Tansley review

Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration

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Contents

Summary

Plant carbon metabolism is impacted by rising CO_2 concentrations and temperatures, but also feeds back onto the climate system to help determine the trajectory of future climate change. Here we review how photosynthesis, photorespiration and respiration are affected by increasing atmospheric CO_2 concentrations and climate warming, both separately and in combination. We also compile data from the literature on plants grown at multiple temperatures, focusing on net CO_2 assimilation rates and leaf dark respiration rates measured at the growth temperature (A_{growth} and R_{growth}, respectively). Our analyses show that the ratio of A_{growth} to R_{growth} is generally homeostatic across a wide range of species and growth temperatures, and that species that have reduced A_{growth} at higher growth temperatures also tend to have reduced R_{growth}, while species that show stimulations in A_{growth} under warming tend to have higher R_{growth} in the hotter environment. These results highlight the need to study these physiological processes together to better predict how vegetation carbon metabolism will respond to climate change.

I. The importance of plant carbon metabolism for climate change

Since the Industrial Revolution, atmospheric CO_2 concentrations have risen from 280 ppm to over 410 ppm (Ciais *et al.*, 2013), a 45% increase. These higher CO_2 concentrations, along with increasing concentrations of other greenhouse gases, have led to a 0.8°C rise in mean annual global temperatures as of 2017 (Hansen *et al.*, 2010). Depending on how aggressive we are about reducing CO_2 (and other greenhouse gas) emissions, atmospheric CO_2 concentrations will probably be between 550 and 1000 ppm by the end of the century, leading to global mean air temperature increases

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of another 1–3.7°C (Ciais *et al.*, 2013). Because CO_2 is a well-mixed gas, there is only minor spatial or temporal heterogeneity in the CO_2 concentration across the Earth's surface at any time (on the order of *c.* 10 ppm), mainly due to regional differences in weather patterns, as well as plant and soil activity (Chahine *et al.*, 2008). In contrast to this pattern of global CO_2 increase, warming will be more severe in some regions than others: high latitudes could warm by 10°C by the year 2100, while the tropics will see smaller temperature increases of *c.* 3–4°C (Ciais *et al.*, 2013). Warming will also be greatest during the winter months and at night: a 10°C mean annual air temperature rise in the Arctic could translate into 12°C increases in minimum winter temperatures (Ciais *et al.*, 2013).

These climatic changes are predicted to have enormous impacts on the Earth's vegetation. Temperature is one of the most important controls on species distribution across the globe (Woodward, 1987), and most biological processes are temperature-sensitive. Not only will higher temperatures alter the thermal environment of plants, but the atmosphere is likely to become drier in the future as the driving force for evapotranspiration increases (Ficklin & Novick, 2017). Rising CO_2 will thus indirectly impact plant performance through its effect on air temperature and water stress. However, CO_2 also directly affects plant metabolism, most importantly through its role in photosynthesis, which is the entry point for carbon into the biosphere (Box 1, Fig. A). Elevated CO_2 concentrations are therefore expected to increase leaf photosynthetic rates, but the degree to which this will actually occur is unclear, given that the stimulation of photosynthesis by CO_2 depends on leaf temperature, and water and nutrient availability (Leakey *et al.*, 2009; Zhu *et al.*, 2017).

Plants are not only affected by climate but are themselves key regulators of global and regional climate (Zhu *et al.*, 2017; Fig. 1), making it imperative that we understand how vegetation will respond to future climate conditions. Photosynthesis in terrestrial plants absorbs *c.* 123 Gt C from the atmosphere every year and about half of the carbon fixed by leaves (*c.* 60 GT C) is then returned to the atmosphere annually via autotrophic respiration (Amthor & Baldocchi, 2001; Beer *et al.*, 2010; Ciais *et al.*, 2013). Vegetation thus helps determine atmospheric CO_2 concentrations, and through this effect, global climate. Terrestrial ecosystems currently absorb *c.* 30% of the anthropogenic CO_2 emitted every year (Le Quéré *et al.*, 2016), slowing climate change by preventing atmospheric CO_2 concentrations from rising as quickly as they would without this mitigating effect. Because carbon fluxes from vegetation are much larger than the CO_2 emitted by human activities (*c.* 10.3 Gt C yr^{-1}; Le Quéré *et al.*, 2016), large-scale alterations in plant carbon fluxes could either mitigate or accelerate climate change (Smith & Dukes, 2013). If elevated CO_2 and temperatures increase net photosynthetic CO_2 fixation, plants may continue to slow climate change, but only if this extra carbon finds its way into recalcitrant pools in the soils or deep oceans rather than in rapidly cycling carbon fluxes and pools, such as leaf litter or labile soil carbon. However, if climate change reduces plant net CO_2 uptake on a global scale (either through direct effects on carbon fluxes or by reducing vegetation cover), then vegetation could accelerate the rate of CO_2 increase and lead to a more rapidly

warming world than we currently predict (Fig. 1). While the responses of stem, root and soil respiration to climate change will play a large role in determining future ecosystem carbon fluxes, we will concentrate on leaf-level processes in this paper, as photosynthesis and respiration in leaves comprise significant global carbon fluxes that are intimately linked within a plant through biochemical and physiological mechanisms.

II. Rising atmospheric CO_2 and carbon metabolism

Higher CO_2 concentrations stimulate net photosynthesis by increasing CO_2 substrate availability for Rubisco and simultaneously suppressing photorespiration (Drake *et al.*, 1997). However, this effect is not linear (Farquhar *et al.*, 1980). At low internal CO_2 concentrations (C_i), Rubisco carboxylation rates limit photosynthesis, and net CO_2 assimilation rates (A_{net}) rise steeply as C_i increases. As C_i increases further, photosynthesis becomes limited by the ability to regenerate RuBP (i.e. the photosynthetic electron transport rate), and then by the ability to use triose phosphates to produce starch and sucrose (Sharkey *et al.*, 1986). These processes are less CO_2-sensitive than Rubisco carboxylation, so for a given increase in C_i, photosynthesis is stimulated more when C_i is low than when C_i is higher (Farquhar *et al.*, 1980; Sharkey *et al.*, 2007). Accordingly, rising CO_2 should have the greatest effects on plant carbon uptake in conditions where C_i is low, for example when stomatal conductance is low and diffusion of CO_2 into the leaf is restricted (Ainsworth & Rogers, 2007). This also implies that the increases in CO_2 concentration that
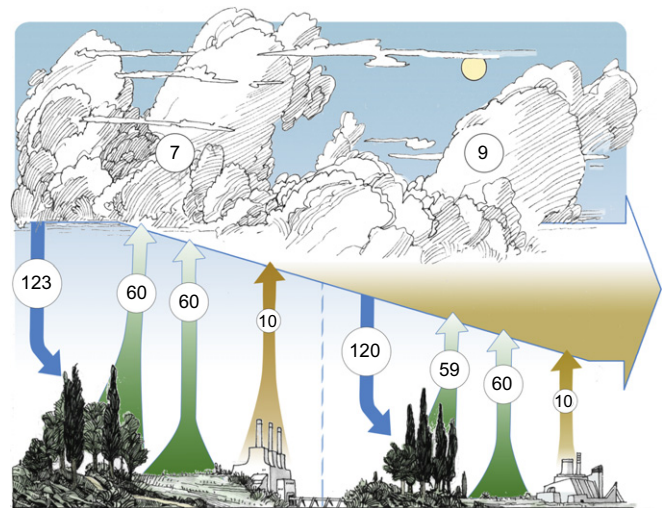

Fig. 1 A simplified schematic of the interplay between the climate system and carbon (C) fluxes in vegetation. Circles in the arrows indicate fluxes of CO_2 in Gt C yr^{-1}; circles in the sky show the balance of CO_2 resulting from those fluxes. Left panel, terrestrial vegetation absorbs CO_2 from the atmosphere through photosynthesis (blue arrow). Respiration (green arrows) releases CO_2 back to the atmosphere from both vegetation and soil. Anthropogenic CO_2 emissions are depicted with a brown arrow. Right panel, a hypothetical future scenario where climate change reduces global photosynthesis and plant respiration, although soil and anthropogenic CO_2 emissions remain unchanged. The net effect of these reductions in vegetation carbon fluxes is a greater accumulation of CO_2 in the atmosphere.

Box 1 Plant carbon metabolism: photosynthesis, photorespiration and respiration

For the purpose of this review, we focus on three metabolic processes that dominate carbon fluxes in vegetation: photosynthesis, photorespiration and respiration (Box Fig. 1 below). Other physiological processes, including the formation and release of volatile organic compounds and root exudates, can consume substantial amounts of carbon (Penuelas & Matamala, 1990; Pausch & Kuzyakov, 2018), but these topics are beyond the scope of this paper. Each metabolic process is composed of a suite of biochemical, biophysical and physiological reactions that have different sensitivities to temperature and CO_2, which, taken together, dictate how photosynthesis, photorespiration and respiration respond to climate change drivers. In the following section, we give a brief overview of these three processes, but for more detailed descriptions, please see Taiz *et al.* (2014).

Photosynthesis begins with the absorption of a photon, which excites a specialized chlorophyll, P680, leading to the ejection of an electron from P680. This electron is transported through the photosynthetic electron transport chain to the final electron acceptor ($NADP^+$) via a series of redox reactions that include the absorption of a second photon by the antenna system of photosystem I, producing the reductant NADPH. Along the way, a proton gradient is created across the thylakoid membrane and this gradient generates ATP via an ATP synthase.

Much of the energy and reducing power created in photosynthetic electron transport is used in the chloroplast stroma in the Calvin–Benson cycle. CO_2 is fixed to ribulose-1,5-bisphosphate (RuBP) by the enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase), producing 3-phosphoglycerate (PGA). This PGA is converted to 1,3-bisphosphoglycerate (which requires ATP), and then reduced to glyceraldehyde 3-phosphate (G3P), a reaction that consumes NADPH. Some of the G3P is used to regenerate RuBP (a process that also uses ATP), while the rest is used to make glucose, sucrose and other carbon-based molecules.

While Rubisco can fix CO_2 in photosynthesis, Rubisco is a dual function enzyme that can both carboxylate and oxygenate RuBP (Spreitzer & Salvucci, 2002). In contrast to the two molecules of PGA produced in a carboxylation event, oxygenation of RuBP by Rubisco produces one molecule of PGA and one of 2-phosphoglycolate (PG). As PG is toxic if it accumulates in plant cells (Zelitch *et al.*, 2009), it must be processed via photorespiration. The PG is converted to glycolate, which is shuttled to the peroxisome, where it is converted to glyoxylate and then (with the addition of NH_2) into glycine. This glycine is converted to serine in the mitochondria, releasing a molecule each of CO_2 and NH_4, and consuming $NADH_2$. The serine is shuttled back to the peroxisome where it is converted to pyruvate and then glycerate, with the latter reaction consuming more $NADH_2$. The glycerate can then be phosphorylated to form PGA in the chloroplast, at the cost of an ATP, while another ATP is used in photorespiration to produce the glutamate needed to provide NH_2 for the production of glycine. Thus, overall, photorespiration consumes ATP and reducing power, while releasing previously fixed CO_2. In addition, glyoxylate (a photorespiratory metabolite) can inhibit Rubisco activity (Cook *et al.*, 1985; Campbell & Ogren, 1990). Photorespiration is one of the biggest metabolic fluxes in plants, and photorespiratory rates can be c. 25% of photosynthetic rates in C_3 leaves at 25°C (Sharkey, 1988).

Respiration involves the breakdown of glucose formed via photosynthesis to produce ATP to fuel plant metabolism. Glucose is initially broken into pyruvate in glycolysis, which is oxidized to form acetyl-CoA, releasing a molecule of CO_2. The acetyl-CoA then enters the tricarboxylic acid pathway, where it is oxidized to CO_2, producing reductants for use in the mitochondrial electron transport chain. Oxidation of these reductants (and succinate, which is also created in the citric acid cycle) generates a proton gradient across the inner membrane of the mitochondria that drives ATP synthesis. Both respiration and photorespiration consume O_2 and release CO_2, but mitochondrial respiration occurs in both the light and the dark, unlike photorespiration, which operates only in the light. While respiration is thought to be suppressed by light by c. 30% (Sharp *et al.*, 1984), the exact effect of light on mitochondrial respiration is difficult to assess in leaves and is a matter of current debate (Tcherkez *et al.*, 2017).
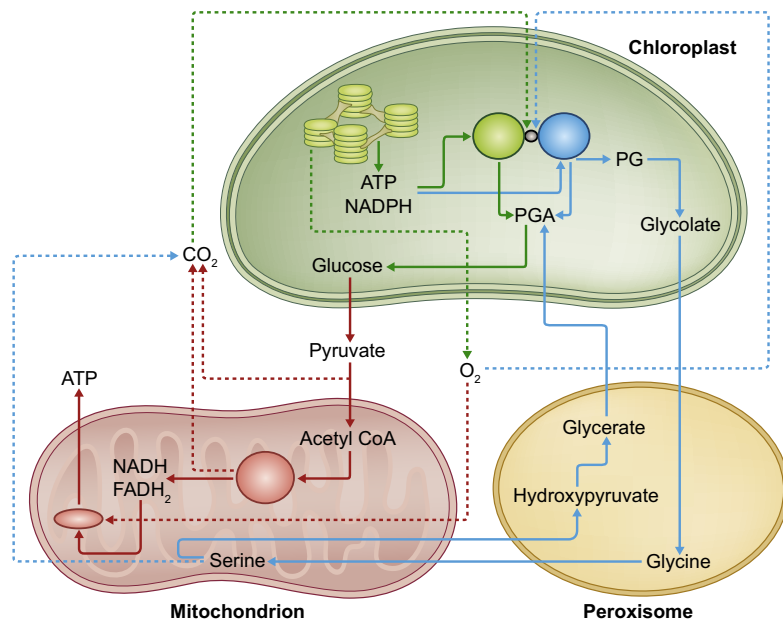
Box Fig. 1 Simplified depiction of the major biochemical linkages between photosynthesis, photorespiration and respiration. Rubisco, small grey circle; the Calvin-Benson cycle, green circle; photorespiration, blue circle; citric acid cycle, red circle. The thylakoids and photosynthetic electron transport are represented by the drawings in the chloroplast and the respiratory electron transport chain is shown by the dark red oval in the mitochondrion. Gas fluxes are represented by dashed arrows. Acetyl CoA, acetyl coenzyme A; ATP, adenosine triphosphate; $FADH_2$, flavin adenine dinucleotide; NADH, nicotinamide adenine dinucleotide; NADPH, nicotinamide adenine dinucleotide phosphate; PG, phosphoglycolate; PGA, phosphoglycerate.

have occurred since the Industrial Revolution probably led to large stimulations in photosynthesis (Polley *et al.*, 1993; Gerhart & Ward, 2010), but that future CO_2 increases may have less dramatic effects on plant carbon uptake, consistent with the saturating response to rising CO_2 noted in crop yield studies (Long *et al.*, 2006).

Much of our early information on how rising CO_2 alters plant carbon fluxes came from studies in growth chambers and glasshouses where CO_2 concentrations can be easily manipulated. While this approach answered a range of physiological questions about high CO_2 effects on plant carbon metabolism (Garbutt & Bazzaz, 1984; Sage *et al.*, 1989), it also has its limitations for understanding how plants and ecosystems will respond to elevated CO_2 in the field (Curtis & Wang, 1998). The need to grow plants in pots imposes an artificial rooting environment (Mcconnaughay *et al.*, 1993), and most glasshouse studies provide ample nutrients and water, conditions rarely found in nature (Poorter *et al.*, 2016). There are, however, ways to determine how high CO_2 affects vegetation in more realistic settings, including open-top chambers and Free Air CO_2 Enrichment (FACE) experiments. FACE studies, where vegetation grown in the field is surrounded by pipes blowing CO_2 over the plots, have explored the effects of elevated CO_2 on plant and ecosystem carbon dynamics in forests, deserts, crop fields and grassland ecosystems (e.g. Rogers *et al.*, 2004; McCarthy *et al.*, 2010; Smith *et al.*, 2014; Obermeier *et al.*, 2017). Determining the response of plants in these more natural systems when possible is important, as there can be significant differences in the results from studies between pot and field studies (Poorter *et al.*, 2016). The effect of elevated CO_2 on photosynthesis from FACE studies was > 50% lower than that from pot studies of crop species, with similar levels of disparity between the two types of experiments in terms of biomass and yield stimulations (Long *et al.*, 2006). Thus, while pot experiments evaluate physiological responses to CO_2 in a highly controlled setting, translating those results into ecologically realistic predictions of how vegetation will respond to rising CO_2 is best evaluated in the field.

The stimulation of photosynthesis in plants grown at elevated CO_2 is well characterized (Ainsworth & Rogers, 2007). Across a range of FACE experiments, maximum rates of A_{net} were 31% higher in the elevated CO_2 plots (Ainsworth & Long, 2004). While this figure is often used to describe the effect of increased CO_2 on photosynthesis, the same meta-analysis found that the mean degree of stimulation varied between plant functional types (PFTs), with trees showing the strongest response to CO_2 (a 47% increase in maximum photosynthesis) and forbs showing a weaker response (a 15% increase in maximum photosynthesis). Importantly, this stimulation is not necessarily constant over time, but tends to decrease as the duration of exposure to a high CO_2 environment increases (Leuzinger *et al.*, 2011; Wang *et al.*, 2012; Warren *et al.*, 2015). Over time, the accumulation of sugars in high-CO_2-grown leaves leads to a down-regulation of Rubisco concentrations, providing a negative feedback on photosynthesis (Moore *et al.*, 1999). This acclimation results in a lower degree of photosynthetic stimulation in plants grown at high CO_2 concentrations than would be expected from short-term exposure to elevated CO_2. Down-regulation of photosynthesis, or a weaker photosynthetic

response to elevated CO_2, is particularly common in plants grown in small pots or with low nutrient availability (Arp, 1991; Jablonski *et al.*, 2002) and often reflects the sink strength of the vegetation (Clough *et al.*, 1981; Ainsworth *et al.*, 2004). For example, *Eucalyptus* growing on phosphorus-poor soils showed only a 19% stimulation of maximum A_{net} when exposed to high CO_2 over 3 years (Ellsworth *et al.*, 2017), while sweetgum and loblolly pine trees grown at elevated CO_2 for three or more years in a fertile site showed 30–67% increases in maximum A_{net} (Herrick & Thomas, 2001; Ellsworth *et al.*, 2012). In the majority of cases, photosynthetic rates measured at the growth CO_2 are still stimulated in high-CO_2-grown plants compared to plants grown under current CO_2 despite this acclimation (Leakey *et al.*, 2009). However, in some studies, field-grown plants exposed to high CO_2 eventually have identical A_{net} at their growth CO_2 as control plants from ambient CO_2 plots (e.g. Norby *et al.*, 2010), negating the expectation of a CO_2 fertilization effect in these experiments.

Elevated CO_2 reduces stomatal conductance (g_s), which affects both the carbon and the water dynamics of vegetation (Medlyn *et al.*, 2001). Averaged across the FACE sites, increased growth CO_2 resulted in a 20% decrease in g_s (Ainsworth & Long, 2004), although in some studies, this reduction of g_s disappeared over time (Uddling *et al.*, 2009) or was not seen (Pathare *et al.*, 2017). The lower g_s in high-CO_2-grown vegetation partially offsets the stimulation of Rubisco carboxylation rates, because it increases resistance to CO_2 diffusion into the leaf and lowers C_i. The reduction in g_s of vegetation under high CO_2 environments could lead to considerable soil water savings (Volk *et al.*, 2000; Wullschleger *et al.*, 2002; Fay *et al.*, 2012; Ukkola *et al.*, 2016; but see Pathare *et al.*, 2017), helping offset the higher evaporative demand of a warmer climate in the future and thereby promoting plant productivity (Fatichi *et al.*, 2016; Swann *et al.*, 2016). There is even evidence that traits affecting g_s have already adapted to the rise in CO_2 that has occurred since the Industrial Revolution, with a reduction in maximum g_s over the last century via decreases in stomatal density or stomatal pore size (Lammertsma *et al.*, 2011). However, in some studies, where the maximum leaf area carrying capacity has not been reached, plants grown under elevated CO_2 concentrations have larger canopies (Ainsworth & Long, 2004; Norby & Zak, 2011). If lower g_s is paired with more leaf area in a high CO_2 environment (Field *et al.*, 1995), these responses can cancel each other out in terms of water lost via transpiration per plant (Tor-ngern *et al.*, 2015; Knauer *et al.*, 2017; Jin *et al.*, 2018).

High CO_2 suppresses photorespiration, a process generally viewed as a wasteful side reaction of Rubisco. This opinion is bolstered by the enhanced productivity of some plant lines engineered with metabolic bypasses to circumvent photorespiration (Kebeish *et al.*, 2007; Maurino & Peterhansel, 2010). However, many photorespiratory mutants grow poorly in current CO_2 conditions (Timm & Bauwe, 2013), indicating that this process has an important role in plant carbon metabolism, and there is growing evidence that photorespiration provides stress tolerance to plants (Voss *et al.*, 2013). Photorespiration can be beneficial during drought stress or high light conditions, which both reduce the capacity of the Calvin–Benson cycle to consume the NADPH and ATP generated in photosynthetic electron

transport. This imbalance between photosynthetic electron transport rates and rates of the use of its products leads to increasing excitation pressure, photoinhibition and reactive oxygen species (ROS) formation; by consuming reducing equivalents, photorespiration can help relieve this acceptor limitation and ROS damage (Takahashi & Badger, 2011). Because low CO_2 concentrations induce a similar imbalance between photosynthetic electron transport and the Calvin–Benson cycle, high rates of photorespiration are also necessary to cope with low CO_2 conditions (Eisenhut *et al.*, 2017). Additionally, photorespiration is intimately connected with plant nitrogen cycling, as NH_2 is used to produce glycine and ammonium is then produced during the formation of serine. Photorespiration has been linked to increased nitrogen uptake capacity (Rachmilevitch *et al.*, 2004; Bloom *et al.*, 2010, 2012, 2014; Dellero *et al.*, 2015; Busch *et al.*, 2018), particularly nitrate, posing the question of whether rising CO_2 may reduce plant nitrogen uptake when nitrate is the main nitrogen source available. This is particularly relevant for crop yield, because nitrate is the dominant soil nitrogen source for most crop plants in cultivated aerated soils (Crawford & Glass, 1998; Hawkesford *et al.*, 2012); by reducing nitrate assimilation, rising CO_2 concentrations may also threaten food quality by depleting crop protein concentrations (Bloom, 2009; Carlisle *et al.*, 2012). Cheng *et al.* (2012) showed that, across a range of studies, elevated CO_2 lowered nitrate uptake capacity by 16%, but had no impact on NH_4^+ use. Recent work with an *Arabidopsis* mutant with impaired nitrate uptake activity found stronger reductions in growth of the mutant at high CO_2 than at lower CO_2 concentrations (Takatani *et al.*, 2014), consistent with an exacerbated reduction in the ability of the mutant to assimilate nitrate at elevated CO_2. Nitrate-preferring species may therefore show a weaker response to rising CO_2 than species that preferentially assimilate ammonium (Rubio-Asensio & Bloom, 2016). The degree to which increases in nitrogen use efficiency (i.e. the ratio of A_{net} to leaf N) due to rising CO_2 (Leakey *et al.*, 2009) will help compensate for reductions in nitrogen assimilation in nitrate-preferring species is unclear. If plant N demand declines proportionally with decreased N uptake capacity, these two responses may counterbalance one another.

The question of whether rising CO_2 will alter plant respiration rates is still open (Way *et al.*, 2015; Xu *et al.*, 2015). There is no immediate effect of high CO_2 on mitochondrial respiration rates (Amthor, 2000). However, in some studies, plants grown at elevated CO_2 have higher respiration rates than control plants (e.g. Wang *et al.*, 2001), in other studies, respiration rates decline (e.g. Curtis, 1996) and the remaining studies show no effect of growth CO_2 on respiration (e.g. Gauthier *et al.*, 2014). Decreased respiration rates in vegetation that develops at elevated CO_2 (e.g. Gifford *et al.*, 1985; Loreto *et al.*, 2001; Crous *et al.*, 2012; Ayub *et al.*, 2014) is often thought to be linked to decreased leaf N (Cotrufo *et al.*, 1998; Ainsworth & Long, 2004), associated with photosynthetic down-regulation and lower metabolic demands. However, Curtis (1996) found little evidence for this hypothesis in woody species, and reductions in respiration are not always correlated with reductions in leaf N (e.g. Haworth *et al.*, 2015). Cases where high CO_2 increases respiration (Thomas *et al.*, 1993; Wang *et al.*, 2001; Rogers *et al.*, 2004; Shapiro *et al.*, 2004; Markelz

et al., 2014) may be related to higher carbohydrate concentrations and hence a higher substrate availability for respiration (e.g. Rogers *et al.*, 2004; Tjoelker *et al.*, 2009). Li *et al.* (2013) found that while higher respiration rates in elevated CO_2-grown tomato were correlated with increased leaf carbohydrate concentrations, supplying leaves with extra sucrose had no effect on respiration rates. Instead, they noted an up-regulation of respiratory genes in plants grown at high CO_2, indicating that higher respiration rates were regulated at the transcriptional level, consistent with work by Markelz *et al.* (2014). Li *et al.* (2013) also found that high CO_2-grown leaves had more mitochondria, which agrees with earlier work in other species (Griffin *et al.*, 2001; Wang *et al.*, 2004). In other cases, an apparent increase in respiration in vegetation from elevated CO_2 can be explained by an increase in leaf mass per unit area (Aspinwall *et al.*, 2017). Taken together, the picture that emerges from these studies is that responses of respiration to changes in growth CO_2 are highly variable. We therefore currently lack a consistent theoretical basis for making strong predictions for how respiration will change in a high CO_2 world.

In natural ecosystems, the effect of the increases in CO_2 that have occurred over the last few decades can be assessed from several sources. Eddy covariance data can be used to measure net ecosystem exchange (NEE), the sum of the plant and microbial carbon fluxes in the ecosystem. NEE, in turn, reflects the balance between gross primary productivity (GPP) and ecosystem respiration (R_{eco}, which includes both autotrophic and heterotrophic respiration). At the ecosystem level, high CO_2 effects on photosynthesis (i.e. GPP) and respiration (i.e. R_{eco}) are likely to be more tightly coupled than in leaves or plants, particularly in sink-limited regions. This is because elevated CO_2 stimulates photosynthesis and carbohydrate production, but if the carbon is not used in growth or autotrophic respiration, it will predominantly be used in heterotrophic respiration, thereby increasing R_{eco}. As eddy covariance also estimates evapotranspiration, this method provides insight into how both carbon and water fluxes are responding to rising CO_2. Tree ring data can also be used to examine tree responses to changes in atmospheric CO_2 concentrations, through both estimates of growth and isotopic analyses of tree rings for water use efficiency (WUE, the ratio of A_{net} to transpiration). Work using eddy covariance data shows that rising CO_2 has stimulated both GPP and WUE in forests in the northern hemisphere since 1990 (Keenan *et al.*, 2013). By combining eddy covariance and tree ring isotopic data, Dekker *et al.* (2016) argued that WUE has increased by c. 48% over the 20th century, largely due to CO_2 effects on photosynthesis and g_s. By contrast, Frank *et al.* (2015) used tree rings to calculate WUE changes since 1900 and found a much smaller stimulation of 14–22% in European forests, with broadleaf species showing smaller increase in WUE than conifers. The large increases in WUE found by Keenan *et al.* (2013) and Dekker *et al.* (2016) have instigated debate about the actual extent of WUE stimulations by rising CO_2, as the values reported are much larger than those predicted by our knowledge of the physiological processes underlying WUE (Knauer *et al.*, 2017; Mastrotheodoros *et al.*, 2017). Some of the difference between measured changes in WUE- and CO_2-based predictions may be due to warming-related increases in vapor pressure deficit (VPD) that occur concurrently

with increasing CO_2, changes that also drive stomatal closure and thereby increase WUE (Ficklin & Novick, 2017). Regardless, these data highlight that climate change is already impacting the carbon and water dynamics of vegetation globally, emphasizing the need to understand the mechanisms generating these changes.

III. Rising temperatures and carbon metabolism

Rising CO_2 predominantly affects plants through its effects on Rubisco biochemistry and stomatal conductance, but increasing temperatures impact almost every biological process in a plant, including morphogenesis, membrane lipid fluidity and composition, and cambial activity (Pearcy, 1978; Falcone *et al.*, 2004; Begum *et al.*, 2013; Quint *et al.*, 2016). Thus, while the effects of warming on photosynthesis, photorespiration and respiration can be evaluated individually, the diverse impacts of higher temperatures on other metabolic processes are likely to feed back on carbon metabolism in ways that we do not currently appreciate.

Increasing temperatures stimulate enzyme activity rates (recently reviewed by Arcus *et al.*, 2016), explaining most of the immediate effects of temperature on leaf carbon fluxes in moderate thermal environments (i.e. *c.* 5–40°C for most C_3 species). For example, respiration increases exponentially with increasing leaf temperature (Hofstra & Hesketh, 1969; Clark & Menary, 1980; Heskel *et al.*, 2016), up to a species- and environment-dependent maximum temperature of 48–60°C (Tjoelker *et al.*, 2001; Heskel *et al.*, 2014; Weerasinghe *et al.*, 2014), largely due to direct impacts of temperature on enzyme function. As leaf temperatures increase, photorespiration rates rise faster than do photosynthetic rates (Long, 1991). The greater stimulation of photorespiration than photosynthesis at higher temperatures occurs for two reasons. First, the specificity of Rubisco for CO_2 vs O_2 decreases at higher temperatures, making it more likely that an oxygenation reaction will occur (Ku & Edwards, 1977a; Jordan & Ogren, 1984). Second, the solubility of O_2 decreases less rapidly than does the solubility of CO_2 as temperatures rise (Ku & Edwards, 1977b), so there is relatively more O_2 available to react with in warm conditions. The different temperature sensitivities of photosynthesis, photorespiration and respiration combine to generate an A_{net} thermal response curve that usually peaks between 25 and 30°C in C_3 photosynthetic species (Sage & Kubien, 2007; Yamori *et al.*, 2014), although some C_3 species can maintain high A_{net} at temperatures as high as 45°C (e.g. Lawson *et al.*, 2014).

Given that climate warming will increase both the mean temperatures experienced by leaves and the risk of extreme heat waves (Coumou & Robinson, 2013; Yao *et al.*, 2013), understanding what limits net carbon uptake at high temperatures will become increasingly important. Two main biochemical hypotheses have been put forward to explain why photosynthesis decreases above the thermal optimum of A_{net}: Rubisco activase heat lability and electron transport declines. The first hypothesis is based on the decline in the activation state of Rubisco as leaf temperatures increase (Crafts-Brandner & Salvucci, 2000; Yamori & Von Caemmerer, 2009). Even when Rubisco acts as a carboxylase, misfire products are frequently produced and these must be removed from the active site by Rubisco activase (recently reviewed

by Carmo-Silva *et al.* (2015) and Bracher *et al.* (2017)). As Rubisco's catalytic activity and production of misfire products increases with rising temperature, so does the role of Rubisco activase in maintaining Rubisco function. Rubisco activase is relatively heat labile (Crafts-Brandner & Salvucci, 2000; Salvucci *et al.*, 2004), so the ability of Rubisco activase to maintain the activation state of Rubisco is expected to decline at high temperatures, and plants expressing a more thermotolerant Rubisco activase have higher A_{net} at high temperatures (Itzhak Kurek *et al.*, 2007; Kumar *et al.*, 2009). However, the effect of Rubisco activase on A_{net} at high temperatures is often small (e.g. Yamori & Von Caemmerer, 2009; Yamori *et al.*, 2012). The second hypothesis states that a decline in photosynthetic electron transport rates, and the production of ATP and NADPH, at high temperatures limits photosynthesis (Schrader *et al.*, 2004; Wise *et al.*, 2004). Teasing out the initial cause of the decrease in A_{net} at high temperatures is complicated by the fact that a reduction in photosynthetic electron transport decreases ATP production, thereby limiting the activity of Rubisco activase, which requires ATP (Cen & Sage, 2005). Recently, Busch & Sage (2017) showed that combining gas exchange and chlorophyll fluorescence measurements at varied CO_2 and O_2 conditions can pinpoint the biochemical limitation of A_{net}, an approach building on that of Long & Bernacchi (2003). While this approach is time-consuming, establishing the limitation to A_{net} above the photosynthetic thermal optimum in a range of species should provide insight into whether one of these limitations is dominant.

The effect of increased temperature on carbon metabolism differs depending on the timescale over which the warming is imposed. When plants are grown at elevated temperatures, both photosynthesis and respiration usually acclimate (Smith & Dukes, 2017). For most C_3 plants, this involves an increase in the thermal optimum of A_{net} (Berry & Björkman, 1980; Yamori *et al.*, 2014) and higher maximum Rubisco carboxylation rates at the growth temperature (Smith & Dukes, 2017). However, these shifts do not necessarily translate into improved A_{net} at the growth temperature (A_{growth}) when comparing a warm-grown plant with a plant grown at a lower, control temperature (Way & Yamori, 2014). In many cases, particularly in evergreen woody species, A_{growth} is lower in the plant grown at elevated temperature, implying that acclimation cannot fully compensate for the change in temperature in some species (Way & Yamori, 2014).

In contrast to photosynthesis, respiration tends to acclimate to increases in growth temperature to a similar degree in species from different biomes and PFTs (Slot & Kitajima, 2015; Smith & Dukes, 2017). This acclimation is evidenced by a lower respiration rate in plants grown at higher temperatures compared to control plants when both are measured at a common temperature (Atkin & Tjoelker, 2003). Plants grown at higher temperatures may reduce the Q_{10} for respiration (the increase in respiration for a 10°C increase in leaf temperature) compared to control plants, and/or have a lower respiration rate at low leaf temperatures (Atkin & Tjoelker, 2003). Thermal acclimation of respiration can lead to perfect homeostasis, where respiration rates at the respective growth temperatures (R_{growth}) are identical for plants grown in different thermal conditions (Atkin *et al.*, 2005), but partial homeostasis of

respiration is more common (Slot & Kitajima, 2015) and in some studies, no significant effect of growth temperature on respiration is found (e.g. Gauthier *et al.*, 2014). While thermal acclimation can reduce respiration by 80% compared to control plants (Reich *et al.*, 2016), the mechanisms leading to thermal acclimation of respiration are not known. Reductions in respiration under elevated temperature are often correlated with decreases in leaf nitrogen (Tjoelker *et al.*, 1999b; Crous *et al.*, 2017) and changes in mitochondrial density or structure (e.g. Armstrong *et al.*, 2006). Thermal acclimation of respiration also often involves respiratory substrate limitation and adenylate control on respiration rates (Atkin & Tjoelker, 2003). However, while we know that these processes are often involved in respiratory thermal acclimation, a general framework to mechanistically explain the long-term response of respiration to growth temperature is currently lacking.

As with rising CO_2, eddy covariance data can provide insight into how the effects of temperature on plant carbon dynamics scale to the ecosystem. Because photosynthesis and respiration in plants both acclimate to prevailing temperatures, and these fluxes constitute the majority of the CO_2 signal measured by eddy covariance, it is perhaps unsurprising that the thermal response of NEE is correlated with regional temperature regimes, with NEE peaking at a higher optimum temperature in warmer locations (Niu *et al.*, 2012). Thermal acclimation can also be detected in the NEE signal, with the NEE thermal optimum increasing in warmer years at a given site. While this NEE thermal acclimation was related to both increases in the thermal optimum of GPP and decreases in the Q_{10} of R_{eco}, the photosynthetic shift accounted for more of the change in the NEE thermal response (29%) than did changes in respiration (7%) (Niu *et al.*, 2012). Thus, even at the ecosystem level, carbon metabolism is likely to shift in a concerted manner as temperatures increase, although this acclimation process may not maintain NEE at a similar value as temperatures warm at a particular site.

IV. Thermal acclimation responses of carbon metabolic processes can be best understood when studied together

While it has long been known that variation in A_{net} and respiration tend to be correlated (Gifford, 1995; Reich *et al.*, 1998; Whitehead *et al.*, 2004; Atkin *et al.*, 2007), thermal acclimation of photosynthesis and respiration are often studied separately (although not always, e.g. Way & Yamori, 2014; Smith & Dukes, 2017). Because of the coupling between these physiological processes, plants that show strong thermal acclimation of photosynthesis might also be expected to show strong acclimation of respiration under warming. One metric of this is the ratio of A_{net} to dark respiration, which is homeostatic across growth temperatures in some studies (e.g. Loveys *et al.*, 2003) but not others (e.g. Way & Sage, 2008).

To evaluate how A_{net} and leaf dark respiration acclimate to changes in growth temperature, we collated information from 58 studies that grew plants at two or more temperatures and then measured net photosynthesis and leaf dark respiration at the growth temperature (A_{growth} and R_{growth}, respectively) (Appendix A1). Studies were restricted to experiments in controlled environments (i.e. glasshouses and growth chambers); while this excludes field studies, we focused on data where growth temperatures could be clearly defined, building on the database used in Yamori *et al.* (2014) and Way & Yamori (2014). Data were extracted directly from the text or taken from figures using DataThief III (v.1.5, www.datathief.org). Because not every study had measurements of

Table 1 Parameter estimates from the linear regression model (LM) of the relationship between changes in leaf dark respiration rate measured at growth temperature (ΔR_g) as a function of changes in growth temperature (ΔT_g); and generalized least squares models (GLS) of the relationship between changes in net CO_2 assimilation rate measured at growth temperature (ΔA_g) and ΔT_g, between ΔR_g and ΔA_g, and the relationship between ΔT_g and the ratio of ΔA_g to ΔR_g ($\Delta A_g / \Delta R_g$)

Model used	Parameters	PFT	Slope	Intercept	σ	P-value (slope)	P-value (intercept)	R^2	F	df	Overall model P-value
GLS	ΔA_g vs ΔT_g	C₃	−0.54	−5.49	6.03	<0.001	<0.001	0.05		316	<0.001
		C₄	−0.39	3.95		0.003	0.13				
		Deciduous	−0.06	3.50		0.28	0.33				
		Evergreen	0.56	5.58		0.03	<0.001				
LM	ΔR_g vs ΔT_g	C₃	0.01	−0.04	0.62	0.67	0.92	0.32	7.01	103	<0.001
		C₄	−0.03	0.87		0.90	0.73				
		Deciduous	0.19	−0.21		0.009	0.75				
		Evergreen	0.02	−0.08		0.58	0.84				
GLS	ΔR_g vs ΔA_g	C₃	−0.004	0.12	0.58	0.5	0.16	0.13		105	<0.001
		C₄	0.16	−0.04		0.058	0.86				
		Deciduous	0.2	0.59		<0.001	0.07				
		Evergreen	0.06	0.05		0.019	0.49				
GLS	$\Delta A_g/R_g$ vs ΔT_g	C₃	−0.09	7.46	36.66	0.95	0.74	0.04		104	0.89
		C₄	−0.95	6.48		0.94	0.96				
		Deciduous	−0.70	3.20		0.87	0.93				
		Evergreen	−2.29	11.72		0.32	0.64				

The main effect of all models included the interaction between the response variable and plant functional type (PFT: C₃ herbs, C₄ species, deciduous woody species and evergreen woody species). σ, residual standard error; *F*, F-statistics; df, degrees of freedom.
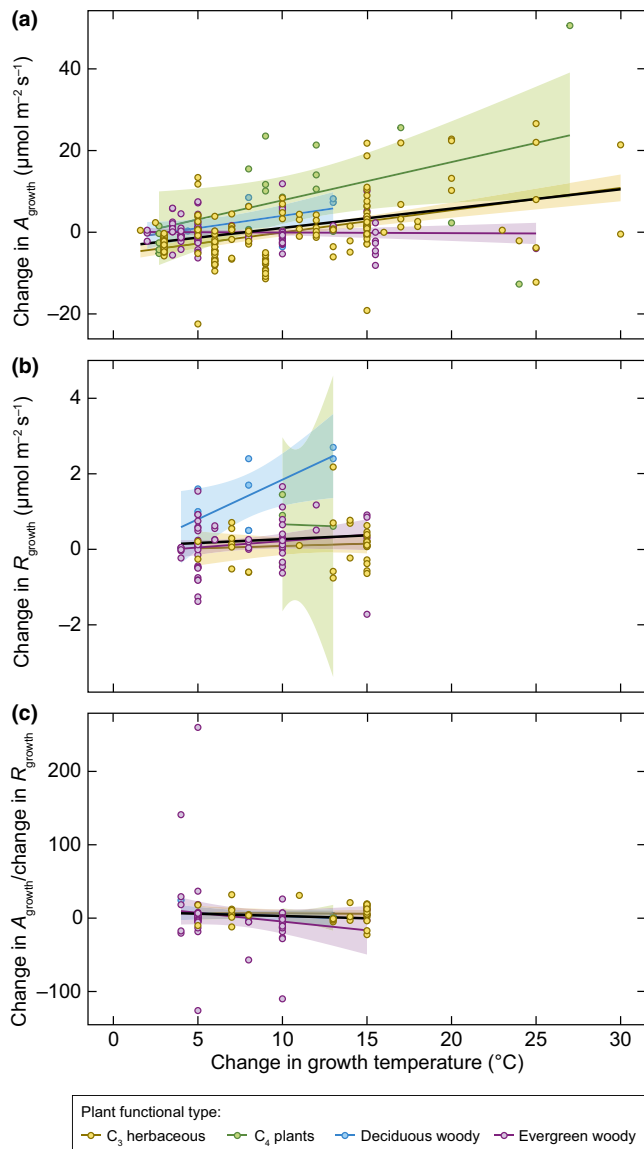
(a)

(b)

(c)

Fig. 2 The relationship between the change in growth temperature (T_{growth}) and changes in (a) net CO_2 assimilation rate at T_{growth} (A_{growth}), (b) leaf dark respiration rate at T_{growth} (R_{growth}) and (c) the ratio of A_{growth} to R_{growth}. Plant functional types (represented by different colours): C_3 herbaceous species, C_4 species, deciduous woody plants and evergreen trees. Circles represent individual observations, lines are regressions and shaded regions represent 95% confidence intervals.

Fig. 3 The relationship between changes in net photosynthesis and leaf dark respiration measured at the growth temperature (A_{growth} and R_{growth}, respectively). Circles represent individual observations, lines are regressions and shaded regions represent 95% confidence intervals. Plant functional types (represented by different colours): C_3 herbaceous species, C_4 species, deciduous woody plants and evergreen trees.

both A_{growth} and R_{growth}, this generated 316 contrasts for A_{growth} from 57 studies, 111 contrasts from 22 studies for R_{growth}, and 105 contrasts from 21 studies where both A_{growth} and R_{growth} were assessed on the same material, allowing us to calculate the ratio of A_{growth} to R_{growth}. All data were expressed on a μmol CO_2 m^{-2} s^{-1} basis and were converted as needed into these units using relevant data from the paper of interest. As our goal was to determine how carbon fluxes varied with continuous variation in growth temperature and changes in growth temperature, we took the analytical approach of Way & Oren (2010). Thus, unlike other types of meta-analyses determining an overall effect size, we did not weight the data by sample size. In total, 83 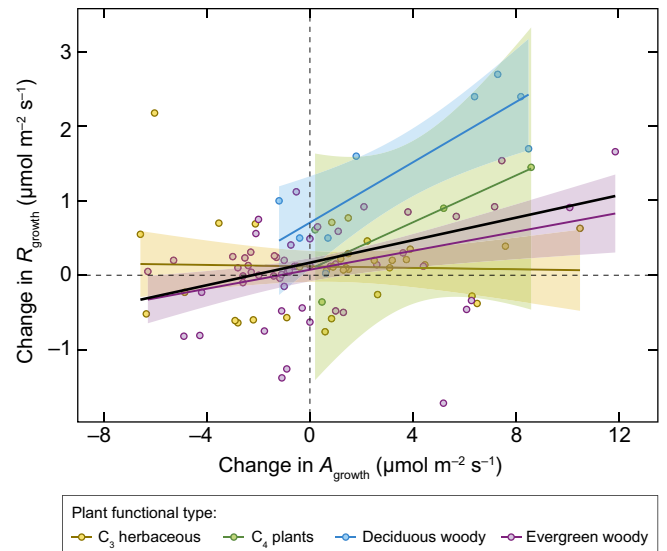plant species (Supporting Information Table S1) belonging to each of four PFTs (C_3 herbaceous, C_4, deciduous woody and evergreen woody) were included.

The relationship between changes in R_{growth} in response to changes in growth temperature (T_{growth}) was analyzed using a linear regression model with the explanatory variable, PFT, and the interaction between the explanatory variable and PFT. The relationship between changes in A_{growth} in response to T_{growth}, the relationship between changes in A_{growth} and changes in R_{growth}, and between the ratio of A_{growth} and R_{growth} (A_g/R_g ratio) with changes in T_{growth} were tested using generalized least squares models to account for deviations from normality present in these relationships, and included the response variables, PFT, and their interaction. All analyses were performed in R (R Core Team, 2013, v. 3.4.3).

Consistent with previous reports (Way & Yamori, 2014), an increase in T_{growth} was correlated with an increase in A_{growth} in some PFTs (Fig. S1a–d). As the change in T_{growth} increased, the change in A_{growth} increased in C_3 herbaceous plants ($P < 0.001$) and C_4 species ($P = 0.003$), but remained constant in deciduous woody species ($P = 0.28$), and declined in evergreen trees ($P = 0.03$) (Table 1; Fig. 2a). Across the same dataset, R_{growth} increased significantly with warming only in deciduous trees ($P = 0.009$), remaining constant in C_3 herbs ($P = 0.67$), C_4 ($P = 0.90$) and evergreen woody ($P = 0.58$) species (Table 1; Figs 2b, S1e–h), indicating a tendency for partial or complete homeostasis of respiration across growth temperatures, as seen in Slot & Kitajima (2015).

More interestingly, the data can be studied to evaluate patterns of concurrent shifts in A_{growth} and R_{growth}. The ratio of A_{growth} to R_{growth} was constant across a wide range of growth temperatures in all PFTs, indicating that most species are able to maintain a homeostatic balance between these processes ($0.32 < P < 0.95$;

Table 1; Fig. 2c). The photosynthetic and respiratory data can also be examined by plotting them against each other. There was a positive relationship between changes in R_{growth} and changes in A_{growth} in response to warming in C_4 species ($P = 0.058$), and deciduous ($P < 0.001$) and evergreen trees ($P = 0.019$), although there was no significant relationship between the parameters in C_3 herbaceous species ($P = 0.5$), where the relationship was constrained by relatively small changes in R_{growth} in response to changes in T_{growth} (Table 1; Fig. 3). Thus, plants that have higher A_{net} in warm growth conditions also tend to show only partial homeostasis of respiration, implying that some of the extra fixed carbon in warm-grown plants is being consumed via elevated respiration rates or that higher respiration rates stimulate A_{net} in warm conditions. This also indicates that in plants where A_{net} is suppressed by warming, perhaps by sink limitations, respiration tends to overcompensate (i.e. thermal acclimation reduces respiration rates more than is needed to maintain homeostasis). This overcompensation is relatively uncommon, occurring in only 10 of 105 contrasts in the meta-analysis by Slot & Kitajima (2015), but our data show that this phenomenon may be linked to reductions in carbon availability for respiration at higher growth temperatures. Overall, our analysis shows that thermal acclimation patterns in photosynthesis and respiration are probably operating in an interlinked manner, emphasizing the need to consider these physiological processes in tandem.

V. Will elevated CO_2 offset warming-induced changes in carbon metabolism?

Many of the impacts of rising CO_2 on plant carbon metabolism are offset by increasing temperatures, so these global change factors must be assessed together to build a realistic picture of how a changing climate will impact plants (Norby & Luo, 2004). For example, because the suppression of photorespiration by elevated CO_2 is temperature-dependent (Long, 1991), CO_2 fertilization is expected to be stronger in the tropics than in cooler climates (Hickler *et al.*, 2008; Baig *et al.*, 2015). High CO_2 also increases the thermal optimum of A_{net} (Sage & Kubien, 2007) and can increase the heat tolerance of photosynthesis in C_3 plants (Taub *et al.*, 2000; Wang *et al.*, 2008; Rodrigues *et al.*, 2016). However, rising CO_2 and warming can have compounding effects on plant carbon dynamics. Elevated CO_2 concentrations decrease g_s (Ainsworth & Long, 2004), as do the high VPD conditions that normally accompany elevated temperatures (Franks & Farquhar, 1999; Oren *et al.*, 1999). Not only will lower g_s reduce A_{net} by restricting CO_2 availability for photosynthesis (Franks & Farquhar, 1999; Oren *et al.*, 1999), but it also warms leaves by reducing latent heat loss (Long *et al.*, 2004; Kimball & Bernacchi, 2006). These high leaf temperatures further stimulate photorespiration rates and may also expose leaves grown under future climates to critically high temperatures. In the field, trees grown under elevated CO_2 shed more leaves during a hot drought than did control trees, which correlated with lower g_s in the high CO_2 trees and probably increases in damaging, high leaf temperatures (Warren *et al.*, 2011). The net effect of global change on carbon dynamics will therefore depend on plant responses to concurrent changes in CO_2 and temperature. For example, even

though rising CO_2 will suppress photorespiration as temperatures increase, eliminating photorespiration could still increase gross photosynthesis by 12–55% in a future warmer and high CO_2 climate (Walker *et al.*, 2016).

The clearest evidence of how rising CO_2 and temperature will alter plant carbon fluxes therefore comes from studies that manipulate both factors. A meta-analysis by Wang *et al.* (2012) showed that the effect of elevated CO_2 on A_{net} does not vary between plants grown at ambient and elevated temperatures, with high CO_2 stimulating A_{net} by 14–20%. There was some indication that elevated CO_2 can alter A_{net} in plants exposed to heat stress, with positive CO_2 effects on legumes and negative effects on C_4 species (Wang *et al.*, 2012). However, the average responses of photosynthesis to CO_2 and temperature in meta-analyses such as Wang *et al.* (2012) do not necessarily tell the whole story. Instead, these data imply that plant carbon flux responses to temperature (which vary across species) may be more critical for understanding future carbon cycling than responses to CO_2 (which are largely consistent across studies). For example, elevated CO_2 increased A_{net} in field-grown soybean, but warming reduced A_{net}, so the combination of warming with high CO_2 led to similar or even lower rates of A_{net} than in high CO_2 plots alone (Ruiz-Vera *et al.*, 2013). A similar effect has been seen in other studies (Wang *et al.*, 1995). In contrast, in studies where A_{net} is not reduced by warming, either because the species thermally acclimates or the degree of warming imposed is small, elevated CO_2 stimulates A_{net} in the combined CO_2 and temperature treatments (Teskey, 1997; Lewis *et al.*, 2001, 2015; Ghannoum *et al.*, 2010; Edwards *et al.*, 2017; Lamba *et al.*, 2018). So while high CO_2 may stimulate A_{net} across a wide range of temperatures, plants may still have decreased carbon uptake compared to current growth conditions.

Given that thermal acclimation of respiration is common while the impact of rising CO_2 on respiration is mixed, we might expect that growth temperature effects will dominate when the two factors are changed concurrently. This is indeed what we see in many studies. Tjoelker *et al.* (1999a,b) showed that the effects of temperature and CO_2 on respiration were largely independent in a suite of boreal tree species, with warming reducing respiration rates and high CO_2 having little effect on respiration in most species. These conclusions are similar to those from another boreal tree study, where the effect of growth temperature on respiration was greater than that of growth CO_2 (Zha *et al.*, 2003). Ziska & Bunce (1993) found that respiration (on a leaf area basis) was suppressed by high CO_2, but only in the lowest temperature treatment, while there was no effect of CO_2 on respiration in plants grown between 20 and 30°C. Other studies find only weak effects of CO_2 and warming on respiratory fluxes (e.g. Tingey *et al.*, 2007; Kroner & Way, 2016; Lamba *et al.*, 2018), and some find the effect of CO_2 to be stronger than that of temperature (Lamba *et al.*, 2018). While there are few studies addressing this question, the temperature sensitivity of respiration appears to be similar in vegetation grown under current conditions and future conditions of combined elevated temperature and CO_2 concentrations (Gauthier *et al.*, 2014; Kroner & Way, 2016; Lamba *et al.*, 2018).

Combining the results from many studies on how plant carbon fluxes are altered by warming and high CO_2 allows for the type of

generalizations necessary for modeling future plant carbon fluxes. Dynamic global vegetation models rely on photosynthetic and respiratory parameters to estimate plant–atmosphere carbon exchange. In many of these models, species are grouped into PFTs (Poulter *et al.*, 2011), as species within these groups may respond to global change in similar ways. However, while some studies find similar responses of carbon dynamics across species to warming and CO_2 (Xu *et al.*, 2014), the variation in how species respond to climate treatments can be substantial, even within a single PFT (Reich *et al.*, 1998). When both Scots pine and Norway spruce were grown at a range of elevated temperatures and CO_2 concentrations, pine showed thermal acclimation of A_{net} and respiration, and thus maintained high net carbon uptake rates at higher temperatures, while A_{net} and respiration showed little acclimation to either CO_2 or warming in spruce, leading to a suppression of net carbon gain in warm-grown spruce trees (Kurepin *et al.*, 2018). As we move forward, it is therefore important to consider not only the mean responses on plant carbon fluxes to climate change, but also the extreme responses, especially when they occur in species with outsized ecological or agricultural impact.

VI. No plant is an island: water and nutrient limitations define plant responses to climate drivers

When water or nutrients are limiting, as is common in terrestrial ecosystems and many agricultural settings, the positive effects of rising CO_2 and warming are likely to be lower than those predicted from well-watered and fertilized systems. For example, elevated CO_2 had no impact on biomass of a temperate grassland when water and nitrogen were both limiting (Reich *et al.*, 2014), the ability of a temperate forest to accumulate carbon under high CO_2 was limited by both soil fertility and water availability (Oren *et al.*, 2001), and the impacts of elevated CO_2 and temperature on photosynthesis and respiration were erased during drought in *Eucalyptus* (Duan *et al.*, 2013). Here we briefly review some of the recent work on how photosynthetic, photorespiratory and respiration responses to CO_2 and temperature are affected by water and nutrient availability.

The impact of elevated CO_2 on plant carbon metabolism is predicted to be greatest in dry conditions where reductions in photosynthesis are primarily due to low g_s and C_i (Drake *et al.*, 1997). While this is seen in some studies (Roden & Ball, 1996; Wullschleger *et al.*, 2002; Robredo *et al.*, 2007), in others, the effect of elevated CO_2 on photosynthesis is actually reduced in dry conditions (e.g. Gunderson *et al.*, 2002). This may be partly due to the different ways that species can respond to rising CO_2 when water availability varies. In dry regions, increasing CO_2 over the past century is linked to increasing WUE (i.e. a higher ratio of A_{net}/g_s), while moister regions show an increase in C_i, implying that g_s is not reduced to the same extent in wet sites as it is in dry sites by high CO_2 (Drake *et al.*, 2017). Importantly, high CO_2 may also alter the way in which plants respond to drought at a physiological and biochemical level. Soybeans grown at high CO_2 were more sensitive to abscisic acid, a plant hormone that induces stomatal closure, so that C_i declined more rapidly in response to water stress in high CO_2 plants than control plants (Gray *et al.*, 2016). In the same study, the direct reduction in g_s and transpiration by elevated CO_2 was partly offset by a larger canopy size, while lower g_s increased leaf temperatures and therefore the leaf to air VPD, driving even more transpiration (Gray *et al.*, 2016). Taken together, these changes in leaf function and canopy structure meant that the stimulation of growth and yield in soybeans under high CO_2 in the field diminished or disappeared during droughts (Gray *et al.*, 2016).

Water stress should also enhance the impacts of warming on plant carbon metabolism, partly because drought reduces evaporative cooling, and partly because low g_s during water stress reduces C_i, which stimulates photorespiration (Feller, 2016). Some of these effects can be seen at a large scale. In a tropical rainforest, GPP was reduced 10% in a hot, dry El Niño year, contributing to a weaker forest carbon sink (Cavaleri *et al.*, 2017). Similarly, unusually warm and dry conditions in large parts of North America in 2012 promoted early budburst and therefore enhanced spring carbon uptake, but decreased summer GPP through heat and drought effects, with the depletion of soil moisture being exacerbated by the earlier leaf development in the spring (Wolf *et al.*, 2016). These effects of temperature and water can also be seen at the global scale. Summer warming tends to stimulate net primary productivity (NPP) in high-latitude northern regions, while decreasing it in other areas of the globe where hotter summers are also dry (Xia *et al.*, 2014). There can also be positive interactions between warming and drought stress with regard to carbon metabolism (Killi *et al.*, 2017). Water stress can provide photosynthetic heat stress tolerance (Havaux, 1992, 1993), as both heat and drought stress alter chloroplast membrane composition in similar manners, facilitating cross-protection between drought and warming. These changes in membrane composition may similarly underlie drought-related modifications of the temperature response of respiration. In *Eucalyptus* grown under elevated CO_2, elevated temperatures and water stress, the temperature at which respiration peaked before declining was increased in water-stressed plants (Gauthier *et al.*, 2014).

Soil nitrogen availability could significantly impact the ability of plants to respond to rising CO_2 by altering soil nitrogen dynamics (Díaz *et al.*, 1993; Reich *et al.*, 2006) or by limiting the nitrogen supply needed to build nitrogen-rich tissues at a rate that matches the CO_2 supply. Elevated CO_2 effects on photosynthesis (and growth) were therefore expected to diminish over time in the field, an idea known as the Progressive Nitrogen Limitation (PNL) hypothesis (Luo *et al.*, 2004, 2006). Recent work has instead shown that gross nitrogen immobilization and mineralization rates in soils are stimulated to a similar degree by elevated CO_2 in FACE studies (Rütting & Andresen, 2015). Elevated CO_2 stimulates plant nitrogen acquisition in experiments where growth is enhanced by high CO_2 (Luo *et al.*, 2006; Finzi *et al.*, 2007; Feng *et al.*, 2015), possibly because plants can explore larger soil volumes to access more nitrogen (Finzi *et al.*, 2007). Thus, while elevated CO_2 decreased leaf nitrogen across a range of FACE studies, growth stimulations were relatively consistent over a decade or so, and there was little evidence for PNL (Feng *et al.*, 2015). In the FACE studies where growth responses to elevated CO_2 were negative or only weakly positive, nitrogen acquisition was instead decreased by high

CO_2 (Feng *et al.*, 2015), implying that growth declines may be related to low photorespiration rates suppressing nitrate uptake capacity (Bloom *et al.*, 2010, 2014). CO_2 effects on nitrogen have also been linked to mycorrhizal status. Terrer *et al.* (2016) showed that elevated CO_2 increases biomass more strongly in ectomycorrhizal plants than in arbuscular mycorrhizal species, a result they attribute to a greater nitrogen supply from ectomycorrhizae to their host plants.

While we know that changes in leaf nitrogen are often strongly correlated with changes in carbon metabolism in plants grown under elevated temperatures (e.g. Tjoelker *et al.*, 1999a; Lewis *et al.*, 2004), surprisingly few studies have directly assessed how nitrogen supply alters the effect of warming on plant carbon metabolism. The little data we have indicate that while warming and high nitrogen availability can separately increase A_{net}, combining these treatments further increased photosynthetic performance in pine seedlings, but reduced A_{net} compared to the warming treatment in spruce (Zhao & Liu, 2009). More data are needed before any broad-scale conclusions can be drawn regarding the interaction between nitrogen availability and rising temperatures.

VII. Conclusions

It is important to remember that changes to the carbon fluxes discussed here do not necessarily lead to changes in biomass (Fatichi *et al.*, 2014; Körner, 2015), because carbon can be lost through other venues, such as volatile organic carbon and soil exudates. For example, Ellsworth *et al.* (2017) showed that A_{net} was stimulated by 19% in high CO_2 but tree above-ground productivity did not increase. Thus, while both A_{net} and growth tend to be impacted by combined CO_2 and temperature in a similar manner (Dieleman *et al.*, 2012; Baig *et al.*, 2015), changes in growth may be related to climate change effects on traits other than photosynthetic rates per se. High CO_2 can promote faster development of spring photosynthetic capacity, as can warming (Linkosalo *et al.*, 2017), highlighting the need to consider how climate alters photosynthetic phenology when comparing studies that measure growth and carbon metabolism. Perhaps even more importantly, plant growth (and the cell division and elongation that underlies growth) is temperature-dependent, and the carbon demand from growth may drive photosynthetic rates, rather than the other way around (Körner, 2015).

Despite these caveats, the impact of elevated CO_2 and warming on growth responses is largely determined via shifts in photosynthesis, photorespiration and respiration, which include both carbon sources and sinks. Plant carbon metabolism underpins the ability of plants to obtain the carbon they need to grow and produce the seeds we consume in major crop species. There has thus been considerable interest in finding ways to improve plant carbon uptake to increase food productivity and combat climate change, including modifying photoprotective mechanisms in crop canopies (Kromdijk *et al.*, 2016), inserting photorespiratory by-passes into plants (Kebeish *et al.*, 2007), improving the kinetics of Rubisco carboxylation (Sharwood *et al.*, 2016), and engineering synthetic carbon fixation pathways into leaves (Bar-Even, 2018). Understanding the combined effects of rising temperatures and CO_2 concentrations on plant carbon metabolism, particularly in the context of changing water and nutrient availability, is critical for the success of these efforts and for predicting the impact of climate change on vegetation carbon fluxes. We therefore advocate for the need to expand our studies of plant carbon metabolic processes under combined CO_2 and temperature, to provide the information we need to guide strategies for improving plants for a future climate. Our results also highlight the need to address the responses of photosynthesis, photorespiration and respiration to climate change in a concerted way, to provide broad insights into climate change effects on carbon metabolism and to open new avenues for mitigating and adapting to the impacts of rising CO_2 and temperatures on vegetation.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article:

Fig. S1 The relationship between growth temperature (T_{growth}) and either net CO_2 assimilation rate at T_{growth} (A_{growth}), leaf dark respiration rate at T_{growth} (R_{growth}) or the ratio of A_{growth} to R_{growth}.

Table S1 List of species used in the meta-analysis, including the plant functional type, biome where the species is found and the study from which the data were taken

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Appendix A1

References used in the meta-analysis

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