

## 34 • Global change and photosynthesis

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The phrase global change is generally associated with alterations of climate (temperatures, fluctuations in precipitation, etc.) that stem from changes in atmospheric composition. In reality, global change also encompasses more than changes in climate or atmospheric composition; any global-scale change that influences biota directly or indirectly can be considered global change. Global change has influenced the biosphere throughout geological time, with changes occurring over periods that allow for either species to evolve to these changes when they occur over long periods, to adapt or acclimate to the changes or to perish when neither of the previous two responses is effective. Although we are currently in the midst of abrupt global change, it certainly is not the first time that rapid global change has occurred. What differentiates the current changes to our planet from all other global-change events is that these abrupt changes are brought about through anthropogenic influences and that they are occurring more rapidly than in previous occasions.

One of the major challenges of a chapter focused on plants and global change is that the topic is extensive. Many chapters of this book focus on photosynthesis responses to most of the predicted global-change scenarios, and entire volumes can be devoted to these and other global-change scenarios. Further, many reviews have been published that address photosynthetic responses to single environmental-change factors (Ceulemans *et al.*, 1999; Saxe *et al.*, 2001; Ainsworth *et al.*, 2002; Long *et al.*, 2004; Ainsworth and Long, 2005; Hikosaka *et al.*, 2006; Sage and Kubien, 2007; Wittig *et al.*, 2007). Our goals in writing this chapter are: (1) to provide a synopsis of global-change trends; (2) to identify the potential impacts of these trends on photosynthesis; (3) to identify the potential for photosynthesis to mitigate global change; and (4) to present ecosystem and general-circulation models as predictors of the interactions between plants and global change.

### 34.1. GLOBAL CHANGE: A BRIEF SYNOPSIS OF OBSERVED AND PREDICTED GLOBAL-CHANGE TRENDS

There are numerous changes that are occurring throughout the planet as a result of anthropogenic activities. The combination of large-scale changes in the composition of atmospheric constituents, changes in climate for many regions of the planet and clear evidence of the impacts of these changes on ecosystems, ice fields, sea levels and a number of other events all confirm that global change is occurring.

#### 34.1.1. Atmospheric CO<sub>2</sub> is increasing

Atmospheric concentrations of CO<sub>2</sub> are increasing at a rate unprecedented since the Oligocene-Miocene transition approximately 20–25 million years ago. The rise in CO<sub>2</sub> is a direct consequence of two main activities, the burning of fossil fuels and land-use change. Since the beginning of large-scale industrialisation, concentrations of CO<sub>2</sub> have increased by over 30% (Fig. 34.1). Fossil fuels consist of high-energy organic molecules that are the remnants of ancient biological organisms. Over long time periods, the remains of these organisms were buried under sediment and the carbon in these remains was removed from the global carbon cycle for millions of years. The total amount of organic matter stored in sediment is unknown; however, evidence suggests that the size of this pool is large. For example, during the Cambrian era (~500 MA) atmospheric CO<sub>2</sub> concentrations were as much as 12 times above present (Berner, 1990). It was during this period and the following periods of the Paleozoic era that most fossil-fuel reserves were formed. The component of the rise in CO<sub>2</sub> that is attributed to the burning of fossil fuels is a direct consequence of releasing carbon that was sequestered for millions of years. Although formed under different epochs and attributed to different

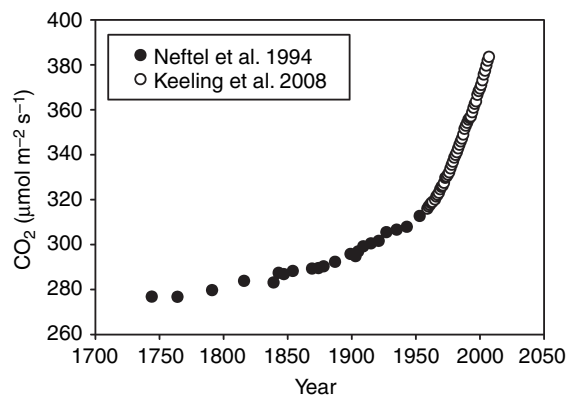


Fig. 34.1. Plots showing the increase in atmospheric concentrations of  $\text{CO}_2$  since the Industrial Revolution. Data in the filled symbols represent ice core data from the Siple Station Antarctic ice cores (Neftel *et al.*, 1994) and the open symbols from measurement made atop Mauna Loa in Hawaii (Keeling *et al.*, 2009).

organisms, burning of coal and natural gas are similarly influencing global atmospheric trace gas concentrations.

Changes in land use have impacted atmospheric  $\text{CO}_2$  concentrations as a result of numerous activities, including deforestation and the spread of agriculture. Despite the occasional disturbance, most ecosystems prior to large-scale industrialisation and the spread of agriculture were under steady state conditions. When the forests or grasslands were cleared for urbanisation or agriculture, these ecosystems were disturbed from their steady state conditions. The carbon sequestered in plant tissues and soils was released to the atmosphere during this disturbance. For example, simulations suggest that the soil carbon pool in Midwestern U.S. agricultural soils has decreased by 60% since it was converted from pre-settlement prairie (Donigian *et al.*, 1994; Lal, 2004a).

The IPCC has presented numerous model scenarios to predict how  $\text{CO}_2$  will continue to increase over the next century (Meehl *et al.*, 2007). Model scenarios for the year 2100 based on the IPCC Fourth Assessment Report predict an increase in atmospheric  $\text{CO}_2$  ranging from 700 to over 1000  $\mu\text{mol mol}^{-1}$  (Meehl *et al.*, 2007), which is higher than the range predicted from the IPCC Third Assessment Report (Prentice *et al.*, 2001). Current evidence shows that increasing demand for fossil fuels is resulting in the rates of  $\text{CO}_2$  emissions to exceed the ‘worst-case’ scenarios from the most recent IPCC report (Raupach *et al.*, 2007). This suggests that the increase in atmospheric  $\text{CO}_2$  that has been observed

as the dawn of the industrial revolution is not showing any signs of stabilisation and that the rise might actually continue at an increasing rate.

The premise that  $\text{CO}_2$  will rise at an unprecedented rate throughout this century suggests that vegetation responses to these changes will become more apparent.  $\text{CO}_2$  has risen over 30% over the last two centuries and the implications to date are uncertain owing to a lack of preliminary data collected prior to the Industrial Revolution. Therefore, effects of global change and of the green revolution are confounded and make assessments of current responses difficult (e.g., Phillips *et al.*, 2008). Large-scale field campaigns are now providing baseline data in order to assess the implications of changes in  $\text{CO}_2$  in the coming decades. In addition to the long-term experiments associated with the steady increases in global  $\text{CO}_2$ , numerous studies employing a variety of techniques, including FACE, open-top chambers, growth chambers, greenhouses and natural  $\text{CO}_2$  sources are allowing researchers to predict how vegetation will respond to substantially higher concentrations at the leaf, whole-plant, ecosystem and global scales.

#### 34.1.2. Tropospheric ozone is increasing

Tropospheric ozone ( $\text{O}_3$ ) is a highly reactive gas that damages any living tissue with which it comes in contact. It has been increasing at a faster rate than  $\text{CO}_2$ . Prior to large-scale emissions of pollutants,  $\text{O}_3$  concentrations were relatively low; however, since the Industrial Revolution concentrations have increased several-fold (Wang and Jacob, 1998). Although  $\text{O}_3$  is a naturally occurring constituent of the atmosphere, fossil-fuel combustion has increased the emission of the precursors to ozone formation by more than an order of magnitude from pre-industrial concentrations (Fowler *et al.*, 1998). In order for  $\text{O}_3$  to form, both VOC and  $\text{NO}_x$  must occur in the presence of sunlight. VOC are released to the atmosphere by both anthropogenic activities and natural processes, including fuel consumption, industrial processes, forest fires and natural geologic and biological emissions (Etiopie and Ciccioli, 2009). The release of  $\text{NO}_x$  occurs naturally as a result of biological activity in soils, lightning, forest fires, etc., but the release as a result of anthropogenic activities far exceeds that from natural sources (Fowler *et al.*, 1999b). Ozone formation is relatively complex and is dependent on the relative concentrations of the precursors. For example, maximum  $\text{O}_3$  formation will occur with optimal concentrations of  $\text{NO}_x$  for a given concentration of VOC (Fig. 34.2). Higher or lower concentrations of either of these

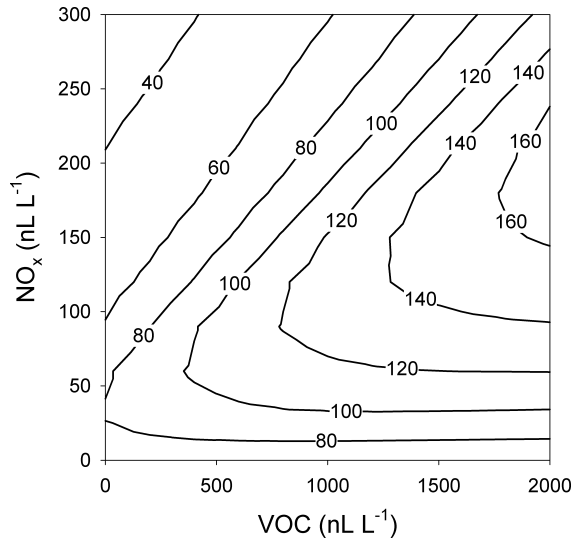


Fig. 34.2. An ozone isopleth graph modelled for Champaign, IL, USA on August 15, 2008. The lines on the plot show the predicted ozone concentration ( $\text{nL L}^{-1}$ ) for a given concentration of the two main precursors, nitrogen oxides ( $\text{NO}_x$ ) and volatile oxygenic compounds (VOCs). Note that for a given concentration of VOC, data is modelled using the Ozone Isopleth Plotting Program (OZIP; <http://www.shodor.org/ekma/>).

substrates reduce the formation of  $\text{O}_3$ . Ozone concentrations are predicted to continue increasing over the next 50 years with average concentrations reaching 20% over current (Grewe *et al.*, 2001; Hauglustaine and Brasseur, 2001), although changes in  $\text{O}_3$  formation are highly variable. Some locations are experiencing rapid increases in  $\text{O}_3$  formation while other locations are experiencing decreases (Forster *et al.*, 2007). Thus, unlike rising  $\text{CO}_2$ , the impacts of rising  $\text{O}_3$  will be highly variable and will depend on local and regional factors that drive the abundance of the substrates to  $\text{O}_3$  formation, as well as the meteorological conditions that might favour the formation of  $\text{O}_3$ .

#### 34.1.3. Global warming will continue

As a potent greenhouse gas,  $\text{CO}_2$  is the major driver for global warming and combined with emissions of other important greenhouse gases, e.g.,  $\text{N}_2\text{O}$ ,  $\text{CH}_4$ , halocarbons and  $\text{O}_3$ , along with other anthropogenic activities, it will result in a net increase in radiative forcing of over  $1.5 \text{ W m}^{-2}$  (Forster *et al.*, 2007). Radiative forcing represents a shift in the balance of incoming versus outgoing energy at the ground surface. While  $1.5 \text{ W m}^{-2}$  is small relative to

peak total solar radiation, it is substantially large enough to have already impacted global mean temperatures (Forster *et al.*, 2007). It is highly likely that global temperatures will continue to increase (Meehl *et al.*, 2007). However, not all parts of the planet are expected to experience temperature increases uniformly. For example, warming will be greatest at northern latitudes, and land surfaces are expected to experience temperature increases double that of the oceans (Meehl *et al.*, 2007). The rate of predicted temperature increase over land is variable, with mean increases ranging from about  $1.8^\circ\text{C}$  to over  $6^\circ\text{C}$  by the year 2100 depending on the region (Christensen *et al.*, 2007). In addition to variability over terrestrial regions, there is predicted seasonality to temperature increases although the most prominent seasonality is predicted in the arctic region, Eastern Canada and Greenland (Christensen *et al.*, 2007).

#### 34.1.4. Extreme events are likely to increase

Although most GCM predictions suggest gradual changes, there is increasing evidence that extreme events are likely to increase in frequency and magnitude in the coming decades. Of the potential extreme events, both high temperature and precipitation are predicted to have the most significant impact on vegetation (Diffenbaugh *et al.*, 2005), although higher probabilities of high  $\text{O}_3$  days can induce highly damaging acute responses to vegetation.

### 34.2. IMPLICATIONS OF GLOBAL CHANGE

Each of the above global-change constituents are likely to have both direct and indirect implications for vegetation. Most of these effects have been described in previous chapters of this book however not always in the context of global change scenarios. Thus, the effects of these changes are described briefly below, followed by a more thorough discussion of interacting factors.

#### 34.2.1. $\text{CO}_2$

As discussed in Chapter 17, rising  $\text{CO}_2$  generally increases rates of photosynthesis, which in turn increases productivity. Early studies demonstrated that increases in photosynthesis were quite large and that these increases led to much higher productivity for most  $\text{C}_3$  species (e.g., Curtis, 1996; Ainsworth *et al.*, 2002). Recent research in which  $\text{C}_3$  plants are grown in elevated  $\text{CO}_2$  under field conditions in experiments that utilise the FACE design suggests increases in

photosynthesis are common (Kimball *et al.*, 1995; Man and Lieffers, 1997; Noormets *et al.*, 2001a,b; Bernacchi *et al.*, 2003b, 2005a, 2006; Centritto *et al.*, 2004). However, it was observed that photosynthetic rates do not increase as much as enclosure-based studies and that the observed increase in biomass is less than earlier non-FACE studies (Long *et al.*, 2006b, 2007; Ainsworth *et al.*, 2008b). Experiments in which C<sub>4</sub> plants are grown in elevated CO<sub>2</sub> using FACE are much less common; however, the limited studies on this topic suggest little or no increase in photosynthesis (Leakey *et al.*, 2004, 2006; Ainsworth and Long, 2005). Evidence does suggest that under certain conditions, i.e., water stress, elevated CO<sub>2</sub> does increase photosynthetic rates of C<sub>4</sub> plants (Leakey *et al.*, 2004), suggesting that impacts of global change should be considered not only in the context of individual factors but also in the context of interacting factors.

Ecosystem functions and plant productivity have likely responded to the increase in CO<sub>2</sub> that has already occurred, although clear documentation of any change to the present is relatively difficult to assess. This is mostly owing to the lack of baseline measurements prior to the industrial revolution and large-scale changes in land use dominating ecosystem responses. Agricultural productivity has increased by more than an order of magnitude over the last century; however, the portion of this increase that is attributed to rising CO<sub>2</sub> is small relative to the impact that the 'Green Revolution' had on productivity with the use of high-yielding crop varieties, chemical fertilisers and pesticides, irrigation, etc. (Matson *et al.*, 2007). Forest ecosystems are likely to have responded to the increase in CO<sub>2</sub> since pre-industrial times, but separating the climate-change component (i.e., temperature, N deposition, etc.) from the CO<sub>2</sub> increase has been shown to be difficult and uncertain (Jacoby and D'Arrigo, 1997). Some evidence for these changes is apparent (Phillips *et al.*, 2008) and suggests that CO<sub>2</sub>-induced changes in plant physiology are already altering various aspects of the environment. Despite the difference in photosynthetic responses for C<sub>3</sub> and C<sub>4</sub> species, there appears to be a consistent response toward lower water use for both types of vegetation in response to growth in elevated CO<sub>2</sub>. For example, evidence from modelling exercises suggest that the decrease in  $g_s$  associated with elevated CO<sub>2</sub> results in an increase in runoff from major continental regions (Gedney *et al.*, 2006; Betts *et al.*, 2007). This modelling exercise assumes that the decrease in  $g_s$  is enough to lower evapotranspiration at the canopy scale, which has been demonstrated by numerous experiments (Hungate *et al.*, 2002; Burkart *et al.*, 2004;

Triggs *et al.*, 2004; Yoshimoto *et al.*, 2005; Kimball and Bernacchi, 2006; Bernacchi *et al.*, 2007).

### 34.2.3. Ozone

Approximately one-quarter of the forested portion of the planet is presently at risk from tropospheric concentrations of O<sub>3</sub> that exceed 60 nL L<sup>-1</sup> (Fowler *et al.*, 1999b). Despite the continual increases of O<sub>3</sub> in the coming decades, spatial variability is predicted to be high. For example, current trends in tropospheric O<sub>3</sub> demonstrate a divergent response, with some areas of the planet experiencing increases and others decreases or no change (Vingarzan, 2004). The areas that have shown steady or decreasing O<sub>3</sub> concentrations over the last few decades are attributed to changing emissions standards resulting in fewer precursors to O<sub>3</sub> being emitted (Vingarzan, 2004). This suggests that policy decisions can have a large impact on regional concentrations of O<sub>3</sub>.

The damage that is imposed on vegetation from exposure to O<sub>3</sub> can be quite severe for many species. Exposure to increased O<sub>3</sub> induces damage and stress responses that reduce photosynthesis, growth, yields and water use (Feng *et al.*, 2003; Morgan *et al.*, 2004; Fiscus *et al.*, 2005; Long *et al.*, 2005; Dermody *et al.*, 2006; Flowers *et al.*, 2007; Low *et al.*, 2007; Wang *et al.*, 2007). However, there are interactions between O<sub>3</sub> and secondary metabolites emitted by plants that in turn may affect photosynthesis. Plants emitting isoprenoids take up more O<sub>3</sub> from the atmosphere, but because of the higher reactivity of these gases O<sub>3</sub> is efficiently scavenged and damage to photosynthesis is lower in isoprenoid-emitting plants (Loreto and Fares, 2007).

### 34.2.4. Temperature

The impact of increasing temperature on photosynthesis is less certain than the impact of other global-change scenarios. Whereas elevated CO<sub>2</sub> is known to stimulate and elevated O<sub>3</sub> decrease or have no net effect on photosynthesis, the complex interplay between the three major biochemical pathways involved in CO<sub>2</sub> fluxes into and out of the leaf (photosynthesis, photorespiration and mitochondrial respiration) make temperature more complex. Thus, increases in temperature can lead to a wide variety of responses for net photosynthesis.

The impact of rising temperatures on photosynthesis is dependent on whether the increase in temperature results in photosynthesis increasing toward or beyond its optimal temperature. It is also important to consider the

extent to which thermal acclimation might occur and the impact that rising temperatures will have on the supply of CO<sub>2</sub> into the chloroplast and on metabolic pathways downstream from photosynthesis. Most metabolic pathways are highly temperature-dependant over short time periods, and over longer periods thermal acclimation will exhibit varying responses for each pathway. For example, a prolonged increase in temperature can result in thermal acclimation of photosynthesis in order to maximise photosynthetic rates for a given temperature. Consequently, optimum temperatures of photosynthesis may be higher in plants acclimated to higher growth temperatures (Kirschbaum, 2004). Respiration, however, can increase and remain high even after acclimation, which results in decreased biomass accumulation. Thus, inferring the response of temperature on photosynthesis may not be sufficient to accurately predict productivity.

#### 34.2.5. Extreme events

Extreme events can represent a wide range of scenarios, including meteorological or climatic conditions or fluctuations in reactive gases that can have large-scale detrimental effects on vegetation. Although plants are well adapted to changes in their environment, events that cause conditions to extend beyond those in which plants can cope can lead to damage or death (McDowell, 2011). Drought is considered a climate extreme that causes large-scale destruction (Dale *et al.*, 2001; Xu and Baldocchi, 2003; Kunkel *et al.*, 2006), but moisture excess can also result in large-scale declines in productivity, particularly for crops (Rosenzweig *et al.*, 2002). In addition to extreme fluctuations in precipitation for a given area, there are implications for temperature extremes on vegetation. For example, increasing global mean temperature is increasing growing-season length over many areas. Unseasonably warm temperatures may result in the initiation of plant growth earlier in the season that makes plants more prone to damage induced by early frosts. An example of this is reported for the Eastern U.S. in 2007 in which warm early season temperatures followed by a late-spring severe frost caused large-scale damage to a number of ecosystems in the region (Gu *et al.*, 2008).

Direct impacts of extreme events on photosynthesis are highly variable. For example, as described earlier maize showed higher photosynthetic rates when grown in elevated CO<sub>2</sub> but only when drought conditions were present (Leakey *et al.*, 2004). Drought conditions result in a loss of transpiratory cooling of leaf surfaces that, combined with

warmer temperatures, can induce high-temperature stress more rapidly in future environments. Further, elevated CO<sub>2</sub> is also shown to decrease  $g_s$  having a net warming effect on plant canopies (e.g., Bernacchi *et al.*, 2007) that might potentially lead to higher frequencies of lethal leaf temperatures. Despite the range of potential scenarios, few studies have demonstrated the impact of extreme events in the context of combined global-change scenarios.

In addition to the damage imposed on vegetation health, extreme events can impact ecosystem services. For example, it is well documented that numerous ecosystems across the globe are acting as carbon sinks, which help to mitigate some of the CO<sub>2</sub> emissions to the atmosphere every year (Cox *et al.*, 2000; Dufresne *et al.*, 2002). However, a heatwave that affected Europe over the summer of 2003 was associated with the most important productivity crisis based on over a century of modelled global net primary production. It caused a 30% reduction of GPP, becoming a 0.5 Pg C net source of CO<sub>2</sub>, which is equivalent to four years of carbon sink by the terrestrial ecosystems of Europe (Fig. 34.3; Ciais *et al.*, 2005). Thus, although extreme events can happen over relatively short time periods, the effects can be far reaching and long lasting.

### 34.3. THE INTERACTIVE EFFECTS OF GLOBAL-CHANGE SCENARIOS

Although many chapters of this book focus on the responses of photosynthesis to single factors that are relevant to global-change scenarios, we focus here on the interactive effects of these factors on photosynthesis. Ecosystems indeed experience a combination of numerous environmental changes. Studies that address only single responses are useful in determining the underlying physiological responses of vegetation to these global-change scenarios. This information is then used to feed data into models that can incorporate interactive influences of simultaneous environmental changes. However, plant responses are often confounded by multiple environmental factors. For example, the impact of rising O<sub>3</sub> on photosynthesis might differ based on whether there is a concomitant increase in CO<sub>2</sub>.

A challenge exists in determining plant responses to interacting factors for many reasons. There is a great deal of uncertainty with regard to the amount of change that is expected for each direct effect. Thus, projecting CO<sub>2</sub> concentrations for 50 years into the future and determining the temperature that will correspond with this CO<sub>2</sub> concentration is highly uncertain. The addition of O<sub>3</sub> or water

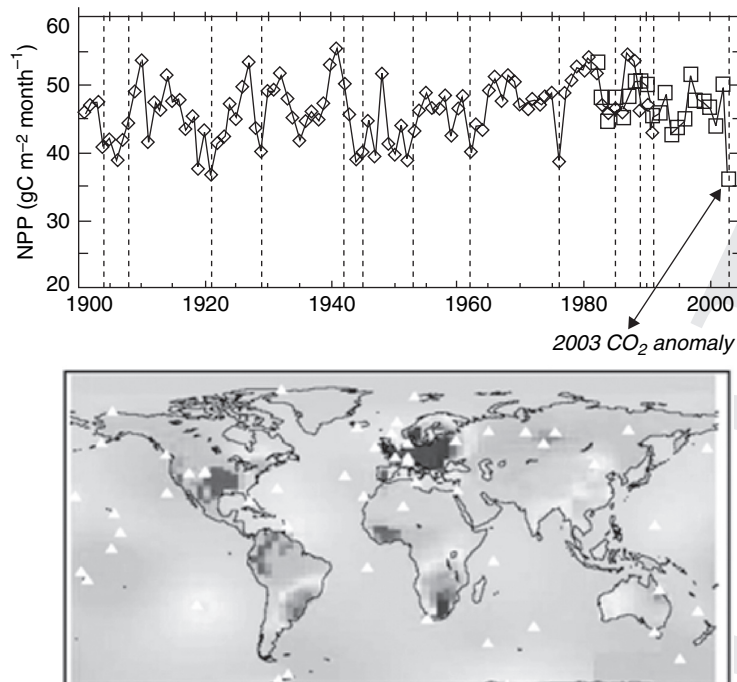


Fig. 34.3. Mean monthly net primary production from 1901 to 2002 and for the drought year, 2003. Data collected from modelled (Mitchell *et al.*, 2004) and measured data (Nemani *et al.*, 2003) for the land surfaces of Italy and France.

availability can further add to uncertainty. Applying numerous interacting treatments to vegetation in a controlled manner is difficult, expensive and often impractical. Various methods for measuring plant responses to their environment have been utilised, including growth chambers, SPAR chambers, open-top chambers, FACE rings, etc., but designing experiments that test two, three or four factors simultaneously result in increasing chambers or plots.

Despite these problems many studies have employed a range of techniques to study interactive effects of global change on photosynthesis. The most commonly studied interactions are presented in more detail below.

#### 34.3.1. The interactive effects of CO<sub>2</sub> and O<sub>3</sub> on photosynthesis

Elevated CO<sub>2</sub> increases the rate of photosynthesis, whereas increases in O<sub>3</sub> result in damage to the photosynthetic apparatus (e.g., Chapter 17). It was originally hypothesised that when these two gases are provided together, a CO<sub>2</sub>-induced reduction in g<sub>s</sub> would result in less opportunity for O<sub>3</sub> to diffuse into the intercellular air spaces (McKee *et al.*,

1995). This hypothesis led to the prediction that elevated CO<sub>2</sub> would provide some protection against the damaging effects of O<sub>3</sub> on photosynthetic tissues. Numerous experiments have provided support for this hypothesis, showing that in elevated CO<sub>2</sub> lower g<sub>s</sub> allows for less diffusion of O<sub>3</sub> into the leaf (McKee *et al.*, 1995, 1997; Fiscus *et al.*, 1997; Morgan *et al.*, 2003). Based on meta-analytic studies of the responses of photosynthesis to combined increases in CO<sub>2</sub> and O<sub>3</sub>, the presence of O<sub>3</sub> alone resulted in over a threefold decrease in photosynthetic rates relative to the combination of CO<sub>2</sub> and O<sub>3</sub> for soybean (Morgan *et al.*, 2003). A meta-analytic study focusing on trees also showed an approximate 20% reduction in saturated photosynthesis (A<sub>SAT</sub>) when exposed to a mean O<sub>3</sub> concentration of 87 ppb, whereas the combined CO<sub>2</sub> and O<sub>3</sub> treatments (mean O<sub>3</sub> concentration of 84 ppb) showed no statistically significant changes in A<sub>SAT</sub> (Wittig *et al.*, 2007). Although the evidence suggests that CO<sub>2</sub> confers protection from elevated O<sub>3</sub> on photosynthesis, such protective responses can be misleading. While CO<sub>2</sub> protects against O<sub>3</sub>, photosynthetic rates in the combined treatment are lower than for elevated CO<sub>2</sub> alone (Ainsworth *et al.*, 2002; Morgan *et al.*, 2003; Ainsworth, 2008).

### 34.3.2. The interactive effects of CO<sub>2</sub> and temperature on photosynthesis

The implications of increased temperature concomitant with rising CO<sub>2</sub> suggest, based on theoretical modelling, that photosynthetic rates will increase more than can be attributed to CO<sub>2</sub> itself (Long, 1991). When the photosynthetic model of leaf photosynthesis is considered, net carbon assimilation is a function of three separate biochemical pathways: the gross uptake of CO<sub>2</sub> via photosynthesis; the release of CO<sub>2</sub> via photorespiration; and the release of CO<sub>2</sub> via mitochondrial respiration (see Chapter 4). The synergistic influence of increases in CO<sub>2</sub> and temperature is driven by an increase in the amount of CO<sub>2</sub> as a substrate for photosynthesis, resulting in a higher rate of gross photosynthesis and the suppression of photorespiratory CO<sub>2</sub> release at higher temperatures resulting from fewer oxygenation events. Higher concentrations of CO<sub>2</sub> increase the thermal optimum of photosynthesis and, provided that photosynthesis is operating below the thermal optimum, the higher temperatures will result in higher photosynthetic rates that would be experienced if CO<sub>2</sub> and thus the thermal optimum were lower (Fig. 34.4). The basic understanding of this synergism is elucidated from employing the leaf model of photosynthesis (Farquhar *et al.*, 1980a), assuming that the underlying photosynthetic physiology is not influenced by the elevated temperature (Long, 1991). Modelling results also suggest that even a 40% reduction in the amount of Rubisco would yield higher photosynthetic rates at elevated temperature and CO<sub>2</sub> (Long, 1991).

Experimental evidence shows that the CO<sub>2</sub> enhancement of photosynthesis is increasingly favoured at higher temperatures for soybean, but not for rice (Vu *et al.*, 1997). Using natural variability in climatic conditions across three growing seasons for soybean, a clear trend toward higher CO<sub>2</sub>-induced stimulation in photosynthesis was observed with increasing daytime maximum temperatures (Bernacchi *et al.*, 2006). Research on trees shows variable responses to combined increases in CO<sub>2</sub> and temperature. For example, pine trees showed variable responses in enhancement of photosynthesis to elevated CO<sub>2</sub> and temperature relative to controls (Teskey, 1997). While species that employ the C<sub>3</sub> photosynthetic pathway show a variety of responses to combined CO<sub>2</sub> and temperature, it is likely that a combination of various factors cause the observed variability in results, including downregulation of photosynthetic machinery, stomatal responses, metabolic activities downstream from photosynthesis, canopy architecture and coupling between air and leaf temperatures and a range of other factors.

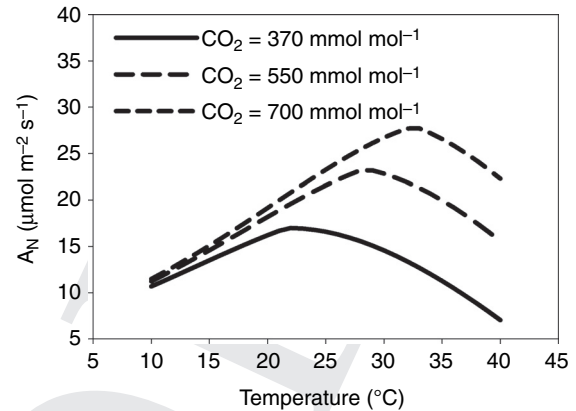


Fig. 34.4. Idealised photosynthetic response to temperature for three CO<sub>2</sub> concentrations using the leaf photosynthesis model of Farquhar *et al.* (1980). For all three scenarios, the parameters included in the model were identical (see Chapter 8) and the temperature responses of the parameters were based on Bernacchi *et al.* (2001, 2003).

### 34.3.3. Modelling plant responses to interactive effects

The reality of global change is that more than two factors that influence photosynthesis will occur. In the above sections, analyses were limited to two main interacting effects owing to the challenges of manipulating three or more global-change scenarios. Given the challenges, the scientific community must rely heavily on models. The mechanistic model of leaf photosynthesis (Farquhar *et al.*, 1980a) can be and has been used to predict responses to a wide range of environmental conditions (e.g., Long, 1991). However, this model is only useful to assess the responses to global-change scenarios if the changes in underlying photosynthetic physiology are well understood. For example, the maximum velocity for carboxylation ( $V_{c,max}$ , see Chapter 8) at 25°C is required for parameterisation of the model. There is evidence for some species that  $V_{c,max}$  changes with growth in elevated CO<sub>2</sub>. Thus, without knowledge of how  $V_{c,max}$  responds to specific growth conditions, it is difficult to model photosynthesis for these conditions. Although a large number of studies report values of  $V_{c,max}$  under single environmental changes or to two changes simultaneously, little data is available to assess how changes in three conditions, e.g., simultaneous increases CO<sub>2</sub>, O<sub>3</sub> and temperature, might influence  $V_{c,max}$ .

Scaling from the leaf to the plant, canopy or ecosystem results in increasing complexity and modelling at higher scales adds to the uncertainty in modelling. While

controlled experiments can be used to assess leaf and whole-plant photosynthetic responses to global change, the observed responses to these treatments at the smaller scales do not often scale to the canopy or ecosystem. Smaller-scale models are also unable to describe the interactions among various different species within an ecosystem. Thus ecosystem models are required to predict the possible influences of interacting global-change effects on plant productivity. For example, four separate ecosystem models were employed to address the impacts on productivity for numerous different ecosystems to varying global-change interactions (Luo *et al.*, 2008). While all four models were fairly consistent in estimation of main effects, e.g., increased CO<sub>2</sub> alone, the authors reported greater variability and inconsistency among the models when interacting effects were modelled. The results of modelling studies that focus on the interactions of numerous global-change scenarios are useful to identify weaknesses in mechanistic understanding of how plants might respond to interacting effects. Models might help investigators to fill in the knowledge gaps, but the model uncertainty is too great for using these tools to predict future ecosystem responses.

#### 34.4. POTENTIAL FEEDBACKS THAT PHOTOSYNTHESIS CAN HAVE ON THE CARBON CYCLE

There is little doubt that if the global-change scenarios presented in the last report of the Intergovernmental Panel on Climate Change (IPCC 2007) are realised, then further disruptions in ecosystem function will occur in coming decades. Arguably, the increases in CO<sub>2</sub> and temperature are going to have the most profound impact on ecosystem functioning and these two global-change factors are not mutually exclusive. While this book addresses photosynthetic responses to global-change scenarios, there is a growing body of research that addresses the potential for vegetation to mitigate many of the changes occurring (e.g., Canadell and Raupach, 2008). Although it is widely accepted that plants cannot reverse the trend toward increasing CO<sub>2</sub> and warmer environments – only improvements in fuel efficiency and alternatives to fossil fuels can accomplish this – there is strong potential for plants to provide offsets to the rise in CO<sub>2</sub>. This section will address three main research areas that use vegetation to: (1) sequester carbon; (2) provide renewable energy sources; and (3) to use vegetation for purposes of geological engineering. It is important to note that these three research areas contain some degree of overlap.

##### 34.4.1. Using photosynthesis to sequester CO<sub>2</sub>

In addition to their importance for food and shelter, plants have long been utilised as a source of energy. The combination of these major demands placed upon vegetation has resulted in food, fuel, fibre and wood industries that are not sustainable. Agricultural demand has resulted in an extensive release of CO<sub>2</sub> into the atmosphere. This includes carbon released through deforestation, which accounts for the second largest flux of CO<sub>2</sub> into the atmosphere behind fossil-fuel consumption (IPCC, 2007), and through the release of carbon from agricultural soils, which are predicted to have lost at least 50% of the organic matter relative to their natural state (Lal, 2004b). Given the amount of CO<sub>2</sub> emitted into the atmosphere as a result of ecosystem disturbances, questions remain whether a similar magnitude of CO<sub>2</sub> storage in woody tissues and soils can once again be achieved to mitigate a proportion of the increases in atmospheric CO<sub>2</sub>.

The opportunity to sequester carbon in soils is anticipated to be quite large provided proper management strategies and proper species are utilised. Predictions suggest that up to 0.9 Pg of carbon can be sequestered per year through a combination of various management practices that include the use of cover crops, optimal nutrient management and a range of other factors (Lal, 2004c). This would offset a large portion of the net ~3 Pg of carbon that is being emitted and retained by the atmosphere each year. In addition to sequestration of carbon in soils, a large amount of carbon can be sequestered in plant tissues through reforestation, restoration of native ecosystems and the establishment of perennial agricultural species to meet the demands for increasing populations and alternative renewable fuels. Further, current estimates suggest that, owing to combinations in CO<sub>2</sub> fertilisation and recovery from past disturbance events, tropical forests alone are sequestering ca 1.3 Pg C yr<sup>-1</sup> (Lewis *et al.*, 2009). Regardless of the technique employed to minimise the loss of carbon from soils, the input of carbon is based on photosynthetic uptake by plants. Given that natural ecosystems once contained a large amount of stored carbon in both soils and in plant tissue, the question remains whether we can utilise ecosystems' services to return carbon to a sequestered state.

##### 34.4.2. Photosynthesis as a renewable source of energy

As mentioned earlier in this chapter, the fossil-fuel reserves are quite likely large given that when these reserves were



formed, atmospheric concentrations were over 12 times their present value (Berner, 1990). Nevertheless, the ability to efficiently extract them from the ground is diminishing, resulting in more emissions associated with extraction of energy. Even with efficient extraction technologies, continued reliance on fossil fuels will have continued negative impacts on the global environment.

Photosynthesis is increasingly considered a viable alternative to reliance on fossil fuels. Both fossil fuels and bio-fuels are products of photosynthesis, however the latter is renewable and in theory does not result in increased emissions of greenhouse gases to the atmosphere. In reality, the agriculture industry relies heavily on fossil fuels for items ranging from diesel for tractors, combines and other farm machinery, nutrient and pesticide production, and transport and processing of the product. Thus, while the carbon emitted from combustion of alternative fuels would be recycled via photosynthesis during the next growing season or seasons, various carbon-lifecycle analyses of plant-based fuel sources estimate a wide range of energy efficiencies. Despite some concern that biofuels provide no net benefit or may consume more energy compared with using fossil fuels, most lifecycle analyses are shown to be inconsistent in their assumptions and are not based on known ecological processes (Davis *et al.*, 2009).

With regards to the traits that make a species 'ideal' for biomass production, long canopy duration, C<sub>4</sub> photosynthesis and high radiation-use efficiency were included among important attributes (Heaton *et al.*, 2004). Each of these three traits is directly related to photosynthesis. Long canopy duration maximises the amount of sunlight absorbed by the canopy over the growing season. Annual species are highly productive over a very short period of time but perennials, with longer growing seasons, can yield much higher rates of season-integrated photosynthesis (Fig. 34.5). While C<sub>4</sub> photosynthesis is listed as one of the traits suited optimally for biomass crops, it must also be considered that C<sub>4</sub> species are not well suited for all environments. Finally, high radiation-use efficiency is a trait that allows for the intercepted light

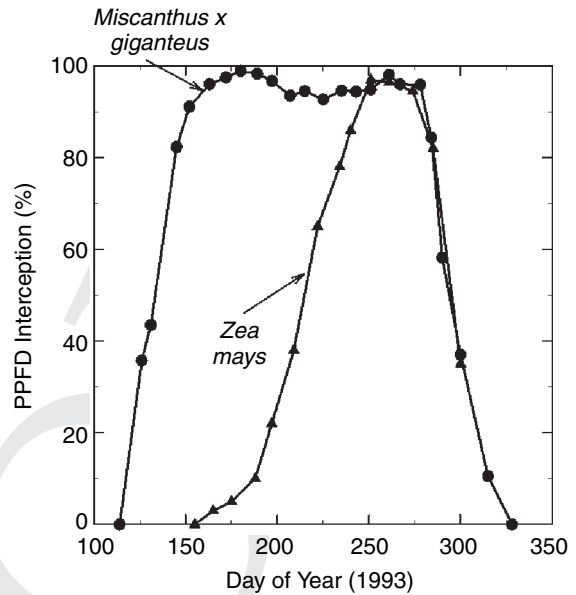


Fig. 34.5. The percentage of light intercepted relative to total available by three different plant canopies over the 1993 growing season. Data is presented for an annual species, *Zea mays*, and a perennial grass species, *Miscanthus X giganteus*. With the longer growing season associated with the perennials, more opportunity was available to convert sunlight into biomass via photosynthesis. Figure redrawn from U.S. DOE (2006).

to be utilised by photosynthesis with little being penetrated in the ground or reflected away. In a recent paper, it was estimated that maximum efficiency of C<sub>3</sub> photosynthesis is 4.6% and of C<sub>4</sub> species is 6.0% based on calculations from the total sunlight hitting a leaf to carbohydrate formation (Zhu *et al.*, 2008). Considering that total sunlight is seldom captured by a plant canopy and in most productive regions of the planet plants are growing for only a few months per year, the efficiency drops to much lower values. Thus, increasing or selecting species that exploit each of these three components can help to ensure that photosynthesis is maximised to increase growth and productivity.