REVIEW

Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO_2

NICHOLAS G SMITH* and JEFFREY S DUKES*†

*Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, IN 47907, USA, †Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907, USA

Abstract

To realistically simulate climate feedbacks from the land surface to the atmosphere, models must replicate the responses of plants to environmental changes. Several processes, operating at various scales, cause the responses of photosynthesis and plant respiration to temperature and CO_2 to change over time of exposure to new or changing environmental conditions. Here, we review the latest empirical evidence that short-term responses of plant carbon exchange rates to temperature and CO_2 are modified by plant photosynthetic and respiratory acclimation as well as biogeochemical feedbacks. We assess the frequency with which these responses have been incorporated into vegetation models, and highlight recently designed algorithms that can facilitate their incorporation. Few models currently include representations of the long-term plant responses that have been recorded by empirical studies, likely because these responses are still poorly understood at scales relevant for models. Studies show that, at a regional scale, simulated carbon flux between the atmosphere and vegetation can dramatically differ between versions of models that do and do not include acclimation. However, the realism of these results is difficult to evaluate, as algorithm development is still in an early stage, and a limited number of data are available. We provide a series of recommendations that suggest how a combination of empirical and modeling studies can produce mechanistic algorithms that will realistically simulate longer term responses within global-scale models.

Keywords: acclimation, carbon cycling, climate change, CO_2, ESM, nutrient limitation, photosynthesis, Q_{10}, respiration, temperature
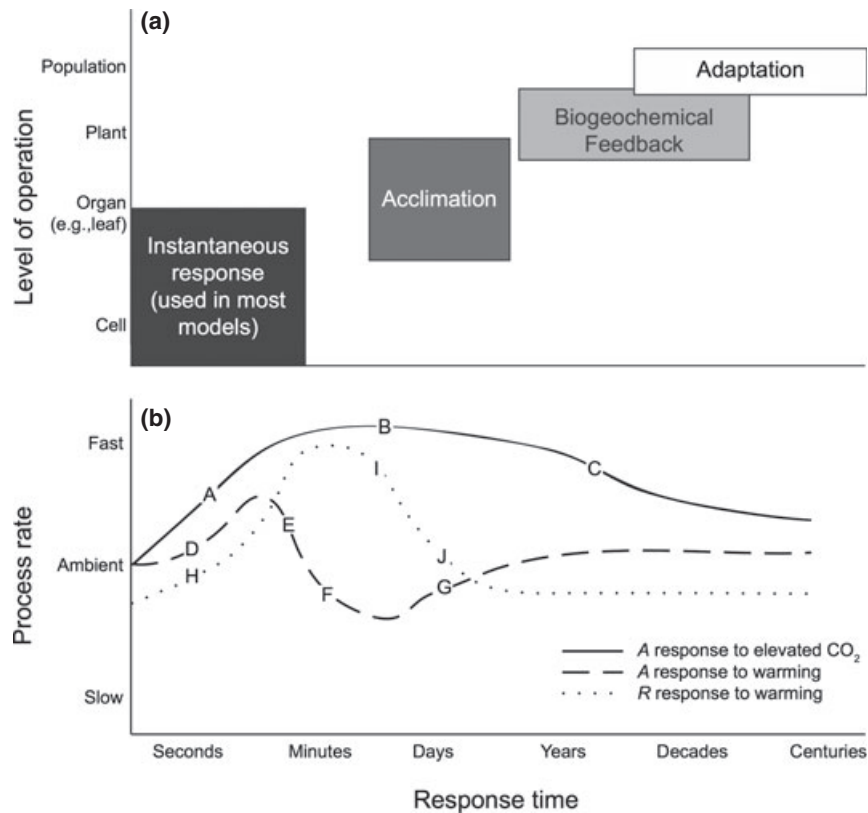
Introduction

The Intergovernmental Panel on Climate Change (IPCC) uses the output of Earth system models (ESMs; Collins *et al.*, 2011) to make projections of future rates of climate change. These models must accurately represent exchanges of carbon between the atmosphere and the land surface if they are to provide reliable estimates of terrestrial feedbacks to atmospheric CO_2 and warming. Thus, realistic simulation of photosynthesis and respiration in plants, two of the largest fluxes between land and atmosphere (IPCC, 2007), is critical.

Despite recent mechanistic improvements to the land model components of some ESMs (e.g., Sokolov *et al.*, 2008; Thornton *et al.*, 2009; Zaehle & Friend, 2010), many potentially important responses have not been incorporated, often because they remain poorly understood (Arneth *et al.*, 2010), or poorly quantified at scales relevant for models. Currently, ESM algorithms for plant carbon uptake and release are derived from equations

Correspondence: Nicholas G. Smith, tel. + 1 765 496 1764, fax + 1 765 494 9461, e-mail: ngsmith@purdue.edu

designed to simulate processes well at small scales (e.g., leaves), and to accurately represent short-term (e.g., minutes) responses to changes in environmental conditions. The mechanisms driving carbon exchange responses that occur over larger scales and longer time periods (see Fig. 1a) are rarely represented. These longer term responses become increasingly relevant in simulations that stretch across decades or centuries.

Here, we review the current understanding and recent implementation into vegetation models of three longer term responses involved in regulating photosynthesis and respiration: plant-level acclimation of (1) photosynthesis and (2) respiration to temperature and CO_2, and (3) nutrient limitation of plant responses to CO_2. We first review empirical evidence for these responses, and then examine the standard structure of carbon cycle models within land models, including those used as components of ESMs. Next, we discuss various methodologies for introducing acclimation processes into models and the implications of including them for regional and global carbon cycling and climate feedbacks. Finally, we propose a series of

Fig. 1 Scales and response times of factors modifying instantaneous plant responses to growth environment. (a) Conceptual graph of processes that determine how plant carbon exchange rates respond to environmental conditions. These processes operate over different scales and response times, and those with longer response times are often omitted from models. (b) Conceptual graph of the three responses mentioned in the manuscript over time: the response of photosynthetic assimilation (A) to elevated CO_2 (solid line) warming (dashed line), and autotrophic respiration (R) to warming (dotted line). Letters along each line indicate the influence of one of the following processes acting to change the shape of the curve: (A) release from diffusion limitation of CO_2, (B) stomatal reduction and closure, (C) biogeochemical (e.g., N, P) limitation, (D) photosynthetic enzyme stimulation, (E) increase in Rubisco deactivation, (F) photosynthetic enzyme degradation, (G) photosynthetic enzyme stabilization, (H) respiratory enzyme stimulation, (I) decrease in substrate availability, (J) respiratory enzyme stabilization. In each panel, the response time indicates the time after a given environmental stimulus (i.e., change in [CO_2] or temperature).

recommendations designed to help facilitate the incorporation of these responses in a mechanistic manner. Terrestrial plants respond to many facets of global change (nitrogen availability, precipitation, etc.), but for the purpose of this review we only address plant responses to projected increases in temperature and atmospheric CO_2. Also, we consider only physiological responses at the tissue level. Long-term changes in biomass allocation are certainly important (Franklin *et al.*, 2012), but are beyond the scope of this review. The goal of this review is not to evaluate model performance or argue for increased model complexity, but rather to highlight mechanisms that have been documented in the field, examine the degree to which they are understood and the degree to which they have been incorporated into leaf-level carbon exchange models, and to consider the barriers to and potential outcomes of their inclusion into global-scale models.

Acclimation of photosynthesis and plant respiration to temperature and CO_2

Plant acclimation, in the context of plant physiology, is a term used to describe a collection of biochemical and physiological responses of an individual plant to an environmental change, in which the plant's response to a sustained change is manifested as alterations in the short-term response functions of physiological processes (see Table 1 for further explanation as well as clarification of these and other terms used in the literature). The extent to which acclimation occurs depends on the stimulus and time since exposure, since these factors influence both substrate availability and the plant's capacity to make physiological, structural, and biochemical adjustments (see Fig. 1b). There now exists a compelling body of evidence in support of the existence of strong acclimatory responses that affect several

Table 1 Definitions of terms used in the discussion of plant responses and acclimation to temperature and CO_2

Term	Definition	Example
Instantaneous response	The initial plant response to an environmental stimulus that manifests before any type of physiological, structural or biochemical adjustment or limitation	Asymptotic increase in photosynthetic assimilation under instantaneously elevated CO_2 as a result of decreased diffusion limitation
Acclimation	A physiological, structural, or biochemical adjustment by an individual plant in response to an experimentally induced environmental stimulus that is manifested as alterations in the short-term response function of a physiological process	An increase in the optimum temperature for photosynthesis as a result of an extended increase in temperature during plant growth
Acclimatization	Similar to acclimation, but responses are a result of natural (e.g., seasonal, latitudinal, altitudinal) changes in an environmental condition. In this context, changes in the environmental condition of interest may co-vary with changes in other environmental conditions	A decrease in the optimum temperature of photosynthesis in plants growing at increasingly high altitudes, where temperature and moisture differences may co-vary
Adaptation	The response of a species over multiple generations to a physical or environmental stimulus that acts to increase growth, survival, and/or reproduction	An alteration in structural cooling mechanisms as a result of an evolutionary response to increased temperature
Homeostasis	The maintenance of a process rate, after an environmental stimulus, at or near the original rate seen before the stimulus. Homeostasis is not necessary for acclimation, and, in terms of plant carbon exchange responses to temperature and CO_2, is likely more the exception than the rule	After extended exposure to an increase in temperature, photosynthesis and respiration rates return to the rates seen prior to the temperature increase
Biogeochemical feedback	Feedback to plant growth, survival, and/or reproduction due to an alteration in the physical environment resulting from an individual or community response to an environmental change	A decrease in environmental nitrogen availability after a sustained period of enhanced photosynthesis in a community responding to elevated CO_2
Type I acclimation	A change in the instantaneous response of a process to a stimulus that results in an alteration of the shape (or slope) of the response and not necessarily the basal rate (or intercept), resulting in larger rate changes only at higher stimulus levels. This type of change is likely a result of biochemical adjustments	A decrease in the Q_{10} of respiration in plants grown under increasingly warmer conditions, resulting in rate changes at high temperatures, but not at low temperatures
Type II acclimation	A change in the basal rate (intercept), but not necessarily the slope of a response to a stimulus. This results in rate changes of a process at all levels of a stimulus. This type of change is likely a result of biochemical adjustments and/or biogeochemical feedbacks	A decrease in low- and high-temperature basal rates of respiration in plants grown under increasingly warmer conditions

key plant responses to environmental forcing. Below, we describe the nature of this evidence, to provide support for our contention that these processes should be represented in land surface models as a matter of course.

Temperature response of plant carbon exchange

The instantaneous response of many plant carbon exchange processes to changes in temperature is attributed to changes in enzymatic activity, where temperature increases stimulate enzyme activity, resulting in an increase in rates up to an optimum temperature at which the rates peak. Beyond the optimum, rates begin to decline. The reason for this decline is not well understood for many processes (including respiration and photosynthesis). The decline in photosynthesis at high temperature may be related to Rubisco; the activation state of Rubisco is an equilibrium between deactivation and activase-promoted activation, both of which increase at high temperatures. At high temperatures, enzyme deactivation may increase to the point that it exceeds the capacity of activase enzymes to promote activation (Crafts-Brandner & Salvucci, 2000).

Respiration is often shown to peak at temperatures higher than that seen for photosynthesis, with decreases possibly resulting from substrate limitation or enzymatic degradation (Atkin & Tjoelker, 2003).

Temperature acclimation is an adjustment of the instantaneous temperature response and can take two forms, known as Type I and Type II acclimation. Type I acclimation refers to adjustments in the shape of the instantaneous response curve as a result of regulatory changes in existing enzymes. This results in little to no change in process rates at low temperatures where rates are limited by enzymatic activity, but instead alters rates at high temperatures at or near the optimum where rates are more limited by substrate availability. Type II acclimation does not necessarily result in changes in the shape of the instantaneous function, but instead results in changes in the base rate or overall capacity of the process (the intercept of the temperature response curve), leading to a decrease in the elevation of the temperature response curve with warming, and consequently a greater degree of homeostasis than Type I acclimation (Atkin & Tjoelker, 2003; Atkin et al., 2005).

Photosynthetic acclimation can be observed as shifts in the instantaneous response of net photosynthesis to temperature, or more specifically the enzymatic processes that drive photosynthesis, such as the carboxylation rate of Rubisco (V_{max}) or the electron transport rate (J_{max}). This is often observed as changes in the shape and/or base rate (Type I and Type II responses, respectively) of the instantaneous response for these processes in response to changes in growth temperature, often resulting in changes in the optimum temperature (T_{opt}; see Fig. 2a). Photosynthetic temperature acclimation has been attributed to increases in enzymatic heat tolerance (Berry & Bjorkman, 1980; Hikosaka et al., 2006), but may also result from a changed expression or activation state of the Calvin cycle enzymes (Stitt & Hurry, 2002), through stomatal adjustment (Lin et al., 2012), or as a result of allocation of enzymes to different metabolic processes such as light capture under higher temperatures (Xu et al., 2012).

Gunderson et al. (2010) studied T_{opt} of net photosynthesis in seedlings of five deciduous tree species under three temperature treatments, and found that T_{opt} was significantly correlated with daytime plot temperature in all treatments, with acclimation potentials ranging from 0.55 to 1.07 °C change in T_{opt} per degree change in daytime temperature. This type of adjustment occurred not only in response to the warming treatments (acclimation), but also on a seasonal basis (acclimatization; see Table 1) (Gunderson et al., 2010). It is important to distinguish between acclimation and acclimatization responses in empirical studies because in
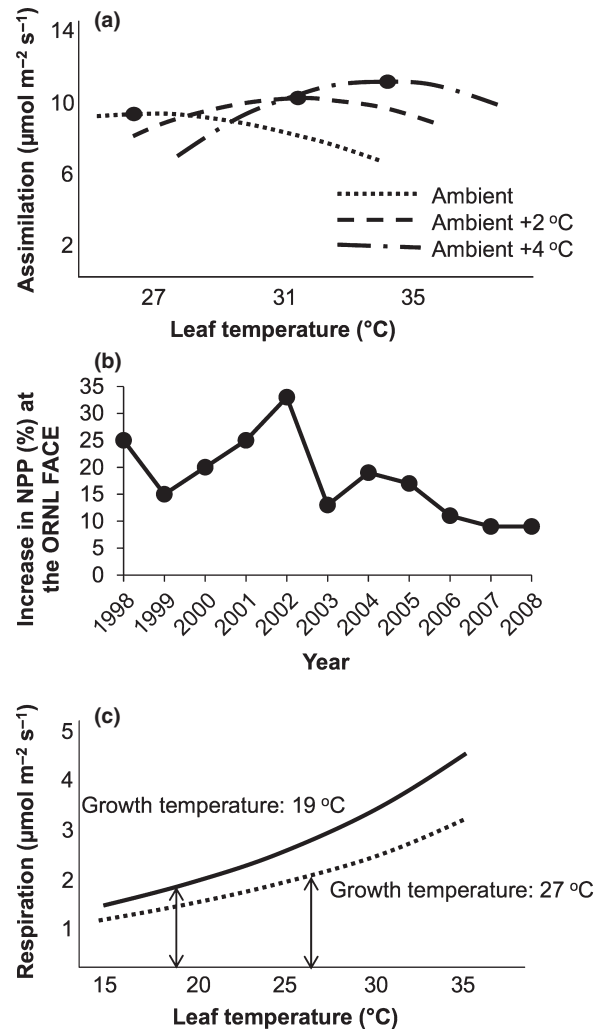
Fig. 2 Empirically assessed responses. (a) The mean photosynthetic response of six field-grown *Quercus rubra* seedlings to instantaneous changes in temperature. The three lines show the response of seedlings grown at the ambient temperature (dotted line), 2 °C above ambient temperature (dashed line), and 4 °C above ambient temperature (dot-dash line). Note the shift in the temperature optimum (circles) in the seedlings grown under elevated temperatures. Modified from Gunderson et al. (2010). (b) The percent increase in NPP under elevated CO_2 (~550 ppm) in a *Liquidambar styraciflua* forest stands over 11 years at the Oak Ridge National Laboratory Free-Air CO_2 Enrichment (ORNL FACE) experiment in Tennessee. Note that the response decreases from year 1 (25%) to year 11 (9%), possibly indicating long-term down-regulation of photosynthetic machinery in response to nutrient limitation. Modified from Norby et al. (2010). (c) The instantaneous response of leaf respiration to temperature in *Populus balsamifera* grown under two different day/night temperature treatments: 19/10 °C (solid line) and 27/16 °C (dotted line). The circles denote the respiration rate at the growth temperature for each treatment. The respiration rate at the growth temperature is very similar in both treatments, indicating acclimation of the seedlings to their respective growth temperature. Modified from Silim et al. (2010).

studies examining acclimatization, which occurs across a natural (e.g., seasonal, altitudinal, latitudinal) temperature gradient, an array of environmental factors may co-vary with temperature and alter the acclimation response, which results only from the change in temperature. However, this distinction is not necessarily important for modeling studies that systematically isolate temperature responses from other environmental responses (thus examining acclimation only).

Photosynthetic acclimation to temperature has been observed in many species, spanning a wide range of plant functional types, including deciduous trees (Slatyer & Morrow, 1977; Battaglia *et al.*, 1996; Gunderson *et al.*, 2000, 2010; Kositsup *et al.*, 2009), coniferous trees (Hikosaka *et al.*, 1999; Medlyn *et al.*, 2002b), shrubs (Smith & Hadley, 1974), and herbaceous species (Atkin *et al.*, 2006; Hikosaka *et al.*, 2006; Bunce, 2008). An analysis of 36 species of various plant functional types found that plants generally adjust their photosynthetic apparatus to maintain an optimal photosynthetic rate at a given growth temperature (Kattge & Knorr, 2007). However, species vary in whether and to what degree they acclimate (Berry & Bjorkman, 1980). The ability to acclimate may be greater in fast-growing species than that in slow-growing species (Atkin *et al.*, 2006), and may also depend on plant functional type (Tjoelker *et al.*, 1998; Bunce, 2008; Volder *et al.*, 2010). Also, there is evidence that plants that experience a more variable thermal environment, such as temperate species, may have a greater ability to acclimate than plants grown in an environment where temperature does not vary as much during the growing season (Billings *et al.*, 1971; Berry & Bjorkman, 1980; Xiong *et al.*, 2000; Cunningham & Read, 2002) (see Table 2). It is difficult to compare photosynthetic acclimation to temperature across studies because a variety of factors affecting the temperature response of photosynthesis, including biochemical responses, daytime respiration (R_d), and stomatal responses to changes in vapor pressure deficit (D), and soil moisture that are not always accounted for (see Lin *et al.*, 2012).

As the temperature of their growing environment changes, plants can adjust their respiratory rate through adaptive responses that alter the instantaneous temperature response (Berry & Bjorkman, 1980; Atkin & Tjoelker, 2003; Armstrong *et al.*, 2008). Although many studies show that the instantaneous response is exponential over a wide range of temperatures, with Q_{10} values at or near 2, the response is more complex over large temperature ranges. In fact, Q_{10} values have been shown to decrease as temperatures increase along the instantaneous curve, resulting in a peaked response similar to the one seen for photosynthesis (Tjoelker *et al.*, 2001).

Several studies have recorded changes in the instantaneous response of respiration to temperature with changes in growth temperature (see Fig. 2c), either through Type I or Type II acclimation, as a result of changes in mitochondrial abundance, protein composition, and/or electron transport rates (Armstrong *et al.*, 2008). This pattern has been seen in the leaves, stems, and roots of a wide range of plant species from a wide range of ecosystems (Smith & Hadley, 1974; Ziska & Bunce, 1998; Loveys *et al.*, 2003; Wright *et al.*, 2006; Tjoelker *et al.*, 2009). However, the degree to which plants adjust their respiratory rate in response to long-term changes in temperature varies by location (Billings *et al.*, 1971; Larigauderie & Korner, 1995) and plant functional type (Tjoelker *et al.*, 1999; Atkin *et al.*, 2006). There is evidence to support the idea that young plants (Atkin *et al.*, 2006; Campbell *et al.*, 2007) and plants grown in more variable environments (Billings *et al.*, 1971) may possess a greater ability to adjust their respiratory rate in response to changes in temperature. Tissue age and tissue type also affect acclimatory ability (Atkin *et al.*, 2005). In addition, respiratory responses of roots, which have been shown to be less sensitive to temperature than leaves (Loveys *et al.*, 2003), may be influenced by soil symbionts such as arbuscular mycorrhizal fungi, which decreased cold acclimation in *Plantago lanceolata* (Atkin *et al.*, 2009). To better understand the mechanisms behind responses, future studies of whole plants should also consider the responses of specific plant tissues, and not just the leaf.

CO_2 response of plant carbon exchange

Plant photosynthetic machinery can also stabilize in response to elevated levels of atmospheric CO_2. Over short periods of time, CO_2 often accelerates photosynthesis (e.g., Norby *et al.*, 2005), but plants may down-regulate photosynthetic activity over longer timeframes through physiological and biochemical adjustments (Lee *et al.*, 2001, 2011; Ainsworth & Long, 2005; Crous *et al.*, 2010). This often comes as a result of biochemical (Cook *et al.*, 1998; Tjoelker *et al.*, 1998; Juurola, 2003), structural (Kirschbaum, 2011), or resource limitation (Drake *et al.*, 1997; Reich *et al.*, 2006a; Norby *et al.*, 2010; Reddy *et al.*, 2010). As the atmospheric CO_2 concentration increases, intercellular CO_2 (C_i) levels rise, decreasing diffusion limitation of some processes, and leading to short-term increases in photosynthesis. Eventually, although, some of the other processes that regulate plant growth (e.g., light harvesting, carbohydrate export, nitrogen uptake) become unbalanced, there is some evidence that plants reallocate resources away from CO_2 fixation in favor of these newly limiting processes. For example, if the plant is unable to use the

Table 2 Studies documenting sources of variation in acclimation of plant carbon exchange rates to temperature and elevated atmospheric concentrations of carbon dioxide

Source of variation	Photosynthetic response to temperature	Photosynthetic response to CO_2	Respiration response to temperature
Plant species/ functional type	Atkin et al. (2006), Bunce (2008), Dillaway & Kruger (2010), Gunderson et al. (2010), Tjoelker et al. (1998), Volder et al. (2010)	Leakey et al. (2009a), Lee et al. (2011), Reich et al. (2006b), Tjoelker et al. (1998)	Atkin et al. (2006), Loveys et al. (2003), Volder et al. (2010), Wright et al. (2006)
Location/ biome	Berry & Bjorkman (1980), Billings et al. (1971), Cunningham & Read (2002), Smith & Hadley (1974), Xiong et al. (2000)	Leakey et al. (2009a), Reich et al. (2006b)	Billings et al. (1971), Larigauderie & Korner (1995), Smith & Hadley (1974), Wright et al. (2006)
Species/ tissue age	Campbell et al. (2007)		Atkin et al. (2005, 2006), Campbell et al. (2007)
Interactive effects	Dillaway & Kruger (2010), Lin et al. (2012)	Drake et al. (1997), Hickler et al. (2008), Reich et al. (2006b)	Atkin et al. (2008, 2009), Crous et al. (2011), Tjoelker et al. (1999), Wright et al. (2006)
Length of study		Cook et al. (1998), Lee et al. (2011), Norby et al. (2010), Reich et al. (2006b)	

extra carbohydrates that are created through increased photosynthesis, then a decrease in photosynthetic activity follows via feedback inhibition pathways (Drake et al., 1997; Kirschbaum, 2011). Cook et al. (1998) found that the Icelandic grassland species *Nardusstricta* down-regulated its photosynthetic apparatus in response to over 100 years of CO_2 enrichment (790 μmol mol^{-1}). The same study found a decrease in leaf-level photosynthetic capacity at a given C_i (25%), chlorophyll content (33%), and Rubisco content (26%), and activity (40%) in plants grown in an enriched environment compared to those grown in ambient conditions (Cook et al., 1998). A recent 11-year grassland free air CO_2 enrichment (FACE) study found that plants grown under elevated CO_2 down-regulated their stomatal conductance and leaf nitrogen content similarly across four functional groups. These reductions caused a decrease in assimilation compared to what would be expected under elevated CO_2. However, the down-regulation of stomatal conductance and leaf nitrogen did not fully explain the photosynthetic acclimation seen in this study (Lee et al., 2011).

Results from some FACE studies suggest that a CO_2 fertilization effect may be seen even after Rubisco down-regulation (Ainsworth & Long, 2005; Leakey et al., 2009a). However, the fertilization response likely depends on genetic and environmental factors and the length of the study. For example, species limited by Rubisco carboxylation capacity at elevated CO_2 show greater fertilization effect compared to those limited by ribulose-1,5-bisphosphate regeneration capacity at elevated CO_2 (Ainsworth & Rogers, 2007). Also, plants grown in low nutrient systems may exhibit stronger

down-regulation and decreased CO_2 response compared to those in high nutrient systems (Ainsworth & Long, 2005). Similarly, positive responses of photosynthesis to CO_2 may decrease over time in longer term studies due to limitation by nutrients (e.g., nitrogen) needed to sustain the short-term response, a phenomenon known as progressive nutrient limitation (PNL) (Luo et al., 2004; Reich et al., 2006b; Lukac et al., 2010). Observations of a gradual decline in growth stimulation in long-term FACE studies have been attributed to PNL. Researchers at a FACE site in Tennessee, USA observed a significant decline in productivity enrichment under elevated CO_2 over 11 years (see Fig. 2b), which coincided with a decrease in nitrogen uptake in that system (Norby et al., 2010). Also, a grassland FACE study in the north-central USA found that increased plant growth under elevated CO_2 was only sustained where nutrients did not become limiting (Reich et al., 2006a). Plants in some systems, however, may be able to overcome PNL through enhanced root growth, litter decomposition, and microbial nitrogen release (Zak et al., 2011). Reich et al. (2006a) reviewed the effect of PNL, specifically nitrogen limitation, on plant production under elevated CO_2 in a variety of site-level studies. Although they noted that decreased nitrogen availability should eventually decrease photosynthetic enhancement from elevated CO_2, the two studies they reviewed (in managed pasture and temperate grassland) did not detect photosynthetic enhancement under varying nitrogen levels, even though both studies found significant biomass responses. These results indicate that these systems may be more sensitive to carbon-nitrogen interactions at the whole system scale,

as opposed to the leaf scale (Reich *et al.*, 2006b). However, more studies are needed in different systems to better understand these mechanisms.

Most studies suggest plant respiration does not respond directly to increases in atmospheric CO_2 concentration (Ziska & Bunce, 1998; Tjoelker *et al.*, 1999; Gifford, 2003; Gonzalez-Meler *et al.*, 2004; Atkin *et al.*, 2005), but the effect of CO_2 on respiration is still poorly understood (Gonzalez-Meler *et al.*, 2004). Respiration is directly influenced by photosynthesis, in that photosynthesis provides the substrate needed for respiratory metabolism (Bouma *et al.*, 1995; Kromer, 1995). As a result, respiration may respond in a way similar to photosynthesis due to increased growth and maintenance demands under elevated CO_2. Some studies on soybean suggest that elevated CO_2 enhances nighttime respiration due to increased substrate availability and respiratory gene expression (Ainsworth *et al.*, 2006; Leakey *et al.*, 2009a,b), but others have found contradicting results in the same species (Bunce, 2005). More research is needed to more fully understand the response of plant respiration to elevated CO_2 across a wider range of species.

Respiration-photosynthesis coupling

Some empirical studies do not treat plant photosynthesis and respiration as separate entities, but instead measure both rates in response to climatic conditions and describe these rates as a ratio of plant respiration to photosynthesis (*R:P*). The *R:P* ratio of plants directly correlates with carbon use efficiency (CUE) in that CUE = 1 − (R/P) (Gifford, 2003). Some studies show that this ratio remains constrained under many growth conditions (Ziska & Bunce, 1998; Loveys *et al.*, 2002, 2003; Gifford, 2003; Atkin *et al.*, 2005, 2006; Van Oijen *et al.*, 2010). This ratio may, however, increase under high growth temperature (Tjoelker *et al.*, 1999; Loveys *et al.*, 2002; Atkin *et al.*, 2007; Campbell *et al.*, 2007; Harley *et al.*, 2007; Way & Sage, 2008), presumably due to heat stress and the need for plants to allocate more carbon to maintenance respiration than to growth and storage. In addition, although respiration and photosynthesis are physiologically linked (Bouma *et al.*, 1995; Kromer, 1995), the processes have different temperature responses, regardless of time scale (see Fig 2a and c). Finally, the 'threshold' stress level where *R:P* ratio deviations are seen is hard to define empirically due to interactions and co-variations among stressors (e.g., temperature, soil moisture, nutrients, light availability), which makes it difficult to incorporate these deviations into models. At least one long-term field study shows that this ratio is unaffected by CO_2 concentration (Tjoelker *et al.*, 1999). The results from the studies reviewed here provide strong evidence for long-term acclimation of photosynthesis to temperature and CO_2 forcing and respiration to temperature forcing; we conclude that these processes are strong candidates for inclusion into Earth System Models.

Model survey

Process-based models use interactive algorithms to describe plant responses to environmental conditions. These algorithms are designed to replicate physiological rates and responses recorded in lab and field observations and experiments. These algorithms often incorporate prescribed values that are fixed; they do not change. To avoid confusion in the text, we use the term 'parameters' for these fixed numbers within algorithms that are prescribed by the model and do not respond to environmental stimuli. We use the term 'response variables' for variables within algorithms that can change in response to environmental stimuli, often through the use of another algorithm that incorporates one or many parameters. The use of static parameters rather than dynamic response variables to represent plants' responses to environmental forcing leads to algorithms with instantaneous responses that do not adjust in response to changes in the environment (Wythers *et al.*, 2005). These algorithms (many of which are described in detail in the next section) thus assume that plants cannot acclimate to changes in environmental conditions. At some level, all algorithms use fixed parameters; however, to incorporate the acclimation responses mentioned above, the instantaneous response to an environmental stimulus such as temperature or CO_2 must be allowed to change over the duration of exposure to that stimulus (i.e., be represented in the form of a dynamic response variable). An increasing number of models have begun to incorporate algorithms with dynamic response variables that allow models to simulate acclimation and/or optimization of carbon exchange rates in plants, as well as effects of changing nitrogen availability on production, allowing for the possibility of nitrogen cycle feedbacks to photosynthesis when coupled to a nitrogen model (Luo & Reynolds, 1999; Sitch *et al.*, 2003; King *et al.*, 2006; Kattge & Knorr, 2007; Thornton *et al.*, 2007, 2009; Atkin *et al.*, 2008; Sokolov *et al.*, 2008; Kattge *et al.*, 2009; Friend, 2010; Zaehle & Friend, 2010; Zaehle *et al.*, 2010; Ziehn *et al.*, 2011).

We surveyed 17 vegetation models, most of which are primary components of current-generation ESMs, to assess their structure with respect to terrestrial plant carbon exchange. The survey evaluated the physiological processes within each model in terms of their ability to capture the three long-term processes reviewed in

this study: (1) photosynthetic acclimation to temperature, (2) autotrophic respiration acclimation to temperature, and (3) photosynthetic acclimation to CO_2 through photosynthetic limitation by other biogeochemical processes under elevated CO_2. Although some of the models surveyed attempted to account for one or two of the processes reviewed here, none of the 17 models surveyed incorporated dynamic response variables for both photosynthetic and plant respiratory responses to temperature and CO_2, meaning that none of the models could simulate simultaneous plant photosynthetic and respiratory acclimation to temperature and CO_2 concentration (Fig. 3). In the following sections, we review common algorithms used to simulate temperature and
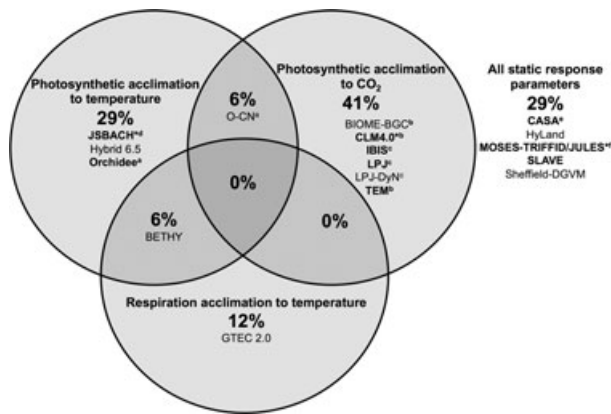
Fig. 3 Incorporation of dynamic plant carbon exchange responses into land models. Results from a review of 17 process-based models, examining which models incorporated dynamic plant carbon exchange responses. Note that none of the models surveyed incorporated all three dynamic responses. Bold names denote models used in the C[4]MIP (Friedlingstein *et al.*, 2006). Note that some of the C[4]MIP models have been updated since 2006 to include the responses evaluated here and are denoted with an asterisk (*). [a]ORCHIDEE and O-CN allow for dynamic response of photosynthesis to temperature only in C[3] grasses. [b]Model mediates photosynthetic response to CO_2 through environmental nitrogen limitation. [c]Model mediates photosynthetic response to CO_2 through optimization of V_{cmax}. Note that IBIS-2 (used in the C[4]MIP) did not use the optimization response of V_{cmax}. [d]Newer unpublished versions of JSBACH exist which include dynamic nitrogen and phosphorus cycles (D. Goll, personal communication). [e]CASA model does include dynamic nitrogen and phosphorus cycles, but these only constrain NPP, not photosynthesis and/or respiration. [f]JULES has been modified to include respiration acclimation in at least one study (Atkin *et al.*, 2008). [g]To the authors' knowledge, SLAVE is not currently in active use or development, but is included in the diagram and Table 3 due to its use in the CMIP[4] simulations. Full citations for each of the models can be found in Table 3. Note that alternate versions exist for some of the models referenced here (e.g., JSBACH-CN). See Table 3 for the full list of citations for the model versions used to construct this diagram.

CO_2 responses of plant carbon exchange in models as well as some recent mechanistic formulations designed to facilitate the incorporation of long-term dynamics of these processes.

Common models of plant carbon exchange

To simulate photosynthesis, many models use a derivation of the Farquhar *et al.* (1980) model of photosynthesis (FvCB). In this biochemical model, photosynthesis is simulated as a function of rate-limiting processes involved in the photosynthetic pathway, including the electron transport rate (A_j), carboxylation rate (A_c), and, in some cases, triose phosphate utilization rate (TPU) such that:

$$A_n = \min(A_c, A_j, TPU) - R_d \quad (1)$$

where A_n is the net rate of photosynthesis. A_c and A_j are described using the maximum rates of each process (V_{cmax} and J_{max} for carboxylation and electron transport, respectively) such that (modified from Medlyn *et al.* (2002a)):

$$A_c = \frac{V_{cmax}(C_i - \Gamma^*)}{C_i + K_c\left(1 + \frac{O_i}{K_o}\right)} \quad (2)$$

and

$$A_j = \left(\frac{J}{4}\right)\left[\frac{C_i - \Gamma^*}{C_i + 2\Gamma^*}\right] \quad (3)$$

and

$$\theta J^2 - (\alpha Q + J_{max})J + \alpha Q J_{max} = 0 \quad (4)$$

where C_i is the intercellular concentration of CO_2, O_i is the intercellular concentration of O_2, Γ^* is the CO_2 compensation point, K_c and K_o are Michaelis–Menton coefficients, θ is the curvature of the light response curve, Q is the photosynthetically active photon flux density, and α is the quantum yield of electron transport. J_{max} and V_{cmax} can be described using fixed parameters or dynamic response variables that (in most cases) respond to temperature and/or leaf nitrogen. Instantaneous temperature functions include basic Q_{10} functions (Collatz *et al.*, 1991) or peaked Arrhenius functions in which the temperature response of either J_{max} or V_{cmax} [$f(T_k)$] is described by the equation [from Medlyn *et al.* (2002a)]:

$$f(T_k) = k_{25} \exp\left[\frac{E_a(T_k - 298)}{298RT_k}\right] \frac{1 + \exp\left(\frac{298\Delta S - H_d}{298R}\right)}{1 + \exp\left(\frac{298\Delta S - H_d}{298T_k}\right)} \quad (5)$$

Table 3 Description of photosynthesis (A) and autotrophic respiration (R) responses for the 17 models reviewed in the model survey

Model Name	Temperature response of A	Temperature response of R	Biogeochemical feedback to A	Main Citations[*]
BETHY	Acclimation of carboxylation and regeneration to previous 30-day temperature	Q_{10}-type function that linearly decreases with temperature	Carboxylation is a function of leaf nitrogen, but does not include nitrogen model	Kattge et al. (2009), Knorr (2000), Ziehn et al. (2011)
BIOME-BGC	Q_{10}-type increase with temperature, when temperature >15 °C. This rate is divided by the Q_{10} when temperatures are <15 °C	Constant Q_{10} function	Carboxylation is a function of leaf nitrogen, and can be used with nitrogen model	Nemani et al. (2009), Wang et al. (2011)
CASA	T_{opt} for NPP is defined by temperature during the month of highest NDVI. A drops off above and below T_{opt}	Not explicitly defined	None, but NPP does respond to environmental nitrogen and phosphorus	Potter et al. (1993), Wang et al. (2010)
Community Land Model (CLM4.0)	Carboxylation has Q_{10}-style relationship	Maintenance: exponential function of temperature. Growth: 30% of total C in new growth	Carboxylation is a function of nitrogen, includes nitrogen model	Oleson et al. (2010), Thornton et al. (2009, 2007)
GTEC 2.0	CO_2 fertilization of NPP increases with temperature	Acclimation to previous four days temperature	None	King et al. (2006, 1997)
Hybrid 6.5	Acclimation of optimum temperature of electron transport	Mitochondrial respiration is modeled using and Arrhenius-type response	Carboxylation and electron transport are directly related to leaf nitrogen, but does not include nitrogen model	Friend (2010)
HyLand	Arrhenius increase in FvCB parameters with temperature	None; constant fraction of A	Carboxylation and electron transport are directly related to leaf nitrogen, but does not include nitrogen	Levy et al. (2004)
IBIS	None	None for leaf, Arrhenius function for stem and root	None, but A is optimized (in IBIS-1 only); which accounts for down-regulation under high CO_2	Friedlingstein et al. (2006), Kucharik et al. (2000)
JSBACH	Acclimation of carboxylation and regeneration to previous 30-day temperature up to 55 °C	Maintenance: constant exponential response to temperature. Growth: 20% of net photosynthesis	None (but see JSBACH-CN and JSBACH-CNP)	Raddatz et al. (2007)
Lund-Potsdam-Jena (LPJ)	Limited at high and low temperatures	Maintenance respiration is described using a constant modified Arrhenius function in response to temperature	None, but A is optimized; which accounts for down-regulation under high CO_2	Sitch et al. (2003)
LPJ-DyN	Limited at high and low temperatures	Maintenance respiration is described using a constant modified Arrhenius function in response to temperature	Similar to LPJ, but includes a full nitrogen cycle. Although, nitrogen does not directly influence A	Xu & Prentice (2008)
MOSES-TRIFFID/ JULES	Carboxylation has Q_{10} dependence with temperature. A drops at very high and very low temperatures that differ based on PFT	Growth respiration is 25% of GPP. Maintenance respiration is 1.5% of V_{cmax} (for C_3 plants). Acclimation to previous 10 days temperature was incorporated in JULES by Atkin et al. (2008)	Carboxylation is a function of leaf nitrogen, no nitrogen sub-model	Atkin et al. (2008), Clark et al. (2011), Cox (2001)

Table 3 (continued)

Model Name	Temperature response of A	Temperature response of R	Biogeochemical feedback to A	Main Citations[*]
O-CN	Arrhenius increase in FvCB parameters with temperature; T_{opt} prescribed, with values shifting with temperature for C_3 grasses	Maintenance respiration is described using a constant modified Arrhenius function in response to temperature	Function of nitrogen availability, and includes full nitrogen model	Krinner et al. (2005), Zaehle & Friend (2010)
Orchidee	Arrhenius increase in FvCB parameters with temperature; T_{opt} prescribed, with values shifting with temperature for C_3 grasses	Maintenance respiration is described using a constant modified Arrhenius function in response to temperature	Function of nitrogen availability, but does not include a full nitrogen model	Krinner et al. (2005)
Sheffield-DGVM	Carboxylation and regeneration change in accordance to a third degree polynomial	Function showing steep increase with temperature, followed by a sharp drop at high temperature	Maximum photosynthesis is constrained by nitrogen uptake, not combined with N model	Woodward et al. (1995)
SLAVE	T_{opt} for NPP is defined by temperature during the month of highest NDVI; P drops off above and below T_{opt}	Not explicitly defined	None	Field et al. (1995), Friedlingstein et al. (1995)
Terrestrial ecosystem model (TEM)	Increases with temperature up to T_{opt}	Q_{10}-type response with Q_{10} decreasing with temperature via third degree polynomial	Function of nitrogen availability, and includes full nitrogen model	McGuire et al. (1992), Sokolov et al. (2008)

[*]Not all references for a given model incorporate the process responses for that model in the same way.

where k_{25} is the rate of J_{max} or V_{cmax} at 25 °C, E_a is the increase in the response below the temperature optimum, T_k is the leaf temperature in Kelvin, R is the universal gas constant (8.314 J mol^{-1} K^{-1}), H_d is the rate of decrease above the optimum, and ΔS is an entropy term related to the temperature optimum (T_{opt}) such that:

$$\Delta S = \frac{H_d}{T_{opt}} + R \ln\left[\frac{H_a}{H_d - H_a}\right] \qquad (6)$$

where T_{opt} describes the optimum temperature for J_{max} or V_{cmax} and H_a is the exponential increase below the optimum; analogous to E_a in Eqn (5). This relationship allows Eqn (5) to be written in an equivalent form such that:

$$f(T_k) = k_{opt} \frac{H_d \exp\left(\frac{H_a(T_k - T_{opt})}{T_k R T_{opt}}\right)}{H_d - H_a\left(1 - \exp\left(\frac{H_d(T_k - T_{opt})}{T_k R T_{opt}}\right)\right)} \qquad (7)$$

where k_{opt} is the rate of J_{max} or V_{cmax} at the optimum. These algorithms, unless adjusted, assume that photosynthetic response to temperature and CO_2 does not change over time due to the fixed nature of the parameters k_{25}, E_a, H_d, H_a, T_{opt}, and k_{opt}. Nitrogen response functions within the FvCB model usually follow the often-observed linear response of V_{cmax} to leaf nitrogen (e.g., Kattge et al., 2009). The models have the potential to facilitate the incorporation of nitrogen limitation under elevated CO_2, but only if they are used in conjunction with a nitrogen cycling model (see following section).

Of the models that do not use a version of the FvCB, model many instead use a light use efficiency (LUE)-type algorithm, which is based on the observations of Monteith (1972), Monteith & Moss (1977) that productivity or photosynthesis is proportional to light interception. Net photosynthesis is described as:

$$A_n = LUE^* APAR \qquad (8)$$

where LUE is a term describing the efficiency of the plant to convert light into usable sugars and APAR is the fraction of radiation absorbed by the canopy. LUE models only respond to light; they cannot account for plant responses to growth temperature or carbon dioxide level unless they are adjusted (e.g., Medlyn, 1996).

To date, a detailed mechanistic model for autotrophic respiration, similar to the FvCB model for photosynthesis, has not been created. So, models must use more generalized calculations to simulate responses of respiration to temperature. As such, most models either use a function with a fixed Q_{10} parameter or assume that an unchanging portion of the carbon fixed through photosynthesis is lost via respiration. A function incorporating

a fixed Q_{10} parameter does not facilitate temperature acclimation and assumes that respiration increases exponentially with temperature (but see discussion of temperature dependent Q_{10} below). In contrast, a fixed ratio of respiration to photosynthesis (*R:P*) does allow for changes in the temperature response of respiration over time as a consequence of changes in photosynthesis. This function is acclimatory in a sense, but the validity of the *R:P* assumption has been debated by the empirical community (see above). *R:P* models are further discussed in the following section.

Adjusting models to incorporate acclimation

The absence of long-term plant carbon exchange responses in most process-based models (see Fig. 3) can no longer be attributed to a lack of suitable algorithms. Initial versions of carbon exchange algorithms have been designed to incorporate (1) photosynthetic acclimation to temperature,(2) respiratory acclimation to temperature, (3) a dynamic photosynthetic response to atmospheric CO_2 concentration (in the form of progressive nitrogen limitation), and (4) coupling of respiration to photosynthesis.

Dynamic response of photosynthesis to temperature

Two different algorithms have been created to incorporate photosynthetic acclimation to temperature change (Kattge & Knorr, 2007; Friend, 2010) into the commonly used FvCB model of photosynthesis. The first algorithm, formulated by Friend (2010), adjusts the temperature response of the electron transport rate (*J*) described by June *et al.* (2004) (Eqn 9 below) to include temperature acclimation. This algorithm, in accordance with empirical evidence, allows the optimum temperature for *J* to respond to changes in growth or leaf temperature such that:

$$J(T_L) = J(T_o)\exp\left[-\frac{T_L - T_o}{\Omega}\right]^2 \qquad (9)$$

where T_L is the leaf temperature, T_o is the optimum leaf temperature for *J*, and Ω is a parameter controlling the response on either side of T_o. Friend (2010) then assumed that T_o decays toward an equilibrium during daylight hours following:

$$\frac{dT_o}{dT} = -\lambda(T_o - T_e) \qquad (10)$$

where T_e is the equilibrium temperature and λ is the decay constant set to -3.3e-6. Finally T_e was described as having a linear relationship with T_L that maximized GPP in a Pennsylvania deciduous forest, using the following equation:

$$T_e = 17 + 0.35 T_L \qquad (11)$$

where T_L is defined using daylight hours only. Inclusion of this dynamic algorithm into a global model only stimulated NPP by 2.55% globally compared to a model run with a static formulation (i.e., Eqn 9 only). However, in regions cooler than Pennsylvania, where the algorithm was optimized, NPP was stimulated up to 20%, whereas decreases in NPP in warmer regions offset this stimulation. These results highlight the need for acclimation to be represented in a plant type- and/or location-specific way (Friend, 2010).
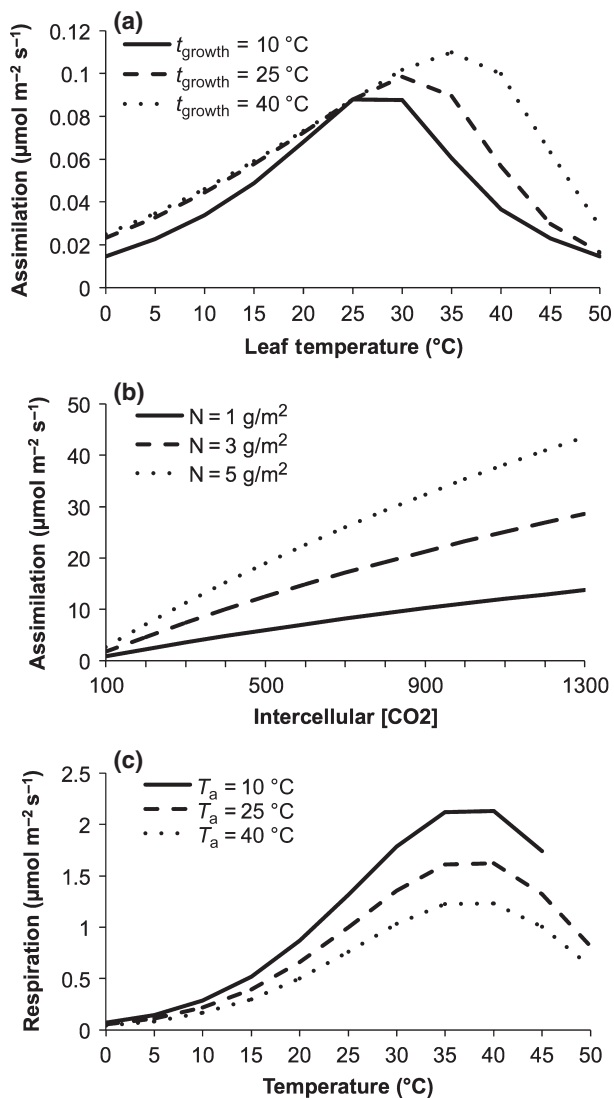
A second algorithm, formulated by Kattge & Knorr (2007), allows for temperature acclimation of J_{max} and V_{cmax} (see Fig. 4a). The adjustment is based on the linear response of the optimum temperature for J_{max} and V_{cmax} to growth temperature from an analysis of 36 species. The algorithm follows from Eqn (5) above and allows the ΔS term for J_{max} and V_{cmax} as well as the ratio of J_{max} to V_{cmax} (r_{jv}) to respond linearly to the average growth temperature of the past 30 days (t_{growth}) in the following way:

$$x_i = a_i + b_i t_{growth} \qquad (12)$$

where x_i is ΔS or r_{jv}, and b_i and a_i are the slope and intercept, respectively, defined separately for each relationship. Empirically derived values for a_i and b_i can be found in Kattge & Knorr (2007). In addition, posterior values gained from a Markov Chain Monte Carlo simulation can be found in Ziehn *et al.* (2011). The algorithm is specifically designed for incorporation into global models, and has been incorporated into at least two published global simulations (Kattge *et al.*, 2009; Ziehn *et al.*, 2011) (discussed below). One potential problem with this model is that it may underestimate optimum temperature values for J_{max}. The values found by Kattge & Knorr range from 19.2 to 38.8 °C in plants growing under temperatures that varied from 11 to 30 °C (Kattge & Knorr, 2007). Results from at least one recent field study fall within this range (Bauerle *et al.*, 2007). However, tobacco plants grown under high temperature and high light had optimum temperature values for J_{max} values in excess of 40 °C (Yamori *et al.*, 2010). More research is needed to increase confidence in this value across warm-climate functional types.

Dynamic response of autotrophic respiration to temperature

At least two groups (McGuire *et al.*, 1992; Tjoelker *et al.*, 2001) have formulated algorithms to alleviate the problematic issue of using a fixed Q_{10} to model plant respiration by incorporating a temperature-dependent Q_{10} that more closely matches the instantaneous response

Fig. 4 Dynamic responses of plant carbon exchange to temperature and CO_2. (a) The dynamic response of photosynthesis to temperature given by the modified Farquhar *et al.* (1980) model of photosynthesis described by Kattge & Knorr (2007), which incorporates the acclimation of J_{max} and V_{cmax} to growth temperature (shown here as 'tgrowth'). Curves are shown for t_{growth} values of 10 °C (solid line), 25 °C (dashed line), and 40 °C (dotted line). Photosynthesis calculations follow Eqns (1–5) and (12) in the text. Parameterization for Eqn (12) follows from values given in Kattge & Knorr (2007). V_{cmax} is normalized to 1 at 25 °C. $[C_i]$ is set at 380 μmol mol^{-1}, $[O_i]$ at 2100 μmol mol^{-1}, Q at 1500 μmol m^{-2} s^{-1}, θ at 0.9, and α at 0.3 mol electrons mol^{-1} photon. (b) The response of photosynthesis to changes in intercellular CO_2 given by a modified Farquhar *et al.* (1980) model designed by Kattge *et al.* (2009) to incorporate the photosynthetic response to leaf nitrogen content. The solid, dashed, and dotted lines show the response at a leaf nitrogen level of 1, 3, and 5 g m^{-2}, respectively. All three lines show the response of a C_3 meadow forb species, with parameters defined by Kattge & Knorr (2007) and Kattge *et al.* (2009). Photosynthesis calculations again follow Eqns (1–5) in the text with settings similar to panel a. Leaf temperature is fixed at 25 °C. (c) The response of dark respiration to temperature given by a respiratory acclimation algorithm (dotted line) described by Atkin *et al.* (2008) with growth temperatures (defined as T_a in the model) set at 5 °C (solid line), 25 °C (dashed line), and 40 °C (dotted line). The unacclimated rate is defined using Eqns (13) and (14) in the text and is adjusted using a correction factor given by Eqn (19) in the text. T_{ref} in all cases is set to 25 °C, at which respiration rates are normalized to 1 μmol m^{-2} s^{-1}. A C value of -0.00794, the value defined for the log$R$-log$N$ relationship for preexisting leaves by Atkin *et al.* (2008), is used.

of respiration seen in the field. First, designers of the Terrestrial Ecosystem Model (TEM) used an early textbook example (Larcher, 1980) showing the decline of the Q_{10} of maintenance respiration with temperature. They fit a third degree polynomial to a dataset in which the value for Q_{10} stayed at about 2 at moderate temperatures between 5 and 20 °C, increased to 2.5 between 5 and 0 °C and decreased to 1.5 between 20 and 40 °C, with temperatures corresponding to the mean monthly temperature (McGuire *et al.*, 1992). Tjoelker *et al.* (2001) took this a step further by using field data from 56 species spanning from arctic to tropical species to fit a linear model for a temperature-dependent Q_{10} such that:

$$R_T = R_{ref}Q_{10}^{\left(\frac{T-T_{ref}}{10}\right)} \tag{13}$$

and

$$Q_{10} = 3.22 - 0.046T \tag{14}$$

where R_T is the rate of respiration at temperature (T) and R_{ref} is the rate of respiration at a reference temperature T_{ref} (Tjoelker *et al.*, 2001). These alterations cause the increase in respiration to decrease at higher temperatures and, in the case of the Tjoelker *et al.* (2001) model, produce a temperature optimum at which respiration peaks. These formulations are certainly a more realistic representation of the instantaneous response than a fixed Q_{10}, but they still do not incorporate acclimation to longer term growth conditions.

In contrast, a few research groups have formulated algorithms that do simulate acclimation of plant respiration to temperature (Wythers *et al.*, 2005; King *et al.*, 2006; Atkin *et al.*, 2008; Ziehn *et al.*, 2011). The first acclimation algorithm, formulated by King *et al.* (2006), follows from the work of Wythers *et al.* (2005). Wythers *et al.* (2005) used field data, including data from (Tjoelker *et al.*, 2001), on the temperature dependence of Q_{10}, to adjust algorithms used by the PnET family of models to incorporate temperature dependence of the Q_{10} of foliar respiration (an instantaneous adjustment similar to Eqn 14) and full acclimation of foliar respiration to

temperature. However, these algorithms were designed for an ecosystem-scale model. King et al. (2006) adjusted these algorithms for inclusion into a global-scale model. Their first algorithm is a derivation of the temperature-dependent Q_{10} algorithm of Tjoelker et al. (2001) that instead uses the energy of activation (E_{aT}) to describe the rate of respiration at any temperature T (R_T):

$$R_T = R_{ref} \exp \left[\left(\frac{E_{aT}}{RT_{ref}} \right) \left(\frac{1-T}{T_{ref}} \right) \right] \qquad (15)$$

where R_{ref} is the respiration rate at a reference temperature T_{ref}. The second algorithm modifies the first to create a full acclimation adjustment of the instantaneous response (i.e., Eqn 15) where R_a is the rate of respiration acclimated to T_a, which is defined as the average temperature over the four previous days, following:

$$R_a = R_{ref} \frac{R_T (1 - (0.9935 \ln(T_a) - 2.8308)}{R_T - 0.5(R_T - 1)} \qquad (16)$$

where R_T is the rate at T from Eqn (15). This algorithm was created using empirical data from warming experiments, including that of (Gunderson et al., 2000), and other published and unpublished data (A. King, personal communication). A global model incorporating these algorithms simulated greater global carbon storage than was seen in a simulation with a fixed temperature-sensitivity algorithm, with carbon storage being highest in the simulation incorporating the full acclimation model (i.e., Eqn 16) (King et al., 2006). These results are interesting, but the data used to parameterize the model were limited. More empirical research is needed to help quantify the response of respiration to temperature across a wider range of species and plant functional types.

Although they do not report its impact on carbon fluxes, Ziehn et al. (2011) incorporated acclimation of autotrophic respiration in a modified version of BETHY, using a temperature-dependent formulation for the instantaneous response such that:

$$R_T = R_{ref} \exp \left(-\frac{T - T_{ref}}{10} \right)$$
$$\left(\frac{(3.22 - 0.046T)^{(3.22-0.046T)/-0.046*10}}{(3.22 - 0.046T_{ref})^{(3.22-0.046T)/-0.046*10}} \right) \qquad (17)$$

where the relationship between the rate of respiration at the reference temperature (R_{ref}) and the rate of carboxylation at a reference temperature ($V_{cmax, ref}$; similar to k_{25} in Eqn 5) acclimates to 30 day growing temperature (t_{growth}) such that:

$$R_{ref} = \left[i_{Rd} - S_{Rd}(t_{growth} - T_{ref}) \right] V_{cmax,ref} \qquad (18)$$

where i_{Rd} and s_{Rd} are the intercept and slope of the relationship, respectively. The parameterization of the model differed for C_3 and C_4 species. The equation followed from results of a group of empirical studies (Tjoelker et al., 2001; Atkin et al., 2005; Wythers et al., 2005) and the full derivation can be found in the supplementary materials of Ziehn et al. (2011). Although the impact of respiratory acclimation was not explicitly evaluated in this study, the results did show that the model was highly sensitive to changes in s_{Rd} for both C_3 and C_4 species (Ziehn et al., 2011).

A final algorithm has been developed using the log-log relationship between leaf respiration, leaf mass-to-area ratio, and leaf nitrogen content (R-LMA-N) in 19 species of plants grown at four different temperatures, to account for respiratory acclimation to thermal history. Atkin et al. (2008) found that thermal history accounted for 20% of the variability in the log-log R-LMA-N relationship, with the impacts being highly predictable. From these experimentally derived relationships, they created an algorithm for whole plant respiration that incorporates the temperature to which the plant is acclimated using the following relationship:

$$R_a = R_T 10^{C(T_a - T_{ref})} \qquad (19)$$

where R_T is the unacclimated rate of respiration, T_{ref} is the reference temperature, T_a is the average daily temperature in the preceding 10 days, and C is a constant that takes into account variation in the intercept of the log-log relationships that is due to acclimation to T_a. The authors then incorporated this algorithm into a global model using a C value defined for the log-log relationship between leaf nitrogen and respiration for preexisting leaves ($C = -0.00794$) and found that the new algorithms led to large decreases in respiration in warm, tropical regions, and moderate increases in cool, temperate ecosystems. These changes largely offset each other, implying that the incorporation of respiratory acclimation into models may be more important for regional-scale results than for those evaluated on a global scale (Atkin et al., 2008).

Dynamic response of photosynthesis to CO_2

Several new modeling approaches permit dynamic responses of photosynthesis to CO_2 by allowing the CO_2 fertilization response to become limited by environmental nitrogen availability. The models include the CLM-CN (Thornton et al., 2009), TEM (Sokolov et al., 2008), and O-CN (Zaehle & Friend, 2010) models, each of which couple carbon assimilation with environmental nitrogen availability. These models also include full nitrogen cycles as part of the biogeochemical model

that is coupled with the vegetation model, a requirement for incorporating nitrogen limitation responses to photosynthesis. Carbon-nitrogen (CN) coupling has been shown to reduce simulated global carbon uptake in response to elevated CO_2 by up to 74% (Thornton *et al.*, 2007). Zaehle *et al.* (2010) found that this effect was slightly dampened in mid-high latitudes when dynamic temperature effects were considered. However, this dampening was minor on the global scale, due to offsetting responses in tropical regions. Although they are more mechanistically comprehensive, dynamic CN models still do not account for down-regulation of photosynthesis in response to limitation by other factors that might limit photosynthesis (e.g., phosphorus, Lewis *et al.*, 2010), particularly in tropical regions of the world (Townsend *et al.*, 2011; but see Wang *et al.*, 2010).

These models are still very recent, and may be further enhanced by a comprehensive understanding of how nitrogen effects photosynthesis, such as was attained by Kattge *et al.* (2009), who used >700 data points from empirical studies to quantify the linear response of V_{cmax} to leaf nitrogen content for 10 plant functional types. These functions, used in conjunction with the temperature acclimation algorithm mentioned above (Kattge & Knorr, 2007), reduced the error between observed productivity (given by stand-scale data for relevant forest vegetation types) and modeled global productivity by 17% globally, and up to 40% in some regions. However, this simulation did not include a full nitrogen cycle, which likely would have affected these results (Kattge *et al.*, 2009).

Some vegetation models use an optimization principle to model plant carbon exchange [e.g., Lund-Potsdam-Jena (LPJ), IBIS]. The basis behind this principle is that Rubisco capacity (V_{cmax}), which governs photosynthesis and respiration in these models, is optimized by plants to maintain a maximum rate of carbon gain under the ambient PAR levels. Thus, carboxylation is only up-regulated if the increase in carbon uptake is not 'outweighed' by the carbon lost in respiration (see Haxeltine & Prentice, 1996a,b; Sitch *et al.*, 2003). This phenomenon does not correspond to a mechanism observed in the field, but could potentially produce results consistent with Rubisco down-regulation in response to elevated CO_2. These types of optimization models provide a simple alternative to more mechanistically complex models, but the omission of important mechanisms that drive these responses, such as nitrogen limitation of photosynthesis, may decrease the predictive ability of this approach. A recent model of nitrogen optimization has also been developed and has shown promising results in terms of simulating photosynthetic responses to altered environmental conditions such as elevated CO_2

and temperature, but this model uses assumptions that have yet to be fully validated in the field (Xu *et al.*, 2012). More empirical research is needed to investigate the biological relevance of optimization-type responses, as they may prove to be important, overlooked mechanisms.

Respiration to photosynthesis coupling

Many process-based models prescribe a constant *R:P*, or similarly *GPP:NPP*, ratio (Potter *et al.*, 1993; Aber *et al.*, 1996; Landsberg & Waring, 1997; Kucharik *et al.*, 2000; Pepper *et al.*, 2005; Thornton & Rosenbloom, 2005; Van Oijen *et al.*, 2005; Sokolov *et al.*, 2008; Kattge *et al.*, 2009; Nemani *et al.*, 2009; Friend, 2010). This assumes that all plants release the same percentage of CO_2 assimilated through photosynthesis regardless of climate. This relationship is acclimatory in the sense that changes in photosynthesis in response to temperature result in adjustments of the response of respiration to temperature; however, if deviations from this ratio occur under stressful environmental conditions, as has been seen in many empirical studies (Tjoelker *et al.*, 1999; Loveys *et al.*, 2002; Atkin *et al.*, 2007; Campbell *et al.*, 2007; Harley *et al.*, 2007; Gratani *et al.*, 2008; Way & Sage, 2008), then the use of a constant ratio would yield unrealistic results. The validity of the use of a constant *R:P* ratio likely depends on the time scale of interest in the study, as variations in the ratio seen over short time scales may average out over longer periods of time. Additional empirical investigations of carbon flow in terrestrial systems that follow from theoretical analyses (e.g., Van Oijen *et al.*, 2010) are needed to better describe the *R:P* relationship at time scales relevant for climate models.

Suggestions for experimental-modeling collaboration

We have highlighted three processes that have been shown to affect the responses of plant carbon exchange to environmental changes in the field, but that are rarely incorporated into ESMs. We believe these processes constitute ideal examples of areas in which more detailed interactions between experimental and modeling activities would be beneficial. Such combined model-experiment endeavors can lead to the design of field experiments with models in mind (e.g., by measuring responses used in common carbon exchange models) and the use of models to help guide experimental research (e.g., identifying responses that the model does a poor job of simulating).

To design models that more accurately simulate feedbacks between the atmosphere and terrestrial ecosystems, empirical studies should continue to assess

variation in plant acclimatory ability, of which there are many sources (see Table 2). More empirical data can be used to improve confidence in algorithms over a wider range of species; in particular, representatives of the functional types that are used in models, but not often studied experimentally, such as tropical species. However, these measurements must be taken in a way that can benefit modeling studies. For example, photosynthetic acclimation to temperature can be measured relatively simply, by recording how temperature optima of net photosynthesis shift in response to changes in growth environment (e.g., Slatyer & Morrow, 1977; Mooney *et al.*, 1978; Gunderson *et al.*, 2010). However, in most models, specifically those implementing versions of the FvCB model, net photosynthesis is a function of photosynthetic capacity and stomatal conductance. Therefore, the temperature responses of variables within biophysical models (e.g., V_{cmax} and J_{max}) are more important for model formulation. The temperature responses of these variables are less often evaluated (e.g., Medlyn *et al.*, 2002b; Bauerle *et al.*, 2007; Silim *et al.*, 2010) as the measurements are more time-intensive, but these responses should receive greater attention in future studies. Also, researchers should be careful about controlling for additional factors that affect the temperature response of photosynthesis, including daytime respiration responses to temperature and stomatal responses to vapor pressure deficit (Lin *et al.*, 2012). Finally, although most studies examine acclimatory responses of photosynthesis in terms of shifting temperature optima, shifts in the slope and/or intercept of the initial instantaneous response could be of equal or greater importance, particularly at suboptimal temperatures.

Respiratory temperature acclimation is typically treated differently than photosynthetic acclimation. The instantaneous respiratory response to temperature resembles an exponential response over a wide range of temperatures, which leads to the representation of respiratory responses using Q_{10} values and/or basal respiration rates (rates at a standard temperature) rather than temperature optima (e.g., Billings *et al.*, 1971; Smith & Hadley, 1974; Gifford, 1995; Larigauderie & Korner, 1995; Tjoelker *et al.*, 1999, 2009). However, as noted above, the instantaneous response is not truly exponential; rather, it is a peaked function similar to the one seen for photosynthesis (Tjoelker *et al.*, 2001), albeit with a much higher optimum temperature. Investigators should be careful not to treat the response as strictly exponential, particularly in cases where the optimum cannot be reached experimentally. In such cases, researchers should carefully examine changes in the instantaneous response or Q_{10} values between temperature intervals, which might allow for estimation of the

temperature optimum. Since a biochemical model has not been developed for plant respiration, these measurements should be taken with acclimatory models in mind (e.g., King *et al.*, 2006; Atkin *et al.*, 2008) to ensure that the measurements can be easily used to parameterize such models. In the case of temperature responses of photosynthesis and respiration, a great deal of uncertainty remains as to how plants respond at very high temperatures. As such, future studies should examine responses at high temperatures, beyond the optimum.

Acclimation responses can be assessed in as little as a few days, but it may take years to identify and characterize biogeochemical limitations (see Fig. 1). Therefore, longer term experiments are needed to assess these responses in the field. However, more controlled experiments could be used to examine the cumulative effect of elevated CO_2 and experimentally altered nutrient availability on plant carbon exchange processes. There are many regions in which these types of studies are underrepresented – tropical regions in particular (Luo, 2007). Comparisons of the responses of tropical plants with those of temperate plants would help to determine the importance of seasonal climatic variability for acclimation potential. Multi-factor field experiments can help determine the importance of interactive effects of other elements of global change (e.g., water availability (Crous *et al.*, 2011) and temperature effects on nitrogen mineralization (Rustad *et al.*, 2001)) for plant carbon exchange responses to temperature and CO_2 (Luo, 2007). Consideration also should be given to how temperature and CO_2 affect the allocation of carbon within plant leaves (e.g., Loveys *et al.*, 2002) and among different organs (e.g., Ziska & Bunce, 1998), as these likely have important implications for $R:P$ ratios and long-term carbon storage (Franklin, 2007).

The interactive effects of elevated CO_2 and temperature should also be considered, particularly with regard to photosynthesis. Some models, including the FvCB model, predict that stimulation of photosynthesis by elevated CO_2 will be greatest in warm regions of the world (Hickler *et al.*, 2008). Empirical tests of this prediction, as well as simulations using modifications of such models that include the long-term responses mentioned here would provide valuable insight into its validity. Of particular interest would be the evaluation of this response within a model framework that allows for biogeochemical limitation of photosynthesis.

In addition, when considering long-term responses, field studies should give consideration to whether plant tissues developed under new growth conditions. Tissues developed under new growth conditions have been shown to have higher acclimatory potential than those forced to respond to environmental changes after development (Stitt & Hurry, 2002; Atkin & Tjoelker,

2003; Campbell *et al.*, 2007). Over time scales relevant to the ongoing changes in climate (e.g., decades), changes in developmental conditions will likely influence photosynthetic and respiratory plant carbon fluxes.

Model parameterization will also likely benefit from the use of plant trait databases (e.g., TRY (Kattge *et al.*, 2011)), which are becoming more readily accessible. For example, Ziehn *et al.* (2011) used leaf-level plant trait data and a Bayesian random sampling method to constrain a modified version of the Farquhar *et al.* (1980) model. The authors found that this method was able to significantly reduce uncertainty in the global simulation of leaf photosynthesis. However, much of the remaining uncertainty was associated with temperature acclimation and stomatal response to CO_2, implying that more empirical research is needed to refine the understanding of these responses (Ziehn *et al.*, 2011).

Comparisons of results from model simulations that do and do not incorporate these types of acclimation algorithms (e.g., through benchmarking activities (Randerson *et al.*, 2009)) will also have value for the empirical and modeling communities. Early results suggest that incorporation of dynamic responses can lead to gross over- or underestimation of global fluxes of terrestrial carbon relative to those predicted by static models (King *et al.*, 2006; Thornton *et al.*, 2007) and may have even greater influences at local scales (Wythers *et al.*, 2005; Atkin *et al.*, 2008; Kattge *et al.*, 2009; Friend, 2010). Although these results highlight the potential impact of the incorporation of these long-term responses, they do not highlight areas that need further empirical evaluation. Therefore, sensitivity analyses that investigate which parameters have the largest impact on the model output will be useful (e.g., Zaehle *et al.*, 2005; Ziehn *et al.*, 2011; Booth *et al.*, 2012). Such an analysis was performed by Ziehn *et al.* (2011), who found that after using plant trait data to reduce the uncertainty in net leaf assimilation, four parameters associated with temperature acclimation of photosynthesis and respiration and the stomatal response to CO_2 could explain the majority of the remaining variation in net leaf assimilation in a terrestrial biosphere model (BETHY). Additional sensitivity studies can help to identify the most important parameters within models, and also when, to what extent, and at what scales the processes leading to acclimation and biogeochemical limitation are relevant and need to be taken into account in global models. Ultimately, these studies should investigate how the inclusion of these longer term responses of vegetation to changes in temperature or CO_2 translates to long-term changes in the carbon pool size at and above the level of the ecosystem.

Conclusions

Results from field experiments suggest that the algorithms for plant carbon exchange (i.e., photosynthesis and respiration) used in many models do not accurately represent long-term responses. Specifically, plant photosynthesis and respiration can acclimate to long-term changes in temperature and elevated CO_2, and photosynthetic responses to elevated CO_2 can be down-regulated due to biogeochemical limitations. Several groups have devised new, and adjusted old, carbon cycling algorithms to account for these dynamic responses in a mechanistic manner (e.g., King *et al.*, 2006; Kattge & Knorr, 2007; Thornton *et al.*, 2007; Sokolov *et al.*, 2008; Friend, 2010; Zaehle & Friend, 2010). These new algorithms have been incorporated into some models (e.g., King *et al.*, 2006; Thornton *et al.*, 2007, 2009; Atkin *et al.*, 2008; Sokolov *et al.*, 2008; Kattge *et al.*, 2009; Friend, 2010; Zaehle *et al.*, 2010; Ziehn *et al.*, 2011), but to date, to our knowledge, no published model has incorporated independent dynamic responses of both plant photosynthesis and respiration to temperature and CO_2 (Fig. 3). These longer term responses may act to increase (temperature acclimation) or decrease (biogeochemical limitation) terrestrial productivity and carbon storage. As these responses each act on different time scales and may differ by region, the cumulative effect is difficult to predict.

We do not suggest that models incorporating the mechanisms mentioned in this study will immediately simulate observed conditions more accurately; rather, we suggest that the omission of important biological mechanisms for the purpose of matching observed data or simplifying model structure may lead researchers to unwittingly sacrifice the quality of future climate projections in the name of better representing current conditions. Rather than developing models that produce the right answer for what might be the wrong reason, we should seek to incorporate known mechanisms now, and observe how the inclusion of these mechanisms alters projected climate feedbacks. Results from such experiments are important not only for evaluating the models themselves but also for identifying areas that deserve immediate attention from the empirical community.

References

Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. *Oecologia*, **106**, 257–265.

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist*, **165**, 351–371.

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant, Cell & Environment*, **30**, 258–270.

Ainsworth EA, Rogers A, Vodkin LO, Walter A, Schurr U (2006) The effects of elevated CO_2 concentration on soybean gene expression. An analysis of growing and mature leaves. *Plant Physiology*, **142**, 135–147.

Armstrong AF, Badger MR, Day DA et al. (2008) Dynamic changes in the mitochondrial electron transport chain underpinning cold acclimation of leaf respiration. *Plant, Cell & Environment*, **31**, 1156–1169.

Arneth A, Harrison SP, Zaehle S et al. (2010) Terrestrial biogeochemical feedbacks in the climate system. *Nature Geoscience*, **3**, 525–532.

Atkin OK, Tjoelker MG (2003) Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, **8**, 343–351.

Atkin OK, Bruhn D, Hurry VM, Tjoelker MG (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, **32**, 87–105.

Atkin OK, Scheurwater I, Pons TL (2006) High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congeneric. *Global Change Biology*, **12**, 500–515.

Atkin OK, Scheurwater I, Pons TL (2007) Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytologist*, **174**, 367–380.

Atkin OK, Atkinson LJ, Fisher RA et al. (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Global Change Biology*, **14**, 2709–2726.

Atkin OK, Sherlock D, Fitter AH et al. (2009) Temperature dependence of respiration in roots colonized by arbuscular mycorrhizal fungi. *New Phytologist*, **182**, 188–199.

Battaglia M, Beadle C, Loughhead S (1996) Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology*, **16**, 81–89.

Bauerle WL, Bowden JD, Wang GG (2007) The influence of temperature on within-canopy acclimation and variation in leaf photosynthesis: spatial acclimation to microclimate gradients among climatically divergent *Acer rubrum* L. genotypes. *Journal of Experimental Botany*, **58**, 3285–3298.

Berry J, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, **31**, 491–543.

Billings WD, Godfrey PJ, Chabot BF, Bourque DP (1971) Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna-d*. *Arctic and Alpine Research*, **3**, 277–289.

Booth BB, Jones CD, Collins M et al. (2012) High sensitivity of future global warming to land carbon cycle processes. *Environmental Research Letters*, **7**, 024002, pp. 8, doi:10.1088/1748-9326/7/2/024002.

Bouma TJ, De Visser R, Van Leeuwen PH, De Kock MJ, Lambers H (1995) The respiratory energy requirements involved in nocturnal carbohydrate export from starch-storing mature source leaves and their contribution to leaf dark respiration. *Journal of Experimental Botany*, **46**, 1185–1194.

Bunce JA (2005) Response of respiration of soybean leaves grown at ambient and elevated carbon dioxide concentrations to day-to-day variation in light and temperature under field conditions. *Annals of Botany*, **95**, 1059–1066.

Bunce JA (2008) Acclimation of photosynthesis to temperature in Arabidopsis thaliana and Brassica oleracea. *Photosynthetica*, **46**, 517–524.

Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V (2007) Acclimation of photosynthesis and respiration is asynchronous in response to

changes in temperature regardless of plant functional group. *New Phytologist*, **176**, 375–389.

Clark DB, Mercado LM, Sitch S et al. (2011) The Joint UK land environment simulator (JULES), model description – Part 2: carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, **4**, 701–722.

Collatz GJ, Ball JT, Grivet C, Berry JA (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis, and transpiration - a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, **54**, 107–136.

Collins WJ, Bellouin N, Doutriaux-Boucher M et al. (2011) Development and evaluation of an Earth-system model – HadGEM2. *Geoscientific Model Devevelopment Discussion*, **4**, 997–1062.

Cook AC, Tissue DT, Roberts SW, Oechel WC (1998) Effects of long-term elevated CO_2 from natural CO_2 springs on Nardus stricta: photosynthesis, biochemistry, growth and phenology. *Plant Cell and Environment*, **21**, 417–425.

Cox PM (2001) *Description of the "TRIFFID" Dynamic Global Vegetation Model*. Hadley Center Met Office, Bracknell, Berkshire, UK.

Crafts-Brandner SJ, Salvucci ME (2000) Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. *Proceedings of the National Academy of Sciences*, **97**, 13430–13435.

Crous KY, Reich PB, Hunter MD, Ellsworth DS (2010) Maintenance of leaf N controls the photosynthetic CO_2 response of grassland species exposed to 9 years of free-air CO2 enrichment. *Global Change Biology*, **16**, 2076–2088.

Crous KY, Zaragoza-Castells J, Löw M et al. (2011) Seasonal acclimation of leaf respiration in Eucalyptus saligna trees: impacts of elevated atmospheric CO_2 and summer drought. *Global Change Biology*, **17**, 1560–1576.

Cunningham SC, Read J (2002) Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. *Oecologia*, **133**, 112–119.

Dillaway DN, Kruger EL (2010) Thermal acclimation of photosynthesis: a comparison of boreal and temperate tree species along a latitudinal transect. *Plant Cell and Environment*, **33**, 888–899.

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? *Annual Review of Plant Physiology and Plant Molecular Biology*, **48**, 609–639.

Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical-model of photosynthetic CO_2 assimilation in leaves of C-3 plants. *Planta*, **149**, 78–90.

Field C, Randerson J, Malmström C (1995) Global net primary production: combining ecology and remote sensing. *Remote Sensing of Environment*, **51**, 74–88.

Franklin O (2007) Optimal nitrogen allocation controls tree responses to elevated CO_2. *New Phytologist*, **174**, 811–822.

Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, Brännström Å, Dybzinski R (2012) Modeling carbon allocation in trees: a search for principles. *Tree Physiology*, **32**, 648–666.

Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erickson D, Schimel D (1995) On the contribution of CO_2 fertilization to the missing biospheric sink. *Global Biogeochemical Cycles*, **9**, 541–556.

Friedlingstein P, Cox P, Betts R et al. (2006) Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate*, **19**, 3337–3353.

Friend AD (2010) Terrestrial plant production and climate change. *Journal of Experimental Botany*, **61**, 1293–1309.

Gifford RM (1995) Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature: long-term vs short-term distinctions for modelling. *Global Change Biology*, **1**, 385–396.

Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Functional Plant Biology*, **30**, 171–186.

Gonzalez-Meler MA, Taneva L, Trueman RJ (2004) Plant respiration and elevated atmospheric CO_2 concentration: cellular responses and global significance. *Annals of Botany*, **94**, 647–656.

Gratani L, Varone L, Catoni R (2008) Relationship between net photosynthesis and leaf respiration in Mediterranean evergreen species. *Photosynthetica*, **46**, 567–573.

Gunderson CA, Norby RJ, Wullschleger SD (2000) Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. *Tree Physiology*, **20**, 87–96.

Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology*, **16**, 2272–2286.

Harley IP, Heinemeyer A, Ineson P (2007) Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response. *Global Change Biology*, **13**, 1761–1770.

Haxeltine A, Prentice IC (1996a) BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles*, **10**, 693–709.

Haxeltine A, Prentice IC (1996b) A general model for the light-use efficiency of primary production. *Functional Ecology*, **10**, 551–561.

Hickler T, Smith B, Prentice IC, Mjöfors K, Miller P, Arneth A, Sykes MT (2008) CO_2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. *Global Change Biology*, **14**, 1531–1542.

Hikosaka K, Murakami A, Hirose T (1999) Balancing carboxylation and regeneration of ribulose-1,5-bisphosphate in leaf photosynthesis: temperature acclimation of an evergreen tree, Quercus myrsinaefolia. *Plant Cell and Environment*, **22**, 841–849.

Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y (2006) Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. *Journal of Experimental Botany*, **57**, 291–302.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Resport of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York.

June T, Evans JR, Farquhar GD (2004) A simple new equation for the reversible temperature dependence of photosynthetic electron transport: a study on soybean leaf. *Functional Plant Biology*, **31**, 275–283.

Juurola E (2003) Biochemical acclimation patterns of *Betula pendula* and *Pinus sylvestris* seedlings to elevated carbon dioxide concentrations. *Tree Physiology*, **23**, 85–95.

Kattge J, Knorr W (2007) Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant Cell and Environment*, **30**, 1176–1190.

Kattge J, Knorr W, Raddatz T, Wirth C (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, **15**, 976–991.

Kattge J, Diaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

King AW, Post WM, Wullschleger SD (1997) The potential response of terrestrial carbon storage to changes in climate and atmospheric CO_2. *Climatic Change*, **35**, 199–227.

King AW, Gunderson CA, Post WM, Weston DJ, Wullschleger SD (2006) Plant respiration in a warmer world. *Science*, **312**, 536–537.

Kirschbaum MUF (2011) Does enhanced photosynthesis enhance growth? lessons learned from CO_2 enrichment studies. *Plant Physiology*, **155**, 117–124.

Knorr W (2000) Annual and interannual CO_2 exchanges of the terrestrial biosphere: process-based simulations and uncertainties. *Global Ecology and Biogeography*, **9**, 225–252.

Kositsup B, Montpied P, Kasemsap P, Thaler P, Ameglio T, Dreyer E (2009) Photosynthetic capacity and temperature responses of photosynthesis of rubber trees (Hevea brasiliensis Mull Arg.) acclimate to changes in ambient temperatures. *Trees*, **23**, 357–365.

Krinner G, Viovy N, De Noblet-Ducoudre N *et al.* (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, GB1015, pp. 33, doi:10.1029/2003GB002199.

Kromer S (1995) Respiration during photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, **46**, 45–70.

Kucharik CJ, Foley JA, Delire C *et al.* (2000) Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles*, **14**, 795–825.

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Larcher W (1980) *Psyiological Plant Ecology*. Springer-Verlag, New York.

Larigauderie A, Korner C (1995) Acclimation of leaf dark respiration in alpine and lowland plant species. *Annals of Botany*, **76**, 245–252.

Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009a) Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany*, **60**, 2859–2876.

Leakey ADB, Xu F, Gillespie KM, Mcgrath JM, Ainsworth EA, Ort DR (2009b) Genomic basis for stimulated respiration by plants growing under elevated carbon dioxide. *Proceedings of the National Academy of Sciences*, **106**, 3597–3602.

Lee TD, Tjoelker MG, Ellsworth DS, Reich PB (2001) Leaf gas exchange responses of 13 prairie grassland species to elevated CO2 and increased nitrogen supply. *New Phytologist*, **150**, 405–418.

Lee TD, Barrott SH, Reich PB (2011) Photosynthetic responses of 13 grassland species across 11 years of free-air CO2 enrichment is modest, consistent and independent of N supply. *Global Change Biology*, **17**, 2893–2904.

Levy PE, Cannell MGR, Friend AD (2004) Modelling the impact of future changes in climate, CO2 concentration and land use on natural ecosystems and the terrestrial carbon sink. *Global Environmental Change-Human and Policy Dimensions*, **14**, 21–30.

Lewis JD, Ward JK, Tissue DT (2010) Phosphorus supply drives nonlinear responses of cottonwood (Populus deltoides) to increases in CO_2 concentration from glacial to future concentrations. *New Phytologist*, **187**, 438–448.

Lin Y-S, Medlyn BE, Ellsworth DS (2012) Temperature responses of leaf net photosynthesis: the role of component processes. *Tree Physiology*, **32**, 219–231.

Loveys BR, Scheurwater I, Pons TL, Fitter AH, Atkin OK (2002) Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. *Plant Cell and Environment*, **25**, 975–987.

Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK (2003) Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology*, **9**, 895–910.

Lukac M, Calfapietra C, Lagomarsino A, Loreto F (2010) Global climate change and tree nutrition: effects of elevated CO2 and temperature. *Tree Physiology*, **30**, 1209–1220.

Luo YQ (2007) Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology Evolution and Systematics*, **38**, 683–712.

Luo YQ, Reynolds JF (1999) Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. *Ecology*, **80**, 1568–1583.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.

McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, Moore B III, Vorosmarty CJ (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles*, **6**, 101–124.

Medlyn BE (1996) Interactive effects of atmospheric carbon dioxide and leaf nitrogen concentration on canopy light use efficiency: a modeling analysis. *Tree Physiology*, **16**, 201–209.

Medlyn BE, Dreyer E, Ellsworth D *et al.* (2002a) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant Cell and, Environment*, **25**, 1167–1179.

Medlyn BE, Loustau D, Delzon S (2002b) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (Pinus pinaster Ait.). *Plant Cell and, Environment*, **25**, 1155–1165.

Monteith JL (1972) Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, **9**, 747–766.

Monteith JL, Moss CJ (1977) Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,*, **281**, 277–294.

Mooney HA, Björkman O, Collatz GJ (1978) Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. *Plant Physiology*, **61**, 406–410.

Nemani R, Hashimoto H, Votava P *et al.* (2009) Monitoring and forecasting ecosystem dynamics using the Terrestrial Observation and Prediction System (TOPS). *Remote Sensing of Environment*, **113**, 1497–1509.

Norby RJ, Delucia EH, Gielen B *et al.* (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 18052–18056.

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19368–19373.

Oleson KW, Lawrence DM, Bonan GB *et al.* (2010) *Technical description of version 4.0 of the Community Land Model (CLM)*. National Center for Atmospheric Research, Boulder, Colorado.

Pepper DA, Del Grosso SJ, McMurtrie RE, Parton WJ (2005) Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising CO_2, temperature and nitrogen input. *Global Biogeochemical Cycles*, **19**, GB1004, pp. 20, doi:10.1029/2004GB002226.

Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA (1993) Terrestrial ecosystem production – a process model-based on global satellite and surface data. *Global Biogeochemical Cycles*, **7**, 811–841.

Raddatz T, Reick C, Knorr W *et al.* (2007) Will the tropical land biosphere dominate the climate–carbon cycle feedback during the twenty-first century? *Climate Dynamics*, **29**, 565–574.

Randerson JT, Hoffman FM, Thornton PE *et al.* (2009) Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Global Change Biology*, **15**, 2462–2484.

Reddy AR, Rasineni GK, Raghavendra AS (2010) The impact of global elevated CO_2 concentration on photosynthesis and plant productivity. *Current Science*, **99**, 46–57.

Reich PB, Hobbie SE, Lee T *et al.* (2006a) Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature*, **440**, 922–925.

Reich PB, Hungate BA, Luo YQ (2006b) Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology Evolution and Systematics*, **37**, 611–636.

Rustad LE, Campbell JL, Marion GM *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.

Silim SN, Ryan N, Kubien DS (2010) Temperature responses of photosynthesis and respiration in *Populus balsamifera* L.: acclimation versus adaptation. *Photosynthesis Research*, **104**, 19–30.

Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Slatyer RO, Morrow PA (1977) Altitudinal variation in photosynthetic characteristics of snow gum, Eucalyptus pauciflora sieb ex spreng.1. Seasonal-changes under field conditions in snowy mountains area of Southeastern Australia. *Australian Journal of Botany*, **25**, 1–20.

Smith EM, Hadley EB (1974) Photosynthetic and respiratory acclimation to temperature in *Ledum groenlandicum* populations. *Arctic and Alpine Research*, **6**, 13–27.

Sokolov AP, Kicklighter DW, Melillo JM, Felzer BS, Schlosser CA, Cronin TW (2008) Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate*, **21**, 3776–3796.

Stitt M, Hurry V (2002) A plant for all seasons: alterations in photosynthetic carbon metabolism during cold acclimation in *Arabidopsis*. *Current Opinion in Plant Biology*, **5**, 199–206.

Thornton PE, Rosenbloom NA (2005) Ecosystem model spin-up: estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecological Modelling*, **189**, 25–48.

Thornton PE, Lamarque JF, Rosenbloom NA, Mahowald NM (2007) Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. *Global Biogeochemical Cycles*, **21**, GB4018, pp. 15, doi:10.1029/2006GB002868.

Thornton PE, Doney SC, Lindsay K *et al.* (2009) Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences*, **6**, 2099–2120.

Tjoelker MG, Oleksyn J, Reich PB (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. *Tree Physiology*, **18**, 715–726.

Tjoelker MG, Oleksyn J, Reich PB (1999) Acclimation of respiration to temperature and CO2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology*, **5**, 679–691.

Tjoelker MG, Oleksyn J, Reich PB (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. *Global Change Biology*, **7**, 223–230.

Tjoelker MG, Oleksyn J, Lorenc-Plucinska G, Reich PB (2009) Acclimation of respiratory temperature responses in northern and southern populations of *Pinus banksiana*. *New Phytologist*, **181**, 218–229.

Townsend AR, Cleveland CC, Houlton BZ, Alden CB, White JWC (2011) Multi-element regulation of the tropical forest carbon cycle. *Frontiers in Ecology and the Environment*, **9**, 9–17.

Van Oijen M, Rougier J, Smith R (2005) Bayesian calibration of process-based forest models: bridging the gap between models and data. *Tree Physiology*, **25**, 915–927.

Van Oijen M, Schapendonk A, Hoglind M (2010) On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. *Annals of Botany*, **105**, 793–797.

Volder A, Tjoelker MG, Briske DD (2010) Contrasting physiological responsiveness of establishing trees and a C-4 grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology*, **16**, 3349–3362.

Wang YP, Law RM, Pak B (2010) A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, **7**, 2261–2282.

Wang W, Dungan J, Hashimoto H, Michaelis AR, Milesi C, Ichii K, Nemani RR (2011) Diagnosing and assessing uncertainties of terrestrial ecosystem models in a multi-model ensemble experiment: 1. Primary production. *Global Change Biology*, **17**, 1350–1366.

Way DA, Sage RF (2008) Elevated growth temperatures reduce the carbon gain of black spruce *Picea mariana* (Mill.) BSP. *Global Change Biology*, **14**, 624–636.

Woodward FI, Smith TM, Emanuel WR (1995) A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles*, **9**, 471–490.

Wright IJ, Reich PB, Atkin OK, Lusk CH, Tjoelker MG, Westoby M (2006) Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites. *New Phytologist*, **169**, 309–319.

Wythers KR, Reich PB, Tjoelker MG, Bolstad PB (2005) Foliar respiration acclimation to temperature and temperature variable Q_{10} alter ecosystem carbon balance. *Global Change Biology*, **11**, 435–449.

Xiong FSS, Mueller EC, Day TA (2000) Photosynthetic and respiratory acclimation and growth response of antarctic vascular plants to contrasting temperature regimes. *American Journal of Botany*, **87**, 700–710.

Xu RI, Prentice IC (2008) Terrestrial nitrogen cycle simulation with a dynamic global vegetation model. *Global Change Biology*, **14**, 1745–1764.

Xu C, Fisher R, Wullschleger SD, Wilson CJ, Cai M, McDowell NG (2012) Toward a mechanistic modeling of nitrogen limitation on vegetation dynamics. *PLoS ONE*, **7**, e37914.

Yamori W, Evans JR, Von Caemmerer S (2010) Effects of growth and measurement light intensities on temperature dependence of CO_2 assimilation rate in tobacco leaves. *Plant, Cell & Environment*, **33**, 332–343.

Zaehle S, Friend AD (2010) Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, **24**, GB1005.

Zaehle S, Sitch S, Smith B, Hatterman F (2005) Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles*, **19**, GB3020.

Zaehle S, Friedlingstein P, Friend AD (2010) Terrestrial nitrogen feedbacks may accelerate future climate change. *Geophysical Research Letters*, **37**, L01401, pp. 5, doi:10.1029/2009GL041345.

Zak DR, Pregitzer KS, Kubiske ME, Burton AJ (2011) Forest productivity under elevated CO_2 and O_3: positive feedbacks to soil N cycling sustain decade-long net primary productivity enhancement by CO_2. *Ecology Letters*, **14**, 1220–1226.

Ziehn T, Kattge J, Knorr W, Scholze M (2011) Improving the predictability of global CO_2 assimilation rates under climate change. *Geophysical Research Letters*, **38**, L10404.

Ziska LH, Bunce JA (1998) The influence of increasing growth temperature and CO2 concentration on the ratio of respiration to photosynthesis in soybean seedlings. *Global Change Biology*, **4**, 637–643.