

Plant Production and Allocation in Terrestrial Ecosystems in Response to Atmospheric and Climatic Change

A number of environmental factors are expected to affect plant production and carbon allocation, including rising atmospheric $[CO_2]$, warming, altered precipitation regimes, and nitrogen deposition. Observational studies of plant responses to current environmental variation have allowed hypotheses to be formulated on the potential impact of these factors on plant growth and allocation, but experimental manipulations are necessary to determine the mechanisms controlling plant response to environmental change across a range of projected future conditions to which plants are not currently exposed.

Elevated Carbon Dioxide Concentrations

The effects of rising atmospheric CO_2 concentrations on plant production and allocation have been studied for decades. Experiments have included the short-term response of seedlings to elevated [CO_2] in small growth chambers and the longer-term responses of larger plants to elevated [CO_2] in open-top chambers. More recently, plants have been exposed to elevated [CO_2] using free-air CO_2 enrichment (FACE) technology, which allows the fumigation of intact ecosystems with air enriched in CO_2 in large-diameter (generally >8 m) plots without walls (Fig. 36.1). FACE technology has been used to examine the responses of a number of ecosystems to elevated [CO_2], including large, long-lived forest systems, as well as agricultural, annual, perennial, and semiarid grasslands; bog ecosystems across Europe; and a xeric shrub ecosystem in the Mojave Desert of southern Nevada, USA (Norby and Zak 2011).

Long-term experiments using FACE technology indicate that CO_2 enrichment increased plant production in forests, grasslands, and deserts. However, plant production did not increase in response to elevated [CO_2] in all ecosystems, and the relative enhancement of plant production under elevated [CO_2] differed among ecosystems and varied over time within an ecosystem. Given that plant production is often limited by the availability of soil nutrients, it has long been theorized that the CO_2 fertilization effect in natural ecosystems would not be sustained due to insufficient nutrient availability (Norby and Zak 2011). Furthermore, elevated [CO_2] can exacerbate existing nutrient limitation by indirectly affecting microbial carbon and nutrient cycling via changes in inputs of root exudates, the amount of leaf litter, and *litter quality* (i.e., chemical recalcitrance), which can progressively decrease the nutrients available for plant uptake.

The importance of negative feedbacks on plant production from nutrient cycling varies among systems. Limited soil nitrogen availability precluded a sustained productivity response in CO_2 enrichment experiments in some ecosystems (e.g., Norby et al. 2010), but not in others. Nitrogen feedbacks were not previously included in land surface and global models projecting future climatic conditions, and the importance of mineral nitrogen as a critical controller of plant production responses to elevated [CO_2] has been the main focus of recent empirical and modeling efforts. Nutrients other than nitrogen may also influence plant production responses to elevated [CO_2]. Plant production in some ecosystems is limited or co-limited by phosphorus availability, and other nutrients (e.g., potassium), which have received even less attention in measurements and models, may be important in determining the production response of vegetation exposed to elevated [CO_2] in nutrient-limited ecosystems. The degree to which the limited availability of nitrogen or other nutrients will preclude sustained increases in plant production under elevated [CO_2] should be a focus of future studies; long-term and large-scale experimental manipulations of plant communities in intact soil systems will be required.

Carbon partitioning to fine roots generally increases under elevated [CO_2], but the effects of elevated [CO_2] on carbon allocation vary within and among

ecosystem types (Luo et al. 2006). One unifying factor among many CO_2 enrichment experiments was a change in rooting depth distribution. In CO_2 enrichment experiments in forested ecosystems, carbon was increasingly allocated to fine roots deeper in the soil profile, presumably to mine the soil for limited inorganic nitrogen (Iversen 2010). Contrasting responses have been observed in grasslands and agricultural systems, where elevated $[CO_2]$ increased root proliferation in shallow soil. Differences in the response of rooting distribution to elevated $[CO_2]$ in forests and other ecosystems could be due to differences in rooting dynamics among plant functional types or shallower distributions of limited resources such as water and nutrients in grassland and agricultural systems (Iversen 2010).

Elevated $[CO_2]$ is unique among the many environmental change factors in that its only direct effects are on photosynthesis and stomatal conductance. However, direct effects of elevated $[CO_2]$ on stomatal conductance can lead to many indirect effects via changes in soil water availability if whole-plant water use is reduced, though the interplay between increases in plant production under elevated $[CO_2]$ and ecosystem water availability depends on the current water limitation of an ecosystem. Important interactions between elevated $[CO_2]$ and other environmental factors are also expected. There is a strong physiological basis for expecting a $CO_2 \times$ temperature interaction based on the biophysics and biochemistry of photosynthesis, but it is an open question whether a leaf-level $CO_2 \times$ temperature interaction translates to whole-plant or ecosystem properties (Norby and Luo 2004).

Rising Temperatures

The effects of temperature on plant production and carbon allocation are much more complicated than the effects of rising atmospheric $[CO_2]$ and are therefore more difficult to summarize. Temperature is perceived by all plant organs and tissues, and it affects all biological processes. Different reactions can be stimulated or inhibited depending on whether warming brings temperatures closer or farther from the optimum for a given process. The net effect of many process responses occurring simultaneously and in different directions can be difficult to predict as they are integrated into a whole-plant or whole-ecosystem response (Norby and Luo 2004). Furthermore, warming can extend the length of the growing season, which can alter productivity even without direct effects on plant metabolism.

Experiments to examine plant responses to warming have made use of greenhouses, electrical surface soil warming, passive nighttime warming, overhead infrared lamps, and closed- and open-top chambers (e.g., Fig. 36.1, reviewed in Rustad et al. 2001). Aboveground plant productivity response to experimental warming was evaluated at a number of research sites in diverse ecosystems (Rustad et al. 2001). There was considerable variation in response: warming increased plant productivity at a majority of the sites but decreased or had no effect on plant productivity at other sites. When all sites were considered together, meta-analysis showed that experimental warming significantly increased rates of aboveground plant productivity by a mean of 19 %. However, positive responses of plant

production to warming tend to decrease with increasing mean annual temperature (Norby and Luo 2004), and increases in growing season temperature tend to increase plant production at colder, northern sites but decrease plant production at warmer or more arid sites (Peñuelas et al. 2007). Such relationships could be useful for global modeling of ecosystem response to climatic warming, but unfortunately, the analyses are limited by lack of data from tropical ecosystems. Furthermore, plant productivity responses to increased temperature do not necessarily inform us about whole-ecosystem response or net carbon balance in a warmer world, because warming could increase *soil respiration* (i.e., CO_2 efflux from the soil) more than it increases plant production.

As is the case with aboveground production, root production and mortality have optimum temperatures, which vary among species (Pregitzer et al. 2000). Hence, it can be expected that increasing soil temperature could in some cases lead to increased rates of root production or mortality and decreased rates in other cases, and the net effect on root biomass may be difficult to predict. In individual experiments, warming has enhanced both the production and mortality of fine roots and led to a significant decrease in the ratio of root biomass to shoot biomass in trees (e.g., Wan et al. 2004). A contrasting response (i.e., an increase in root production compared with shoot production) has been observed in wetland ecosystems, where water table elevation plays an important role in controlling plant responses to atmospheric and climatic change (Weltzin et al. 2000).

Direct effects of temperature on plant metabolism can be difficult to separate from the indirect effects of temperature on resource (e.g., water and nitrogen) availability. That is, roots may acclimate (i.e., physiologically adapt) to a higher temperature, but nevertheless, root production could increase due to warmer temperatures stimulating nitrogen availability or decrease due to warming-induced drought. These interactions between temperature and resource availability are compounded in mixed-species communities if species respond differentially. In a constructed old-field community exposed to elevated temperature, elevated CO_2, and altered precipitation (Fig. 36.1), total community biomass increased in response to warming, but the increase was due almost entirely to the response of a dominant shrub species (Kardol et al. 2010). Hence, the structure of the plant community changed, and this had secondary effects on the subdominant community.

Changing Precipitation Regimes

Experiments in which precipitation was manipulated in the field span a wide range of experimental treatments and use a variety of methodologies. Uncertain model forecasts of precipitation patterns in future climates, and the importance of variability in the timing and amount of rainfall to rates of plant production, make it difficult to determine logical scenarios for experimental manipulations. The effect of changing precipitation patterns on plant production is determined by resulting changes in soil moisture, which is influenced by several processes, including

rainfall, evaporation from soils, plant transpiration, soil water transport, and the redistribution of water throughout the soil profile by plant roots. Soil moisture has been manipulated in a wide range of ecosystems through both decreases and increases in precipitation, changes in the seasonality of precipitation, and changes in the frequency at which constant amounts of precipitation are delivered. In relatively small-statured ecosystems, drought has been simulated using rain-out shelters, while increases in precipitation have been simulated using a combination of rain-out shelters and irrigation. In forested ecosystems, large-scale displacement and redistribution of *throughfall* (i.e., rainfall in a forest that is not intercepted by the tree canopies) has been used to manipulate soil moisture (Fig. 36.1). In areas where snowfall is an important form of precipitation, snow fences have been used in addition to rain-out shelters to manipulate soil moisture and evaluate the importance of seasonality in precipitation.

Experimental precipitation manipulations have been conducted across a wide array of ecosystems, including relatively small-statured grasslands and shrublands, and large-statured and long-lived temperate and tropical forests. An increasing number of experiments have examined the interactive effects of altered precipitation regimes in various combinations with elevated [CO_2], warming, and nitrogen deposition (e.g., Dukes et al. 2005), on plant community production and carbon allocation.

Plant responses to changing soil water availability depend on whether water availability is limiting to plant growth and whether the plant community is adapted to drought conditions (Hanson and Weltzin 2000). A recent meta-analysis indicated that across a number of studies spanning mainly grasslands and shrublands, plant production responded positively to experimental increases in precipitation and negatively to experimental decreases in precipitation, and plants were more sensitive to increases in precipitation compared with decreases (Wu et al. 2011). Similar responses were observed in some forested ecosystems, but not all (e.g., Hanson et al. 2001).

Intra- and interannual variability in precipitation can affect plant production as strongly as changes in precipitation amount. One of the main conclusions from a long-term manipulation of precipitation inputs in a forested ecosystem was that intra- and interannual variability in precipitation were more important in determining tree growth than large directional changes in the amount of precipitation falling at any given time (Hanson et al. 2001).

Altered precipitation regimes may be more important for future plant production than other environmental change factors. For example, precipitation was a dominant driver in a multifactor experiment in an annual grassland in a Mediterranean climate in California, USA, where increased precipitation increased plant growth more than warming or elevated [CO_2] (Dukes et al. 2005). Precipitation was also the dominant driver in the distribution of an invasive shrub and on plant community production and composition in a relatively mesic old-field system in eastern Tennessee, USA, where drought reduced aboveground plant biomass more than it was increased by elevated temperatures and elevated [CO_2] (Kardol et al. 2010).

Increased precipitation tends to increase both above- and belowground production, but increases in aboveground production are greater than belowground (Wu et al. 2011), leading to decreased root/shoot ratios. Contrasting responses would be expected in manipulations that decreased precipitation. Initial hypotheses, dating back several decades from work conducted on seedlings in pots, assumed that long-term decreases in water availability would lead to increased root biomass and production, increased root/shoot ratios, and deeper rooting distributions. One recent meta-analysis concluded that there were too few experimental precipitation reduction manipulations that measured belowground production to estimate the global mean effects of reduced precipitation on carbon partitioning to fine roots (Wu et al. 2011). Another recent meta-analysis found that decreased precipitation increased allocation to root biomass, but only under extreme drought conditions (Poorter et al. 2012). Some of the long-term stand-level experimental reductions in irrigation that have been conducted saw expected increases in root biomass, increased root/shoot ratios, and deeper rooting distributions (e.g., Joslin et al. 2000). However, responses tend to differ among plant functional types and across regions. Shifts in belowground carbon partitioning may not be necessary for drought to affect ecosystem carbon cycling, as decreased carbon allocation to root exudation can reduce carbon flow to microbial biomass.

Greater air and soil temperatures lead to increased evaporation of water from the soil, making it difficult to tease out the direct effects of temperature and water availability on plant production and carbon allocation without experiments directly testing the effects of each factor individually and in combination. Modeled projections of multiple ecosystem responses to a combination of environmental factors suggest that warming will further increase plant growth in response to increased precipitation and further decrease plant growth under drought conditions (i.e., interactions between precipitation and other environmental factors will be important).

Atmospheric Nitrogen Deposition

Atmospheric deposition of *reactive nitrogen compounds* (i.e., forms of nitrogen that interact with the biosphere and atmosphere) is another by-product of human activity that can have large effects on plant productivity and carbon allocation. The creation of reactive nitrogen continues to increase each year, and through atmospheric transport, nitrogen deposition to large regions of the world exceeds natural (i.e., non-anthropogenic) levels by more than an order of magnitude (Galloway et al. 2008). The focus of most analyses of ecosystem responses has been in temperate regions where the increases in nitrogen deposition have been greatest, but anthropogenic nitrogen deposition also occurs in tropical and high-latitude regions, where it may also be affecting plant and ecosystem processes. Experimental determination of the effects of nitrogen deposition on plant productivity and carbon allocation must be approached differently from determination of

effects of elevated CO_2, warming, or altered precipitation. Nitrogen compounds deposited to ecosystems immediately mix with the endogenous nitrogen cycle either through direct absorption and assimilation by leaves or through available nitrogen pools in soil. Hence, plant responses depend not only on the amount of deposition, which varies widely across the planet, but also with how nitrogen deposition interacts with native soil fertility. Retention of the added nitrogen in an ecosystem varies with the nitrogen status of the ecosystem (nitrogen-saturated systems leach a substantial fraction of added nitrogen), the extent to which nitrifying bacteria are stimulated, and the absorption of dry deposition directly by foliage (Norby 1998).

Some insights as to how plants respond to atmospheric nitrogen deposition come from experiments investigating plant growth and carbon allocation responses to nitrogen fertilizer additions. Plant biomass generally increases with nitrogen additions, and aboveground growth increases more than belowground growth, leading to decreased root/shoot ratios. Responses tend to vary across growth forms, with herbaceous plants responding more than woody plants, although this difference depends on the amount of nitrogen added (Xia and Wan 2008). However, results from nitrogen fertilizer additions are not necessarily informative of the responses of plants to atmospheric nitrogen deposition. A large majority of studies use nitrogen addition rates that are approximately 100-fold higher than background (non-anthropogenic) rates of nitrogen deposition. Nitrogen fertilization studies also usually provide the nitrogen in a single or a few applications, in contrast to atmospheric deposition, which is essentially continuous in the dry form (NO_x, HNO_3 vapor) and in small, frequent pulses as wet deposition (NH_4^+ and NO_3^-) in precipitation. Furthermore, in contrast to fertilizer additions where nitrogen inputs are retained primarily in soil, vegetation accounts for most of the retention of nitrogen deposited from the atmosphere.

Experimental simulation of nitrogen deposition is difficult given the need for small, frequent additions maintained over a long period of time for the simulation to be realistic. Where such experiments have been attempted, simulated nitrogen deposition usually increases aboveground NPP (e.g., Pregitzer et al. 2008). Given the dubious value of fertilizer experiments for informing about effects of atmospheric deposition and the difficulty in simulating atmospheric deposition in experiments, analyses of plant growth and ecosystem responses have relied on observations across nitrogen deposition gradients. Forest inventory analysis of tree species in northeastern and north central USA across a range of nitrogen deposition indicated that nitrogen deposition enhanced growth of some species but decreased growth of others (Thomas et al. 2010). It should also be noted that high rates of nitrogen deposition, or deposition to sites that are already nitrogen saturated, can lead to tree mortality and loss of species diversity.

The possible effect of nitrogen deposition on fine-root production has been assessed through analyses across gradients of nitrogen availability. Nitrogen deposition is likely to stimulate fine-root production but also increase fine-root turnover, resulting in a decrease in fine-root biomass. However, fine-root production could

decrease if chronically elevated nitrogen deposition leads to tree mortality (Nadelhoffer 2000). Other experiments have found that simulated nitrogen deposition led to decreased belowground carbon allocation, which could also result in a decline in mycorrhizal symbioses or a change in mycorrhizal community composition (Pregitzer et al. 2008).

Climate Change Effects in Complex Plant Communities

The effects of climate change factors on plant production and carbon allocation are played out against a background of complex community and ecosystem dynamics that may change in unexpected ways in the face of atmospheric and climatic change. These added layers of uncertainty make it difficult to quantify and model the effects of climate change on plant production.

Differences in NPP among plant communities are determined by the interplay between climatic drivers, edaphic factors, and inherent species characteristics. Inherent differences in production and carbon allocation among individual plant genotypes within a species, and among species within a plant community, will affect how plant community composition responds to atmospheric and climatic change, which will in turn affect NPP, decomposition, and ecosystem carbon storage (Bradley and Pregitzer 2007). Interaction between a plant community and its heterotrophic symbionts, pathogens, and insect herbivores can also affect plant response to atmospheric and climatic change.

One problem with the indirect interactions between plant communities and atmospheric and climatic change is that these complex relationships are not well represented in current models that aim to project future climate conditions (Meehl et al. 2007). Dynamic vegetation models (DVM) and dynamic global vegetation models (DGVM) group plant species into plant functional types (PFT) based on characteristics such as life form (i.e., mosses, graminoids, shrubs, trees), stature, and physiology, and these PFT compete for light and nitrogen to determine future community composition (Euskirchen et al. 2009). DVM indicate that some plant communities will respond more strongly to atmospheric and climatic change than others (Euskirchen et al. 2009). However, large-scale DGVM differ in their projection of the magnitude of plant production and carbon sequestration in response to climate forcing, due to differences in the sensitivity of certain parameters to environmental factors such as drought and elevated temperatures, as well as differences in their treatment of nutrient cycling (Sitch et al. 2008). Furthermore, the representation of plant species or PFT in DVM and DGVM is necessarily coarse (Euskirchen et al. 2009).

Lastly, even if plant community dynamics and carbon uptake in response to atmospheric and climatic change could be perfectly simulated, the effects of disturbances such as fire and land-use change are overwhelmingly important in controlling the species composition, plant productivity, and carbon balance of ecosystems (McGuire et al. 2006). However, disturbances are difficult to predict and therefore difficult to model.

Conclusions

In order to understand and project the consequences of environmental change, we must understand the magnitude of changes in plant carbon uptake from the atmosphere and its ultimate fate in the ecosystem. We have shown here that plant production can increase in response to environmental factors such as elevated [CO_2], warming, increased precipitation, and nitrogen deposition, but that environmental factors can change the allocation of carbon among different plant organs and tissues, with implications for plant fitness, survival, and competition that may influence long-term ecosystem carbon storage (see ▶ Chap. 39, "Biogeochemical Cycling in Terrestrial Ecosystems - Individual Components, Interactions and Considerations Under Global Change"). Furthermore, not all plant communities increased growth in response to changing environmental factors due to nutrient limitation or the countervailing effects of other environmental factors. Drought in particular may be an important factor in limiting carbon sequestration by the terrestrial biosphere. Plant community composition, under current conditions and in response to climatic forcing, may also play an important role in the response of the terrestrial biosphere to atmospheric and climatic change.

It is important that the responses of the plant community are accurately represented in models, and models are continually being improved based on observations from new experimental manipulations and new process-level understanding. For example, the addition of nitrogen feedbacks to plant production in global-level models has altered our estimate of the CO_2 fertilization effect. However, improvements are still needed. While carbon uptake by plants is well understood and represented in models, process-level understanding of carbon allocation remains elusive, and models lag in their representation of allocation as a dynamic process that is responsive to environmental cues. Hence, belowground processes are poorly represented in models, yet we know that belowground responses can be the most important feature of ecosystem responses to atmospheric and climatic change. The situation is exacerbated by the difficultly in measuring belowground responses, especially in long-term field experiments.

Even with all of the information we have to date regarding plant production and allocation in response to atmospheric and climatic change, important questions remain. Long-term experiments are needed to resolve ecosystem responses to changing climate that occur on decadal or greater time scales, such as the effect of environmental factors on long-lived plant species and on plant species composition. New experiments building on the results we have seen to date will continue to increase our understanding of, and ability to project, plant and ecosystems responses to the changing global environment. Technological advances such as large-scale soil and air warming, improved infrared heating, and large-scale FACE rings can improve our ability to quantify the response of large-scale ecosystems to realistic global change scenarios (e.g., Fig. 36.1). On a smaller scale, improved technology can help to advance our understanding of understudied processes, such as root production, root mortality, and CO_2 efflux from the soil. Experiments investigating a single environmental factor in an ecologically simple ecosystem will remain important sources of data and insights for informing and improving

models, especially when implemented in understudied biomes. However, there also is a need to consider the increased complexity that derives from multiple, interacting environmental factors and complex and changing plant communities. The highest priority should be experiments in ecosystems that are critical to the global carbon budget and climate system.

Cross-References

► Biogeochemical Cycling in Terrestrial Ecosystems - Individual Components, Interactions and Considerations Under Global Change
► Soil Organic Matter Dynamics, Climate Change Effects

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