

# Chapter 6

## Leaf Respiration in Terrestrial Biosphere Models

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## Summary

How leaf respiration ( $R_d$ ) is represented in leading terrestrial biosphere models (TBMs) is reviewed, followed by an overview of how emerging global datasets provide opportunities to improve parameterization of leaf  $R_d$  in large-scale models. We first outline how TBMs have historically accounted for variations in respiratory  $\text{CO}_2$  release in mature leaves, using assumed relationships between leaf nitrogen, photosynthetic capacity and  $R_d$ . The need for TBMs to account for light inhibition of  $R_d$  in mature leaves is highlighted, followed by a discussion on how  $R_d$  of upper canopy leaves is used to predict maintenance respiration in whole plants. We then outline how respiratory energy requirements of growth are accounted for in TBMs, pointing out that current assumptions on the costs of biosynthesis are based on theoretical calculations that may not be valid for all plant species and environments. The chapter then considers how improvements might be made to TBMs with respect to the parameterization of leaf  $R_d$ . We show how recently compiled datasets provide improved capacity to predict global variations in baseline  $R_d$  measured at a standard temperature, and how baseline  $R_d$  likely acclimates to sustained changes in growth temperature. Application of this dataset reveals markedly higher rates of leaf  $R_d$  than currently predicted by TBMs, suggesting that TBMs may be underestimating global plant respiratory  $\text{CO}_2$  release. The availability of a new, global dataset on short-term temperature responses of leaf  $R_d$  is highlighted. Analysis of this dataset reveals that leaf  $R_d$  does not exhibit the exponential response assumed by most TBMs; rather, the temperature-sensitivity declines as leaves warm, with convergence in the temperature-response across biomes and plant functional types. We show how equations derived from these datasets may provide the TBM community with a new framework to improve representation of mature leaf respiration in TBMs.

## I. Introduction

Over the past 30 years, increasing efforts have been put into the development of terrestrial biosphere models (TBMs) and associated land surface components of Earth system models (ESMs) (Running and Coughlan 1988; Raich et al. 1991; Woodward et al. 1995; Haxeltine and Prentice 1996a; Ruimy et al. 1996; Cox et al. 1998; Cox 2001; Sitch et al. 2008; Clark et al. 2011; Booth et al. 2012; Prentice and Cowling 2013; Fisher et al. 2014). TBMs are used to

represent carbon exchange between plants and the atmosphere, with  $\text{CO}_2$  release by plant respiration ( $R$ ) being crucial for TBM predictions (King et al. 2006; Huntingford et al. 2013; Wythers et al. 2013), reflecting the fact that  $\sim 60$  Pg carbon are respired by plants into the atmosphere each year (Prentice et al. 2001; Canadell et al. 2007; Denman et al. 2007; IPCC 2013). Because leaf  $R$  represents approximately half of overall respiratory  $\text{CO}_2$  release by whole-plants (Atkin et al. 2007), even small fractional changes in leaf respiration can have large

impacts on net carbon uptake by plants, which in turn can affect ecosystem net carbon exchange and storage (Piao et al. 2010). Moreover, by influencing the  $\text{CO}_2$  concentration in the atmosphere, feedbacks can occur that alter the extent of future global warming (Cox et al. 2000; Huntingford et al. 2013). There is growing acceptance, however, that representation of leaf respiration in TBMs is inadequate and lags behind that of photosynthetic parameterization, leading to large uncertainties in predictions of future climates and vegetation dynamics (Gifford 2003; Leuzinger and Thomas 2011; Huntingford et al. 2013; Smith and Dukes 2013; Lombardozzi et al. 2015). In this chapter, we outline how foliar respiratory  $\text{CO}_2$  release is currently parameterized in TBMs, and identify a range of areas where improvement is now possible.

Both fully-expanded (i.e. mature) leaves and developing leaves contribute to respiratory rates of whole shoots; for both leaf tissue types, variation in the rate of respiratory  $\text{CO}_2$  release can be influenced by factors such as availability of substrate, demand for respiratory products [e.g. adenosine triphosphate (ATP), reducing equivalents and/or tricarboxylic acid (TCA) cycle intermediates] and respiratory capacity (i.e. abundance of active respiratory proteins). Importantly, demand for respiratory products differs markedly between immature (i.e. expanding) and mature (i.e. fully-expanded) leaves (Fig. 6.1; see also Chap. 8 in this volume), with energy demands for biosynthesis being dominant in expanding leaves, whereas maintenance processes (e.g. protein turnover and maintenance of solute gradients) are central to energy demand in mature leaves (Penning de Vries 1975; Amthor 2000; Bouma 2005). Reflecting this difference, a theoretical framework was conceived (Thornley 1970, 2011, Amthor 2000) that recognized that respiratory energy is used to support both growth ( $R_g$ ) and maintenance ( $R_m$ ) processes (the so-called ‘*growth-and-maintenance-respiration paradigm*’–

GMRP) (Amthor 2000). While the GMRP is not without its critics [e.g. respiration in mature leaves is also likely influenced by growth-linked processes such as the energy costs associated with phloem loading (Bouma et al. 1995)], it nonetheless forms the basis of how whole-plant respiration ( $R_p$ ) is parameterized in most TBMs (Gifford 2003; Smith and Dukes 2013; see Table 6.1 for details). For example, in the Community land surface model JULES [Joint UK Land Environment Simulator (Clark et al. 2011)], used as the land surface scheme in the UK Hadley Centre climate models, the starting point for modeling  $R_p$  is to first predict rates of respiration of mature leaves at 25 °C (i.e.  $R_d$ ), with leaf  $R_d$  then used to estimate rates of maintenance respiration in whole shoots and roots ( $R_{pm}$ ) (Fig. 6.2). Whole-plant growth respiration ( $R_{pg}$ ) is then calculated as one quarter of whole-plant gross primary productivity (GPP) minus  $R_{pm}$ , with overall  $R_p$  being estimated from the sum of  $R_{pm}$  plus  $R_g$  (Fig. 6.2). In subsequent sections, we outline how respiratory rates of developing and mature leaves are accounted for in leading TBMs such as JULES, highlighting uncertainties and areas where our growing understanding of how genotypic and environmental variation in leaf respiration across the globe could be used to improve the predictive capacity of TBMs.

When considering how to improve representation of leaf  $R_d$  in TBMs, the ideal solution would be to develop a process-based model that accurately predicts spatial and temporal variations in respiratory fluxes. For photosynthesis, a mechanistic biochemical framework is available (Farquhar et al. 1980), enabling  $\text{CO}_2$  uptake to be modeled in TBMs (e.g. Haxeltine and Prentice 1996a; Cox 2001; Clark et al. 2011; Ziehn et al. 2011; Oleson et al. 2013; Ali et al. 2015). However, while our understanding of the underlying factors that regulate leaf respiratory fluxes has improved markedly in recent years (Plaxton and Podesta 2006; Noguchi and Yoshida 2008; Buckley and Adams 2011;

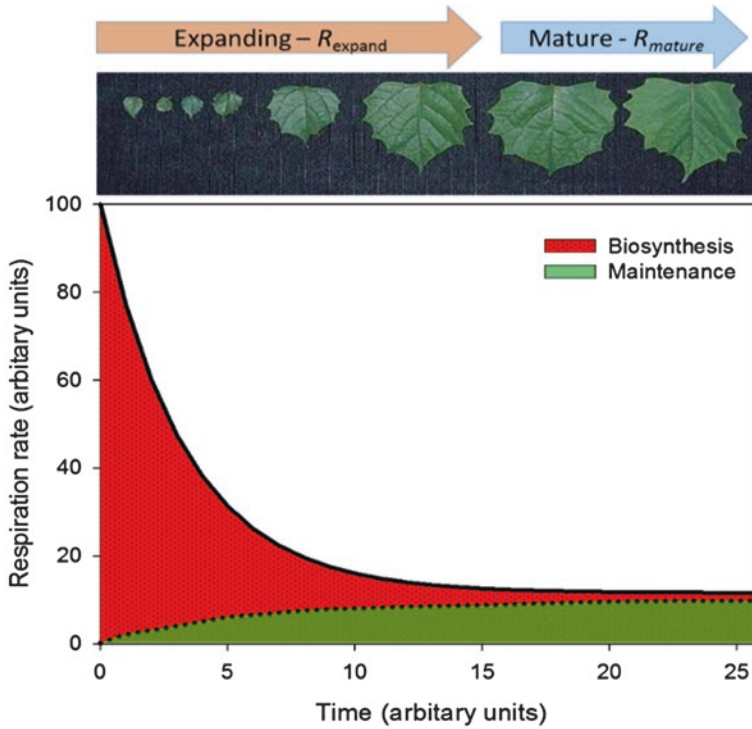


Fig. 6.1. Developmental changes in leaf ( $R$ ). Solid line shows  $R$  declining sharply as leaves expand (Azcón-Bieto et al. 1983; Fredeen and Field 1991; Evans et al. 2000; Armstrong et al. 2006), meeting energy demands associated with biosynthesis (i.e. cell division and expansion) & maintenance (e.g. protein turnover and maintenance of solute gradients) processes (Penning de Vries 1975; Amthor 2000; Bouma 2005). In expanding leaves, demands of biosynthesis are dominant. Maintenance costs become relatively more important as leaves expand, being dominant in mature leaves; potentially, energy demands associated with sucrose and amino acid production/export (Bouma 2005) may also influence rates of mature leaf respiration. Thus, variation in demand for respiratory products from mature leaves – such as might occur when plants vary in whole plant growth rates with concomitant changes in demand for sucrose/amino acid export from mature leaves to meristematic regions – could potentially impact on respiratory rates of mature leaves

Kruse et al. 2011; Millar et al. 2011; Tcherkez et al. 2012; Sweetlove et al. 2013), at present there is no ‘Farquhar-model-equivalent’ for leaf  $R_d$ . Recognizing this, the TBM community has – by necessity – relied on a *phenomenological* approach to predict variation in leaf  $R_d$  in TBMs, using reported relationships between  $R_d$  of mature leaves and associated traits, and chemical analyses of plant tissues to predict whole-plant growth respiration. However, when TBMs were first developed, relatively few data were available on  $R_d$  of mature leaves, requiring them to rely on measurements made on a limited number of species/environments (e.g. Farquhar et al. 1980; Ryan 1991; Collatz et al. 1992; Ryan 1995;

Haxeltine and Prentice 1996a; Ruimy et al. 1996; see Table 6.1 for details).

In subsequent sections, we discuss in detail how variations in leaf  $R_d$  have historically been parameterized in leading TBMs, and highlight key uncertainties in assumed relationships between  $R_d$  of mature leaves and associated traits. How leaf  $R_d$  is scaled to whole plants is also outlined; as part of this section, we discuss the basis upon which growth respiration ( $R_{pg}$ ) is accounted for in TBMs, and discuss whether the assumption by TBMs of a single growth respiration coefficient ( $g_R$  – i.e. respiratory  $\text{CO}_2$  released per unit biomass produced by growth) for all plants is valid. The chapter concludes with a

Table 6.1. Representation of leaf and whole-plant respiration in a range of terrestrial biosphere models, including what assumptions are made on the temperature dependence of respiration

Model	Example papers	Leaf respiration of mature leaves ( $R_d$ ), usually in the upper canopy	Refs	Temperature dependence	Refs	Whole-plant maintenance $R$ ( $R_{pm}$ )	Growth $R$ ( $R_{pg}$ )	Refs
BETHY	Knorr (2000) and Ziehn et al. (2011)	$C_3$ plants: $R_d = 0.011 V_{emax}$ (25 °C) $C_4$ plants: $R_d = 0.042 V_{emax}$ (25 °C) ( $R_d$ units: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Farquhar et al. (1980), Collatz et al. (1991) and Knorr (1997)	Short-term: $T$ -dep. $Q_{10}$ Long-term: via $V_{emax}$ acclimation	Tjoelker et al. (2001) and Katge and Knorr (2007)	Scales with canopy $R$ (calc. assuming LAI and light absorption) and assuming 40% of $R_d$ in canopy, based on assumptions of N allocation and $R_d$ -N relationships	$R_{pg} = 0.25 \text{ NPP}$ and, $\text{NPP} = \text{GPP} - R_{pm} - R_{pg}$	Ryan (1991)
BIOME3	Haxeltine and Prentice (1996a)	$C_3$ plants: $R_d = 0.015 V_{emax}$ (25 °C) $C_4$ plants: $R_d = 0.035 V_{emax}$ (25 °C) ( $R_d$ units: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Farquhar et al. (1980) and Haxeltine and Prentice (1996a)	Combination of $T$ -dep. of $V_{emax}$ and temp- dependent $E_a$	Berry and Björkman (1980), Haxeltine and Prentice (1996b) and Lloyd and Taylor (1994)	Scales with variation in $V_{emax}$ and N through canopy	$R_{pg} = 0.20 \text{ (GPP} - R_{pm})$	Haxeltine and Prentice (1996a) citing Ryan (1991) as the source.
BIOME-BGC	Running and Coughlan (1988), White et al. (2000) and Thornton et al. (2002)	$R_d$ proportion to leaf N $R_d = 0.0106 \text{ mol C (mol N)}^{-1} \text{ h}^{-1}$ (20 °C), converted to: $R_d = 2.525 \mu\text{g C (g N)}^{-1} \text{ s}^{-1}$ (20 °C)	Ryan (1991)	Fixed $Q_{10}$ (2.3)	Running and Coughlan (1988)	Calculated as a function of leaf N	$R_{pg}$ assumed to be fixed fraction of GPP	Ryan (1991)
Century	Parton et al. (1987), Melillo et al. (1993) and Methereil et al. (1996)	$R_d$ proportion to leaf N $R_d = 0.0106 \text{ mol C (mol N)}^{-1} \text{ h}^{-1}$ (20 °C), converted to: $R_d = 2.525 \mu\text{g C (g N)}^{-1} \text{ s}^{-1}$ (20 °C)	Ryan (1991)	Fixed $Q_{10}$ (2.0)	Ryan (1991)	Calculated as a function of leaf N	$R_{pg}$ assumed to be fixed fraction of GPP	Ryan (1991)

(continued)

Table 6.1. (continued)

Model	Example papers	Leaf respiration of mature leaves ( $R_d$ ), usually in the upper canopy	Refs	Temperature dependence	Refs	Whole-plant maintenance $R$ ( $R_{pm}$ )	Growth $R$ ( $R_{pg}$ )	Refs
CLM4.5	Oleson et al. (2013)	$R_d$ proportion to leaf N $R_d = 0.0106 \text{ mol C (mol N)}^{-1} \text{ h}^{-1}$ (20°C), converted to: $R_d = 2.525 \mu\text{g C (g N)}^{-1} \text{ s}^{-1}$ (20 °C) $C_3$ plants; $R_d = 0.015 V_{\text{cmax}}$ (25 °C) $C_4$ plants; $R_d = 0.025 V_{\text{cmax}}$ (25 °C) ( $R_d$ units: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Ryan (1991)	Fixed $Q_{10}$ (2.0)	Oleson et al. (2013)	Whole-plant $R_{pm} \propto$ base rates of $R_i$ , scaled to tissue N	$R_{pg} = 0.3$ total C in new growth	Larcher (2004)
MOSES-TRIFFID (now JULES)	Cox et al. (1998), Cox et al. (2000), Cox (2001), Clark et al. (2011) and Huntingford et al. (2013)	$R_d = 2.525 \mu\text{g C (g N)}^{-1} \text{ s}^{-1}$ (20 °C) $C_3$ plants; $R_d = 0.015 V_{\text{cmax}}$ (25 °C) $C_4$ plants; $R_d = 0.025 V_{\text{cmax}}$ (25 °C) ( $R_d$ units: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Farquhar et al. (1980), Collatz et al. (1991) and Collatz et al. (1992)	Fixed $Q_{10}$ (2.0) Bell-shaped function with peak rates of $R_d$ at 32°C	Cox (2001) and Huntingford et al. (2013)	Uses leaf $R_d$ to predict whole-plant $R_{pm}$ based on: assumed common $R$ -N scaling in roots, stems and leaves; assumed N allocation among organs	$R_g = 0.25$ (GPP- $R_{pm}$ )	Penning de Vries et al. (1983) and Thornley and Cannell (2000)
LPJ	Sitch et al. (2003) and Bonan et al. (2003)	$R_d$ (10 °C) scales with leaf N and is adjusted for C:N ratios (PFT-dependent within biome) Tropical trees: 0.027 Temperate trees: 0.066 Boreal trees: 0.033 $C_3$ and $C_4$ grasses: 0.066 ( $R_d$ units: $\text{g C g N}^{-1} \text{ d}^{-1}$ )	Ryan (1991)	Short-term: Temperature dependent $E_a$  Long-term: allows for growth $T$ -dependent variation in $R_d$ at 10 °C	Lloyd and Taylor (1994), Fukai and Silsbury (1977), Lechowicz et al. (1980), Amthor (1989) and Ryan (1991)	Whole-plant $R_{pm}$ = sum of rates in leaves, sapwood and roots	$R_{pg} = 0.25$ (GPP- $R_m$ )	Penning de Vries et al. (1983) and Thornley and Cannell (2000)

O-CN	Zaehle and Friend (2010)	$R_d$ proportion to leaf N $R_d = 0.0106 \text{ mol C (mol N)}^{-1} \text{ h}^{-1} (20^\circ \text{C}),$ converted to: $R_d = 2.525 \mu\text{g C (g N)}^{-1} \text{ s}^{-1} (20^\circ \text{C})$	Ryan (1991)	Modified $E_a$	Lloyd and Taylor (1994) and Reichstein et al. (2005)	Scaled to tissue level N concentrations	Ruimy et al. (1996) and McCree (1974)
Orchidee	Ruimy et al. (1996) and Krinner et al. (2005)	Based on literature survey of $R_d$ coefficients; $R_d = 7 \text{ mg g}^{-1} \text{ d}^{-1} (20^\circ \text{C})$	Ruimy et al. (1996)	Increases linearly with temperature $R_d = R_{d,0} e^{(1 + 0.016T)}$ modified	Ruimy et al. (1996)	Based on literature survey of $R_{pm}$ coefficients; roots ( $11 \text{ mg g}^{-1} \text{ d}^{-1}$ ) and sapwood ( $0.5 \text{ mg g}^{-1} \text{ d}^{-1}$ ) ( $20^\circ \text{C}$ );	$R_{pg} = 0.28 (GPP - R_{pm})$
Sheffield-DGVM	Woodward et al. (1995) and Woodwardlatter and Lomas (2004)	$R_d$ dependent on N uptake rates, with the foliar N concentrations	Harley et al. (1992)	Modified $E_a$	Robson (1981) and Paomban et al. (1991)	Based on a relationship between overall respiration rate of tissues, times mass of tissue, times a fixed constant (0.35)	For leaves, $R_{pg} = 0.30$ of mass synthesized
TEM	Raich et al. (1991), McGuire et al. (1992) and Melillo et al. (1993)	Rates of $R_d$ estimated by calibrating TEM and plant $R$ that matched autotrophic $R$ for forests/grasslands in USA.	Raich et al. (1991)	Either a $Q_{10}$ of 2.0 across all temperatures, or a $Q_{10}$ of 2.0 between 5-20 °C; linear increase from 2.0 to 2.5 between 5° and 0 °C; linear decrease from 2.0 to 1.5 between 20° and 40 °C	Raich et al. (1991), McGuire et al. (1992) and Larcher (2004)	Whole-plant $R_{pm} = K_r(C_v)^{0.0693T}$ where $K_r$ is the respiratory rate of vegetation per unit biomass C at 0 °C, and T is mean air T. $K_r$ estimated from calibrations of TEM to produce autotrophic R ( <i>i.e.</i> $R_{pm} + R_{pg}$ ) that matched R for forests/grasslands in USA (Raich et al. 1991)	$R_{pg} = 0.20 (GPP - R_{pm})$
							Raich et al. (1991), citing: Chung and Barnes (1977), Vertregt and Penning de Vries (1987), Williams et al. (1987) and Ryan (1991)

Source citations are listed where available

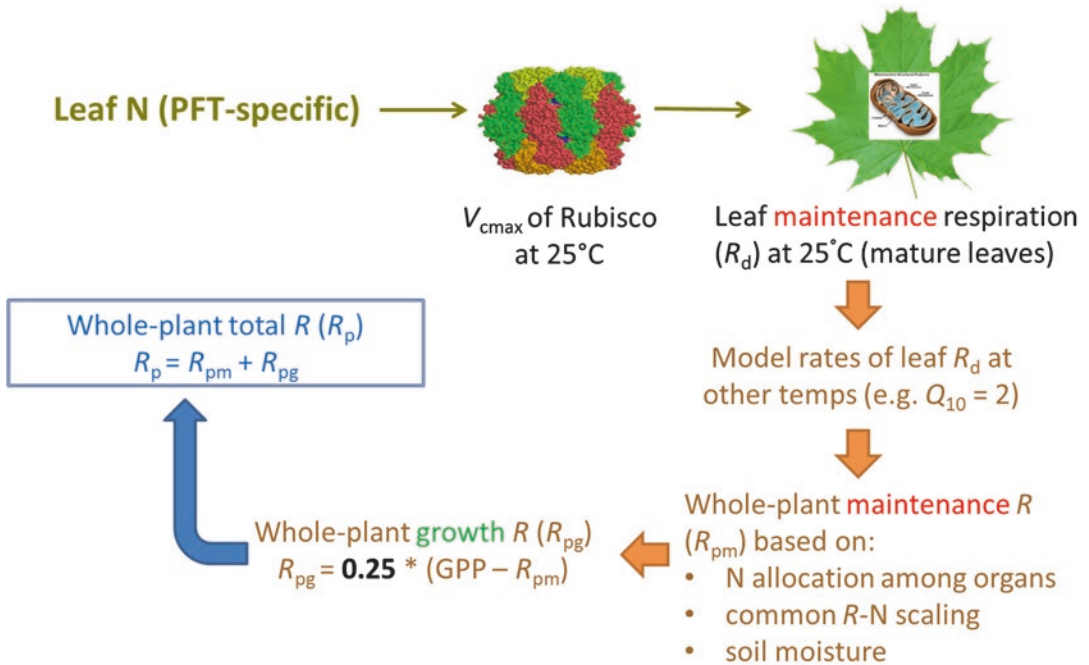


Fig. 6.2. Schematic showing progression via which whole-plant respiration rates ( $R_p$ ) are calculated from leaf nitrogen in the land surface model of JULES (Joint UK Land Environment Simulator) (Cox 2001; Clark et al. 2011). For individual plant functional types (PFTs), assumed foliar N concentrations are used to predict maximum rates of CO<sub>2</sub> carboxylation by Rubisco ( $V_{cmax}$ ) at a standard temperature of 25 °C, based on assumed  $V_{cmax}$ -[N] relationships derived from Schulze et al. (1994). Thereafter, maintenance respiration in mature leaves ( $R_d$ ) at the standard temperature of 25 °C is estimated based on assumed  $R_d$ - $V_{cmax}$  relationships (Farquhar et al. 1980; Collatz et al. 1991, 1992). Then, rates of leaf  $R_d$  at other temperatures are calculated assuming a  $R_d$ -temperature relationship such as a fixed  $Q_{10}$  approach. Whole-plant maintenance respiration ( $R_{pm}$ ) is then estimated via assumptions of how N is allocated among leaves, stems and roots, and respiration-[N] relationships in each organ. Crucially, this approach assumes a common maintenance  $R$ -N relationship in above and below-ground organs. Finally, rates of  $R_{pm}$  are modulated by a soil-moisture correction factor,  $\beta$  to yield the final whole-plant  $R_{pm}$  estimate. Whole-plant growth respiration ( $R_{pg}$ ) is then calculated as being 25% of the residual of gross primary productivity (GPP) minus  $R_{pm}$ .

section on potential ways parameterization of global variations in mature-leaf  $R_d$  over different time scales could be improved in future versions of TBMs. The chapter does not provide a comprehensive update on the role of genotype and environment in determining variations in mature-leaf  $R_d$ , which while important are beyond the scope of this chapter. Here, readers are encouraged to consult relevant reviews and primary literature (e.g. Atkin and Tjoelker 2003; Gonzelez-Meler et al. 2004; Atkin et al. 2005, 2015; Flexas et al. 2005; Rodríguez-Calcerrada et al. 2010; Searle et al. 2011b; Slot et al.

2013, 2014; Smith and Dukes 2013; Ayub et al. 2014; Way and Yamori 2014; Weerasinghe et al. 2014; Slot and Kitajima 2015; Vanderwel et al. 2015; Drake et al. 2016; Heskell et al. 2016b; Reich et al. 2016; Rowland et al. 2016).

Finally, a note on abbreviations used to describe leaf respiration. In most TBMs, respiration of mature leaves is designated as ' $R_d$ '. However, this can occasionally cause confusion when interpreting precisely what the abbreviation ' $R_d$ ' refers to. In leaf-level studies assessing variations in gas exchange rates,  $R_d$  is often used to describe leaf



respiration measured in *darkness* (e.g. Reich et al. 1998; Pons and Welschen 2002; Lee et al. 2005; Liang et al. 2013). However, in the paper that often forms the basis of TBM estimates of GPP,  $R_d$  was defined as non-photorespiratory mitochondrial  $\text{CO}_2$  release in the *light* (Farquhar et al. 1980), with Brooks and Farquhar (1985) subsequently defining  $R_d$  as being ‘day’ respiration (also designated as ‘ $R_{\text{day}}$ ’), and respiration in darkness as being ‘ $R_n$ ’ (i.e. ‘night’ respiration). With the exception of a few studies (Mercado et al. 2007; Clark et al. 2011; Harper et al. 2016), TBMs typically assume that  $R_d = R_n$  (i.e. light does not inhibit leaf respiration). For this reason, in most sections in this chapter, we use the term ‘ $R_d$ ’ to refer to leaf respiration taking place throughout the 24-h cycle (day and night). The only exception is a section devoted to the topic of light inhibition of leaf respiration, where we use the terms  $R_{\text{light}}$  and  $R_{\text{dark}}$  to define fluxes measured in the light and dark, respectively.

## II. Representation of Leaf Respiration in Terrestrial Biosphere Models

As noted above, there is no single approach to estimating plant respiration in TBMs, with Schwalm et al. (2010) reporting 15 unique approaches in a survey of 21 TBMs. However, in models that explicitly represent leaf  $R_d$ , a common approach is to relate  $R_d$  to foliar nitrogen concentration ([N]) and/or photosynthesis (Fig. 6.2, Table 6.1). Such approaches are based, in part, on the fact that variations in foliar [N], and/or photosynthetic rates, impact on the demand for respiratory products (e.g. ATP, reducing equivalents and/or carbon skeletons) by metabolic processes such as phloem loading, N assimilation and protein turn-over (Lambers 1985; Bouma et al. 1994, 1995; Noguchi and Yoshida 2008). Photosynthesis can also impact on respiratory rates via demand for ATP associated with sucrose synthesis,

exchange of excess redox equivalents and substrate supply (Krömer et al. 1988; Raghavendra et al. 1994; Krömer 1995; Hoefnagel et al. 1998). Moreover, as N is a core component of the photosynthetic system, positive relationships are often observed between light-saturated photosynthesis and [N] (Field and Mooney 1986; Evans 1989; Schulze et al. 1994) as well as between leaf  $R_d$  and [N] (Ryan 1991, 1995; Reich et al. 1996, 2008; Wright et al. 2006; Atkin et al. 2015). Hence, the use of foliar [N] and/or photosynthesis to predict leaf  $R_d$  in TBMs is based on a solid empirical and theoretical framework. For models that predict variation in leaf  $R_d$  via assumed relationships with photosynthetic capacity, foliar [N] remains often pivotal, reflecting assumed relationships between photosynthesis and [N] (e.g. Fig. 6.2). In this section, we discuss details on how respiratory fluxes are predicted from foliar [N] and/or photosynthesis in a range of leading TBMs, highlighting, where possible, the source datasets that underpin the assumed relationships.

### A. Using Foliar Nitrogen As a Predictive Trait for Mature Leaf Respiration

Terrestrial biosphere models such as Biome-BGC (Thornton et al. 2005), Century (Parton et al. 1987), CLM (Oleson et al. 2013) and O-CN (Zaehle and Friend 2010) predict rates of leaf  $R_d$  based on  $R_d$ -[N] relationships reported by Ryan (1991; Table 6.1). Foliar N (used as a proxy for N uptake) is also used to predict leaf  $R_d$  in Sheffield DGVM (Woodward et al. 1995; Woodward and Lomas 2004). In LPJ, rates of leaf  $R_d$  are also predicted based on assumed  $R_d$ -[N] relationships that are PFT (plant functional type) and biome specific, corrected for tissue C:N ratios and which are ultimately derived from Ryan (1991). In Ryan (1991), data from nine herbaceous and two coniferous tree species (i.e. 11 species in total) were assembled from published literature to assess the overall relationship between foliar  $R_d$  (mol C mol

$\text{N}^{-1} \text{h}^{-1}$ ) measured at 20 °C and [N] ( $\text{mol N mol C}^{-1}$ ), yielding:

$$R_d(\text{at } 20^\circ \text{C}) = 0.0106 [\text{N}] \quad (6.1)$$

Thus, rates of  $R_d$  at a set measuring temperature can be predicted in TBMs by using information on foliar [N]. TBMs using this approach assume that all PFTs and biomes follow the same  $R_d$ -[N] relationship. In a subsequent comparison of 14 tree species, Ryan (1995) found that the relationship between  $R_d$  and [N] did not differ between boreal and sub-alpine sites and that there was relatively little variability in N-based rates of leaf  $R_d$  among species; thus, the assumption of a common  $R_d$ -[N] relationship across PFTs and biomes appeared to hold. Subsequently, Amthor and Baldocchi (2001) collated published data on N-based rates of leaf  $R_d$  (measured at different temperatures, depending on the study) for 23 species [including data from Ryan (1991)]. For the current chapter, we have normalized rates to 20 °C assuming a fixed  $Q_{10}$  (i.e. proportional change in metabolic rates per 10 °C change in temperature) of 2.2, and excluded data from soybean that exhibited particularly high  $R_d$  [ $17.4 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$ ; (Thomas and Griffin 1994)]; analysis of the resultant dataset revealed three-fold variation in N-based rates of leaf  $R_d$  ( $2.2 - 6.8 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$ ). Contained within this comparison were species from several PFTs ( $\text{C}_3$  grasses and forbs, broad-leaved evergreen trees, broad-leaved deciduous trees, and conifers), suggesting that  $R_d$ -[N] relationships may differ among PFTs. Indeed, a cross-biome comparison revealed that rates of  $R_d$  at a given [N] differ among PFTs [forbs > broad-leaved shrubs > broad-leaved trees > needle-leaved trees; (Reich et al. 1998)]. Later, Reich et al. (2008) found that the y-axis intercept of  $R_d$ -[N] relationships was highest in herbs, followed by woody angiosperms, and with gymnosperms exhibiting the lowest  $R_d$ -[N] intercept. PFTs also

differed with respect to the slope (exponent) of the  $R_d$ -[N] relationship, with the slope ranking: gymnosperms > woody angiosperms > herbs. The slope of the  $R_d$ -[N] relationship was consistently >1.0 (Reich et al. 2008), likely reflecting the combined effects of higher energy requirements and greater allocation of tissue N to metabolism (relative to non-metabolic N pools) in metabolically active tissues (Poorter and Evans 1998; Reich et al. 2008).

Recently, a comparison of 899 species across 100 globally-distributed sites also found that rates of  $R_d$  (at 25 °C) at a given [N] differ among PFTs [ $\text{C}_3$  herbs > shrubs > broad-leaved trees > needle-leaved trees; (Atkin et al. 2015)]. Rates of  $R_d$  (at 25 °C) at a given [N] are also higher in plants growing in cold environments than their warm-grown counterparts (Tjoelker et al. 1999; Atkin et al. 2008, 2015) and higher in plants growing in high-light than low-light environments (Wright et al. 2006). In some studies, nutrient supply and/or soil moisture have also been shown to influence rates of  $R_d$  at a given [N] (Meir et al. 2001; Wright et al. 2001; Atkin et al. 2013; Rowland et al. 2016). Collectively, these observations strongly suggest that there is no common leaf  $R_d$ -[N] relationship across PFTs and environments. Given this, if leaf nitrogen is used as a predictor of  $R_d$  in TBMs, PFT-specific equations that take growth temperature/irradiance, soil moisture, and/or nutrient availability into account are needed. Later, we discuss an example of how this approach can be implemented (Atkin et al. 2015).

Why does the rate of leaf  $R_d$  at a given [N] vary among plants? There are three possible reasons, in principle: (i) differential allocation of nitrogen within leaves to metabolic and non-metabolic components; (ii) factors that might influence the metabolic flux through the respiratory system; and (iii) thermal effects (e.g. acclimation to sustained changes in growth temperature). For (i), it is now well established that the fraction of total

leaf N allocated to photosynthetic processes differs among and within PFTs. For example, a greater fraction of leaf N is allocated to photosynthesis in  $C_3$  herbs than broad-leaved trees (with reduced allocation to non-photosynthetic components such as cell wall and structural proteins), leading to higher rates of photosynthesis per unit leaf N (Field and Mooney 1986; Reich et al. 1997; Poorter and Evans 1998; Hikosaka 2004; Pons and Westbeek 2004; Warren and Adams 2004). N allocation to photosynthesis is also greater in species with low leaf mass per unit leaf area (LMA,  $\text{g dry mass m}^{-2}$ ) than their high LMA counterparts (Takashima et al. 2004; Warren and Adams 2004; Harrison et al. 2009; Bahar et al. 2017). Given tight metabolic coupling between mitochondria and chloroplasts (Raghavendra et al. 1994; Hoefnagel et al. 1998), one would expect increased allocation of leaf N to photosynthetic processes to also be associated with increased allocation of leaf N to respiratory proteins. In turn, this would result in higher rates of leaf  $R_d$  at a given [N], not necessarily because of higher respiratory fluxes *per se*, but because more of the total leaf N pool is linked to metabolism. For (ii) on factors that influence respiratory rates, variability in N allocation could also be important, reflecting the likelihood that proteins involved in metabolism exhibit higher turn-over rates than their structural N counterparts (Nelson et al. 2014), thus increasing ATP demand associated with protein synthesis and repair (Hachiya et al. 2007). Indeed, variation in energy demand is likely to be a major factor responsible for variation in rates of leaf  $R_d$  at a given [N], influenced not only by protein turn-over [which likely accounts for near 20% of nocturnal respiration (Bouma et al. 1994)], but also other maintenance processes (e.g. maintenance of solute gradients) (Amthor 2000; Bouma 2005). Variation in the engagement of non-phosphorylating pathways of mitochondrial electron transport (e.g. alternative oxidase, rotenone-insensitive NADH dehydrogenase, external NAD(P)H dehydroge-

nase), proton leakage through the inner mitochondrial membrane and proton flux via uncoupling proteins (PUMP) could all reduce the efficiency of ATP synthesis (Affourtit et al. 2001; Sweetlove et al. 2006; Armstrong et al. 2008; Millar et al. 2011; Searle et al. 2011a; Kornfeld et al. 2012), leading to variation in the rate of leaf  $R_d$  at a given [N]. For the third point on factors affecting respiratory rates (thermal effects), see section II.C of this chapter.

### B. Links Between Respiration and Photosynthetic Metabolism in Mature Leaves

As noted above, in TBMs that predict  $R_d$  from assumed relationships with photosynthesis, the starting point can still originate with foliar [N]. Strong positive relationships are often reported between light-saturated rates of photosynthesis ( $A$ ) and N, reflecting the importance of leaf N for light harvesting, photosynthetic electron transport and carboxylation capacity (Field and Mooney 1986; Evans 1989; Schulze et al. 1994; Reich et al. 1999). Similarly, maximum carboxylation capacity of Rubisco ( $V_{\text{cmax}}$ ) is often positively correlated with leaf [N] (Meir et al. 2002; Kattge et al. 2009; Domingues et al. 2010; Walker et al. 2014). Reflecting this, many TBMs predict variation in  $V_{\text{cmax}}$  based on assumed relationships with leaf [N]. An example is the TRIFFID dynamic global vegetation model (Cox et al. 1998, 2000; Cox 2001) – implemented in JULES (Clark et al. 2011) – where  $V_{\text{cmax}}$  ( $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) at 25 °C is assumed to be linearly dependent on leaf [N],  $n_i$  in the JULES terminology [ $\text{kg N (kg C)}^{-1}$ ] according to:

$$V_{\text{cmax}} = 0.0008 n_i \text{ for } C_3 \text{ plants} \quad (6.2)$$

and

$$V_{\text{cmax}} = 0.0004 n_i \text{ for } C_4 \text{ plants} \quad (6.3)$$

with the constants being derived from a survey of 23 studies by Schulze et al. (1994), assuming that leaf dry matter is 40% C by mass and that  $V_{\text{cmax}}$  is equal to twice light-saturated net photosynthesis for  $C_3$  plants and equal to light-saturated net photosynthesis for  $C_4$  plants.

TBMs that use  $V_{\text{cmax}}$  to predict rates of leaf  $R_d$  (Table 6.1) adopt a range of coefficients to link the two processes. For example, in BETHY, leaf  $R_d$  was assumed to be 1.1% of  $V_{\text{cmax}}$  for  $C_3$  plants (Knorr 2000; Ziehn et al. 2011), reflecting the *assumed* relationship reported in Farquhar et al. (1980). For  $C_4$  plants, leaf  $R_d$  was assumed to be 4.2% of  $V_{\text{cmax}}$  (Knorr 1997). In both BIOME3 (Haxeltine and Prentice 1996a) and JULES (Cox 2001; Clark et al. 2011), leaf  $R_d$  was assumed to be 1.5% of  $V_{\text{cmax}}$  for  $C_3$  plants (Collatz et al. 1991); interestingly, the latter study cited Farquhar et al. (1980) as its source for the leaf  $R_d$ - $V_{\text{cmax}}$  relationship (although in that reference, leaf  $R_d$  was assumed to be 1.1% of  $V_{\text{cmax}}$  for  $C_3$  plants, not 1.5%). BIOME3 and JULES differ in their predicted leaf  $R_d$ - $V_{\text{cmax}}$  relationships for  $C_4$  plants [4.2% (Knorr 1997) and 2.5% (Collatz et al. 1992), respectively], with neither estimate based on large screening of leaf respiration rates in  $C_4$  plants. Indeed, in Collatz et al. (1992), the estimate was based solely on measurements made on corn. Thus, in none of the models linking  $V_{\text{cmax}}$  to leaf  $R_d$  is the assumed relationship based on comprehensive surveys of respiratory and photosynthetic values in nature. Moreover, no allowance is made for variations in rates of leaf  $R_d$  at a given  $V_{\text{cmax}}$ , even though there is now evidence that leaf  $R_d$ - $V_{\text{cmax}}$  relationships vary among PFTs and environments (Atkin et al. 2015). For example, at 25°C leaf  $R_d$  as a percentage of  $V_{\text{cmax}}$  is higher in  $C_3$  herbs (7.8%) than shrubs (4.5%), needle-leaved trees (3.8%) and broad-leaved trees (3.3%). Further, leaf  $R_d$  at a given  $V_{\text{cmax}}$  (at 25 °C) is greater in plants growing in cold than warm biomes (Atkin et al. 2015). From these observations, two conclusions can be made:

(i) for most species, leaf  $R_d$  as a percentage of  $V_{\text{cmax}}$  is actually greater than that assumed in current TBMs; and (ii) leaf  $R_d$ - $V_{\text{cmax}}$  relationships vary amongst PFTs and biomes. The next generation of TBMs will have to account for these observations, if leaf  $R_d$  continues to be predicted from modeled rates of  $V_{\text{cmax}}$ .

### C. Temperature Dependence of Mature Leaf Respiration in TBMs

In the TBMs listed in Table 6.1, rates of  $R_d$  (predicted from assumed  $R_d$ -[N] and/or  $R_d$ - $V_{\text{cmax}}$  relationships) at a specified reference temperature are used to model rates of  $R_d$  at other leaf temperatures. How leaf  $R_d$  varies with temperature is crucial for TBM predictions, because of the importance of temperature-mediated changes in respiratory  $\text{CO}_2$  efflux in determining future carbon storage in vegetation and atmospheric  $\text{CO}_2$  concentrations (King et al. 2006; Atkin et al. 2008; Huntingford et al. 2013; Wythers et al. 2013; Lombardozzi et al. 2015; Heskell et al. 2016b). Here, consideration needs to be given to how  $R_d$  responds to temperature, both over short (e.g. minutes-hours) and long (days, months, years) periods of time.

In most TBMs, leaf  $R_d$  is assumed to increase exponentially with increasing temperature, with the  $Q_{10}$  value (i.e. proportional increase in  $R_d$  per 10 °C increase in leaf  $T$ ) assumed to be fixed through time (with typical values of 2.0–2.3). Examples of TBM frameworks using a fixed  $Q_{10}$  include BIOME-BGC (Running and Coughlan 1988), Century (Melillo et al. 1993), CLM4.5 (Oleson et al. 2013), JULES (Cox 2001) and TEM (Raich et al. 1991). In an earlier version of JULES (i.e. MOSES-TRIFFID) that modeled global carbon fluxes under a ‘business-as-usual’ emission scenario, the assumption of a fixed  $Q_{10}$  of 2.0 resulted in positive carbon feedbacks that increased future atmospheric  $\text{CO}_2$  concentrations and global temperatures (Cox et al. 2000). Importantly, by assuming a fixed tempera-

ture response of  $R_d$ , global respiratory  $\text{CO}_2$  release was predicted to exceed global GPP by the end of the century, making the land surface a net source of  $\text{CO}_2$  to the atmosphere (Cox et al. 2000). Earlier versions of MOSES-TRIFFID (Cox et al. 1998, 1999) allowed leaf  $R_d$  to follow the same temperature dependency as  $V_{\text{cmax}}$ , with the latter incorporating low and high temperature limit functions into the calculation of temperature dependence. More recently, JULES was modified to yield a bell-shaped temperature function, with peak rates of leaf  $R_d$  at 32 °C (via linking leaf  $R_d$  to  $V_{\text{cmax}}$ , and assuming the latter has a peak rate at 32 °C) (Huntingford et al. 2013). Doing so results in marked increases in carbon storage in land vegetation in the tropics, when compared to model runs that assumed a fixed  $Q_{10}$  of 2.0 (Huntingford et al. 2013). Thus, TBMs predictions are strongly dependent on whether or not a fixed  $Q_{10}$  is used.

The assumption of a constant  $Q_{10}$  (i.e. a  $Q_{10}$  that is independent of leaf temperature) is in some ways surprising, as it has been long recognized that the temperature-response of  $R_d$  is highly variable (James 1953; Forward 1960; Tjoelker et al. 2001). For example, changes in growth temperature that last several days, can alter the short-term  $Q_{10}$  (Atkin et al. 2005; Armstrong et al. 2008), with  $Q_{10}$  values often varying seasonally (Atkin et al. 2000b; Zaragoza-Castells et al. 2008). There is also evidence that temperature-corrected  $Q_{10}$ s can vary with climate of origin amongst woody species (Criddle et al. 1994) and that  $Q_{10}$ s are lower in tissues where substrates and/or energy demand limit respiration (Atkin and Tjoelker 2003). Moreover,  $Q_{10}$  values decline as measurement temperature increases (James 1953; Forward 1960; Tjoelker et al. 2001; Atkin and Tjoelker 2003; Zaragoza-Castells et al. 2008; Heskell et al. 2016b), with the  $Q_{10}$  reaching unity (i.e.  $Q_{10} = 1.0$ ) at high leaf temperatures as  $R_d$  reaches a maximum rate (at  $T_{\text{max}}$ ). Beyond  $T_{\text{max}}$ , further heating results in irreversible declines in  $R_d$  (i.e.  $Q_{10} < 1.0$ ).

Reflecting this, a number of models allow for decreasing temperature sensitivity of  $R_d$  as leaves warm, either using a modified  $Q_{10}$  (Tjoelker et al. 2001) such as in BETHY, or via application of modified Arrhenius activation energy ( $E_a$ ) functions (Robson 1981; Paembonan et al. 1991; Lloyd and Taylor 1994) such as in LPJ, O-CN and Sheffield DGVM.

With the exception of BETHY (Knorr 2000) and LPJ (Bonan et al. 2003; Sitch et al. 2003), rates of leaf  $R_d$  at a standard temperature are static within current generation TBMs, with no allowance made for potential changes in those reference values of  $R_d$  in response to sustained changes in growth temperature. That is, leaf  $R_d$  is not allowed to thermally acclimate despite mounting evidence that leaf  $R_d$  does adjust to sustained changes in growth temperature. Acclimation can result in homeostasis of  $R_d$  in plants grown at different temperatures, when measured at their respective growth temperatures (Larigauderie and Körner 1995; Atkin and Tjoelker 2003). Acclimation also results in  $R_d$  (at a standard temperature) increasing upon cold acclimation and declining upon acclimation to warmer temperature. Growth temperature dependent changes in  $R_d$  at a standard temperature can occur over periods of a few days (Atkin et al. 2000b; Bolstad et al. 2003; Lee et al. 2005; Zaragoza-Castells et al. 2007; Armstrong et al. 2008), suggesting that respiration metabolism acclimates to changes in growth temperature over time scales of several days and longer (Reich et al. 2016). As discussed in later sections, acclimation also manifests itself at the global scale, resulting in higher rates of leaf  $R_d$  at a given measuring temperature in plants growing in cold environments compared to warm habitats (Atkin et al. 2015; Vanderwel et al. 2015). Importantly, acclimation results in a reduction in the long-term temperature-sensitivity of  $R_d$  (Fig. 6.3; Larigauderie and Körner 1995); as such, accounting for thermal acclimation is likely to be important when predicting rates of

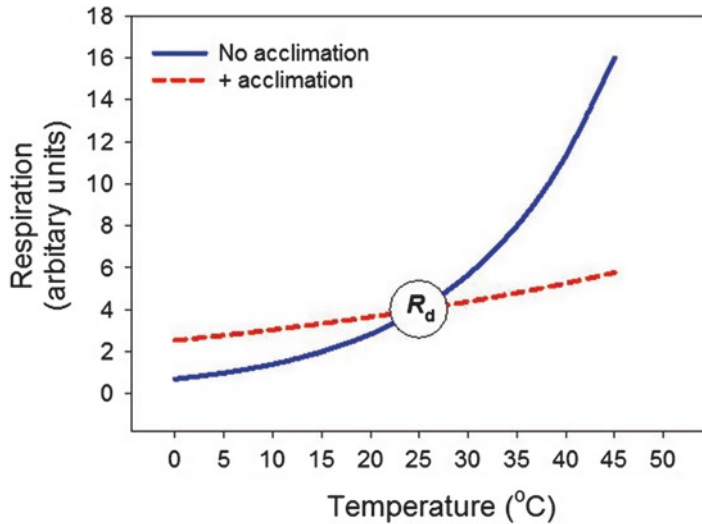


Fig. 6.3. Diagram to illustrate the impacts of thermal acclimation on modeled rates of leaf respiration. In most TBMs, rates of leaf respiration (leaf  $R_d$ ) at a standard measuring temperature (here shown at 25 °C) are used to model rates of leaf  $R_d$  at other temperatures assuming that respiration does not thermally acclimate; the no-acclimation scenario (in blue) shows values where leaf  $R_d$  increases with temperature according to a fixed  $Q_{10}$  approach. The dashed line shows calculated rates of leaf  $R_d$  across a range of temperatures for a scenario where leaf  $R_d$  acclimates to sustained changes in growth temperature. This is achieved via allowing the rate of leaf  $R_d$  at the standard measuring temperature to *increase* and *decrease* when growth temperatures are *below* and *above* the standard temperature, respectively. Thus, when TBMs that have the standard temperature at 25 °C are initially spun-up to equilibrium, accounting for acclimation will result in increased rates of leaf  $R_d$  where daily average growth temperatures are <25 °C (i.e. most environments) compared to models that do not account for acclimation. Similarly, accounting for acclimation will result in reduced rates of leaf  $R_d$  in hot tropical ecosystems (Atkin et al. 2008). Thereafter, as all ecosystems warm, acclimation reduces predicted future increases in leaf  $R_d$ .

respiratory CO<sub>2</sub> release at global and regional levels, especially in response to increasing growth temperatures that are a consequence of global warming (King et al. 2006; Atkin et al. 2008; Smith and Dukes 2013; Wythers et al. 2013; Lombardozzi et al. 2015; Reich et al. 2016). Accounting for acclimation (via growth-temperature mediated changes in leaf  $R_d$  at a standard temperature) is likely to increase overall estimates of leaf  $R_d$  in cool habitats (e.g. arctic and boreal ecosystems), whereas it may lead to lower estimates of leaf  $R_d$  in warmer habitats (Atkin et al. 2008). In recent runs of CLM4.5, Lombardozzi et al. (2015) reported that accounting for thermal acclimation of both photosynthesis and respiration has a marked impact on terrestrial carbon pools, with high latitudes gaining the most carbon under acclimation (reflecting the greater gains through photo-

synthesis than increased carbon losses by respiration), whereas accounting for acclimation had little impact on tropical carbon pools. Similarly, accounting for thermal acclimation of respiration alone in the PnET-CN ecosystem model was found to increase NPP by 9% when averaged across high latitude grassland and forests (Wythers et al. 2013). Thus, failure to account for thermal acclimation of leaf  $R_d$  in TBMs is likely to lead to marked overestimates in the extent to which respiratory CO<sub>2</sub> release increases as global warming heats individual ecosystems.

#### D. Light Inhibition of Leaf Respiration

As noted earlier, most TBMs typically assume that rates of leaf respiration taking place in the light are the same as those in darkness (i.e. light does not inhibit leaf res-

piration). Yet, there is long-standing evidence that rates of leaf respiration in the light/day ( $R_{\text{light}}$ ) are often lower than those in darkness/night ( $R_{\text{dark}}$ ) (Sharp et al. 1984; Brooks and Farquhar 1985; Pärnik and Keerberg 1995; Villar et al. 1995; Atkin et al. 1997; Pärnik et al. 2007; Way et al. 2015). Indeed, when measured at a common temperature,  $R_{\text{light}}$  can be 80% lower than  $R_{\text{dark}}$  (Atkin et al. 2006; Zaragoza-Castells et al. 2007). This issue has been acknowledged and addressed in the latest version of JULES (Clark et al. 2011). Failure to account for light inhibition can lead to large overestimates of daily respiration in individual leaves (Atkin et al. 2006), and whole ecosystems [and hence by necessity net primary productivity (Janssens et al. 2001; Wohlfahrt et al. 2005; Mercado et al. 2007; Bruhn et al. 2011; Heskell et al. 2013; Wehr et al. 2016)]. It can also have important implications for our understanding of the processes controlling the rate of net  $\text{CO}_2$  assimilation in the light ( $A_{\text{net}}$ ), particularly in ecosystems exhibiting low rates of  $A_{\text{net}}$  where assuming that leaf  $R$  takes place at similar rates in the dark and light can result in substantial errors in estimates of carboxylase ( $V_c$ ) and oxygenase ( $V_o$ ) rates of Rubisco.

Given the lack of understanding of how light inhibition varies among terrestrial biomes, attempts to account for light inhibition in TBMs have had to rely on assumed inhibition values. Lloyd et al. (1995) provided one of the earliest attempts to model light inhibition through forest canopies using  $R_{\text{light}}$  versus irradiance curves from work on tobacco by Brooks and Farquhar (1985), where respiration in darkness was assumed to equal respiration in the light when growth irradiance  $< 10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , but with  $R_{\text{light}} < R_{\text{dark}}$  when canopy irradiance  $> 10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , the latter calculated according to the equation:

$$R_{\text{light}} = [0.5 - 0.05 \ln(I_o)] R_{\text{dark}} \quad (6.4)$$

with  $I_o$  being the incoming irradiance at the top of the canopy. This approach has since been applied in JULES (Mercado et al. 2007; Clark et al. 2011). Later, in a study modeling  $\text{CO}_2$  exchange in tropical forests, Lloyd et al. (2010) used data from an evergreen tree species *Eucalyptus pauciflora* (Atkin et al. 2000a) to formulate an equation that modeled the irradiance dependence of leaf respiration according to:

$$R_{\text{light}} = R_{\text{dark}} \left[ 1 - \frac{\alpha I}{\beta + I} + \gamma I \right] \quad (6.5)$$

where  $\alpha$ ,  $\beta$ , and  $\gamma$  are fitted empirical constants with values of 0.9575 and  $29.85 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $5.114 \times 10^{-5} \mu\text{mol photons } \mu\text{mol}^{-1} \text{CO}_2$ , respectively, and  $I$  is the irradiance experienced by a leaf. Using this approach results in a 73%, 82% and 88% inhibition of leaf respiration at irradiances ( $I$ ) of 100, 200 and  $500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , respectively. More recently in studies using the JULES TBM, a uniform 30% inhibition of leaf respiration has been applied in conditions when irradiance  $> 10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Clark et al. 2011; Harper et al. 2016). While the assumption of 30% inhibition has yet to be assessed across a range of habitats and species, a recent analysis of light inhibition in eight tropical forest species growing in North Queensland, Australia, found average light inhibition of 32% (Weerasinghe et al. 2014). Yet, we continue to lack data on patterns of light inhibition across a wider range of species.

Crucial to successful incorporation of light inhibition of leaf respiration into large scale models will be determining whether the degree of light inhibition differs systematically among plant species adapted to contrasting habitats. Whether there are systematic differences among species/biomes in the degree of light inhibition of leaf respiration will depend on: (i) the mechanisms responsible for light inhibition; and

(ii) whether species differ in those traits associated with inhibition. While the factors responsible for light inhibition remain uncertain, past studies have pointed to light-dependent reductions in the activity of the pyruvate dehydrogenase (PDH) complex (Budde and Randall 1990; Gemel and Randall 1992) and malic enzyme (Hill et al. 1992) thought to play a role. Both enzymes play central roles in regulating carbon flow from glycolysis through the tricarboxylic acid (TCA) cycle in mitochondria. Further, transition to a truncated TCA cycle in the light, that results from removal of carbon skeletons to support N-assimilation (e.g. synthesis of glutamate) and transfer of amino groups within the photorespiratory pathway, can result in reduced rates of TCA cycle  $\text{CO}_2$  release (Igamberdiev et al. 2001; Tcherkez et al. 2005, 2008, 2012). Increased use of stored organic acids can also reduce demand for TCA cycle intermediates, potentially slowing rates of  $R_{\text{light}}$  (Gauthier et al. 2010). Metabolic modeling has also suggested that reduced rates of the oxidative pentose phosphate pathway (OPPP) in the light might also contribute to lower  $R_{\text{light}}$  compared to  $R_{\text{dark}}$  (Buckley and Adams 2011). Common to a number of the above factors is a link to photorespiratory metabolism, with high rates of photorespiration being linked to reduced PDH activity and increased demand for TCA intermediates. Similarly, changes in the demand for TCA intermediates by N assimilation could impact on the degree of light inhibition. Thus, it remains possible that criteria that predict variations in the degree of light inhibition might be identified via screening rates of  $R_{\text{light}}$ ,  $R_{\text{dark}}$ , photorespiration and N assimilation in a wide range of plant species representative of PFTs used in TBMs. At present, however, such data are lacking.

Further, despite studies investigating the impacts of atmospheric  $\text{CO}_2$ , water supply, nutrient availability, growth irradiance and temperature on light inhibition (Wang et al. 2001; Pinelli and Loreto 2003; Shapiro et al.

2004; Pärnik et al. 2007; Zaragoza-Castells et al. 2007; Ayub et al. 2011; Crous et al. 2012; Heskell et al. 2012; Atkin et al. 2013; Ayub et al. 2014; Heskell et al. 2014; McLaughlin et al. 2014; Weerasinghe et al. 2014; Way et al. 2015), it remains unclear if there are systematic differences in the  $R_{\text{light}}$  to  $R_{\text{dark}}$  ratio along sustained differences in the growth environment. Finally, uncertainty remains as to the effects of short-term changes in leaf temperature (i.e. second-minutes-hours) on the degree of light inhibition (Way and Yamori 2014). In Bernacchi et al. (2001),  $R_{\text{light}}$  of tobacco exhibited an activation energy ( $46.39 \text{ kJ mol}^{-1}$ ) which is similar to that often reported for  $R_{\text{dark}}$ ; others have also reported little difference in the short-term temperature dependence of  $R_{\text{light}}$  and  $R_{\text{dark}}$  (Shapiro et al. 2004; Griffin and Turnbull 2013; McLaughlin et al. 2014; Way et al. 2015). By contrast, a number of different studies have reported the degree of light inhibition of leaf respiration to increase with rising leaf temperature (Harley et al. 1992; Atkin et al. 2000a; Loreto et al. 2001; Bruhn 2002; Pons and Welschen 2003; Atkin et al. 2006; Zaragoza-Castells et al. 2007), and decrease with increasing temperature in one study (Way and Sage 2008). Given the conflicting nature of these reports, and the importance of the temperature response of leaf respiration for TBM predictions (Huntingford et al. 2013), further work is needed to determine whether there are systematic patterns (across plant taxa and environments) in the effect of leaf temperature on the degree of light inhibition of respiration.

### *E. Whole-Plant Maintenance Respiration – Accounting for Soil Moisture*

A range of approaches are used in TBMs to estimate rates of whole-plant maintenance respiration ( $R_{\text{pm}}$ ), with leaf  $R_{\text{d}}$  of upper-canopy leaves forming the starting point of these calculations in most TBMs (Table 6.1). Here, we focus on scaling up from leaves to



whole-plants in JULES – in that model, upper-canopy leaf  $R_d$  is used to predict equivalent rates of maintenance respiration in whole canopies ( $R_{dc}$ ) via multiplication of leaf  $R_d$  by parameters that account for light attenuation through the canopy. Thereafter, canopy-level  $R_{dc}$  is used to calculate whole-plant  $R_{pm}$  according to the following equation (Cox 2001):

$$R_{pm} = 0.012R_{dc} \left[ \beta + \frac{(N_r + N_s)}{N_l} \right] \quad (6.6)$$

where  $N_l$ ,  $N_s$  and  $N_r$  are the N contents of leaves, stems (sapwood) and roots, and the factor of 0.012 is a unit conversion term. Hence, in JULES, whole-plant  $R_{pm}$  is calculated on the basis of nitrogen partitioning in above and below-ground organs, with scaling between respiration and tissue N being assumed to be constant, an assumption that is challenged by more recent studies (Reich et al. 2008). Canopy-level  $R_{dc}$  is adjusted to account for low soil moisture contents via multiplication by a moisture stress factor ( $\beta$ ).

In Equation (6.6), the moisture stress factor ( $\beta$ ) is a function of soil moisture content ( $\theta$ ) in the rootzone, taking a value of zero if  $\theta$  is below wilting point ( $\theta_w$ ), a value of unity if  $\theta$  is greater than critical moisture concentration ( $\theta_c$ ), and having a linear decrease between  $\theta_c$  and  $\theta_w$  (Cox et al. 1998). Variable  $\theta_c$  is a value below which physiological performance of plants is reduced, and so the ‘ $\beta$ ’ approach similarly can be modeled as impacting on photosynthesis during drought periods. This approach, which was suggested by Cox et al. (1998), therefore assumes that drought reduces canopy-level  $R_{dc}$  by the same proportion as whole-canopy net photosynthesis ( $A$ ) in all plant species; that is, the  $R_{dc}/A$  ratio remains identical in well-watered and moisture stressed plants. However, a growing body of empirical data shows that  $R_d/A$  ratios increase markedly under drought (Flexas et al. 2006; Atkin and Macherel 2009; Ayub et al. 2011; Crous et al. 2011;

Rodríguez-Calcerrada et al. 2011), reflecting the greater sensitivity of photosynthesis than  $R_d$  to drought. Incorrectly accounting for drought-mediated changes in canopy-level  $R_{dc}$  and/or  $A$  is likely to result in large errors in rates of predicted net ecosystem  $\text{CO}_2$  exchange (Flexas et al. 2006), and so a new ‘ $\beta$ ’ but specific for respiration will be considered for future JULES model versions. This may be expected to be particularly important for low productivity ecosystems where leaf  $R_d$  represents a large proportion of overall carbon exchange (Zaragoza-Castells et al. 2008). It is important, therefore, that ecosystem gas exchange models be developed to the state where drought-mediated changes in  $R_{dc}$  are taken into account when simulating ecosystem carbon fluxes and when interfaced with TBMs to predict the impacts of global climate change on carbon exchange in terrestrial ecosystems (Ryan 2002). The impact of drought on temperature responses of leaf  $R_d$  also needs to be considered, with recent literature pointing to drought accentuating downward adjustments (i.e. acclimation) of leaf  $R_d$  in response to rising temperatures in summer (Rodríguez-Calcerrada et al. 2010; Crous et al. 2011).

#### F. Estimating Whole-Plant Respiration – Importance of Growth Respiration

In models that use the ‘*growth-and-maintenance-respiration paradigm*’ (GMRP) (Amthor 2000) to estimate rates of whole-plant respiration ( $R_p$ ), rates of growth respiration in whole plants ( $R_{pg}$ ) need to be estimated. In most of the models listed in Table 6.1,  $R_{pg}$  is calculated on the basis that the energy costs of growth are a fixed fraction of GPP (e.g. BIOME-BGC & Century), or a fixed fraction of GPP minus  $R_{pm}$  (e.g. BETHY, BIOME3, JULES, LPJ, ORCHIDEE and TEM). For the latter, 0.20–0.25 of GPP- $R_{pm}$  (herein termed the ‘growth respiration coefficient’ –  $GRC_{ESM}$ ) is assumed to represent  $R_{pg}$  for all plant functional types

and biomes, according to the following equation:

$$R_{pg} = GRC_{ESM} [GPP - R_{pm}] \quad (6.7)$$

In this section, we discuss the origins of the fixed  $GRC_{ESM}$  values used in some leading TBMs.

According to the GMRP, the rate of respiration in whole plants is the sum of  $R_{pm}$  and  $R_{pg}$ , according to:

$$R_p = R_{pm} + R_{pg} = m_R W + g_R G \quad (6.8)$$

where  $W$  is the dry mass of mature tissues,  $m_R$  is the maintenance respiration coefficient (i.e. respiratory  $CO_2$  associated with maintenance of existing biomass per unit time, with units of  $\text{mol } CO_2 (\text{g biomass})^{-1} \text{ s}^{-1}$ ),  $G$  is the growth rate (e.g.  $\text{g new biomass time}^{-1}$ ), and  $g_R$  is the respiratory  $CO_2$  released per unit biomass produced by growth. Thus,  $R_{pg}$  can be viewed as linked not only to  $G$ , but also to the efficiency of biosynthetic pathways, reflected in the variable of central interest,  $g_R$ . This parameter is central to calculating  $R_{pg}$  as part of the GMRP. Using a biosynthesis ‘pathway analysis method’ to analyze growth costs in several crop species, Penning de Vries et al. (1983) reported an overall average  $g_R$  value of 0.33; in such cases, 33% of the carbon retained in growth is released to the atmosphere by respiration in the production of that growth. Importantly, there was greater than three-fold variation in  $g_R$  [0.13 in carbohydrate-rich tubers to 0.43 in lipid-rich tissues (Penning de Vries et al. 1983)]. Variation in  $g_R$  could have profound implications for estimates of  $R_{pg}$  of individual organs and whole-plants.

The GMRP can also be viewed from a growth ( $G$ ) rate perspective, according to:

$$G = Y_g (A - R_{pm}) = Y_g A - Y_g m_R W \quad (6.9)$$

where  $A$  is the rate of gross photosynthesis with the same units as respiration above, and  $Y_g$  is the yield of growth processes (i.e. fraction of substrate inputs retained in the products of growth). For example, if  $Y_g = 0.8$ , then for every 100 units of C fixed by photosynthesis, 80 units are retained in the resultant biomass while 20 units are released back to the atmosphere by respiration. In Penning de Vries et al. (1983),  $Y_g$  varied from 0.70 in lipid-rich palm nuts to 0.89 in starch-rich tubers, with an average value of 0.75 (Penning de Vries et al. 1983; Thornley and Cannell 2000). That is, 70–89% of the carbon in substrates was retained in tissue biomass (Amthor 2000), with the variability in this parameter further suggesting that no single growth efficiency parameter can be applied universally across plant tissues, organs and/or species. Yet, inspection of Table 6.1 shows that several TBMs assume that respiratory costs associated with growth are indeed constant, both across plant functional types (PFTs) and biomes.

In JULES and LPJ, the ‘growth respiration coefficient’ ( $GRC_{ESM}$ ) used to calculate  $R_{pg}$  is a single value (i.e. 0.25). To understand the origins of this fixed  $GRC_{ESM}$ , it is necessary to show the inverse relationship between  $Y_g$  and  $g_R$ , where increases in the  $CO_2$  requirements associated with biosynthesis ( $g_R$ ) reduce the growth yield ( $Y_g$ ), according to (Thornley 1970; Amthor 2000):

$$Y_g = 1 / (1 + g_R) \quad (6.10)$$

Similarly, increases in the growth yield are associated with a lower  $g_R$  according to, re-writing equation (6.1) as:

$$g_R = (1 - Y_g) / Y_g \quad (6.11)$$

When combined with information on rates of  $GPP$  and  $R_{pm}$ , variation in  $Y_g$  and  $g_R$  influence rates of  $R_{pg}$  according to:

$$R_{pg} = g_R \left[ Y_g (GPP - R_{pm}) \right] \quad (6.12)$$

If one assumes that all species exhibit  $g_R$  and  $Y_g$  values of 0.33 and 0.75, respectively, then the  $GRC_{ESM}$  used to calculate  $R_{pg}$  in equation (6.8) will be 0.25 (i.e.  $GRC_{ESM} = 0.33 \times 0.75$ ). Thus, the ‘universal’  $GRC_{ESM}$  (i.e. 0.25) used in JULES and LPJ turns to be:

$$GRC_{ESM} = g_R \times Y_g \quad (6.13)$$

In JULES and LPJ,  $GRC_{ESM}$  is based on the average  $g_R$  and  $Y_g$  values of several crop species (Penning de Vries et al. 1983; Thornley and Cannell 2000), rather than a comprehensive assessment of  $GRC_{ESM}$  values across PFTs and/or biomes; here, we note that the reliance on crop species data was necessary because there were no wider surveys of  $GRC_{ESM}$  at the time JULES and LPJ were developed. In any case, assuming a fixed  $GRC_{ESM}$  of 0.25 gives undue weight to high-lipid tissues (Penning de Vries et al. 1983). While high lipid concentrations are common in seeds of some species, leaves, stems and roots of plants growing in natural ecosystems are more likely to be dominated by carbohydrates, and therefore exhibit lower  $GRC_{ESM}$  [e.g. akin to a  $GRC_{ESM} = 0.13 \times 0.89 = 0.12$  of carbohydrate-rich tubers (Penning de Vries et al. 1983)]. Given this, relying on average crop-derived  $g_R$  and  $Y_g$  values (Penning de Vries et al. 1983) to parameterize the land surface component of TBMs may result in an over-estimation of global  $R_{pg}$ .

To illustrate the potential impact of different  $GRC_{ESM}$  values, we present the following example where the global average  $GRC_{ESM}$  is closer to 0.12 rather than 0.25, reflecting carbohydrate-rich leaves rather than lipid-rich seeds (Penning de Vries et al. 1983; Amthor 2000). If we assume that global  $GPP - R_{pm} = 50 \text{ Gt C yr}^{-1}$ , then assuming a

$GRC_{ESM}$  of 0.12 would mean that global  $R_{pg}$  is  $\sim 6.0 \text{ Gt C yr}^{-1}$  as opposed to  $\sim 12.5 \text{ Gt C yr}^{-1}$  when  $GRC_{ESM} = 0.25$ . Thus, application of  $GRC_{ESM}$  values across the range reported by (Penning de Vries et al. 1983) could result in a change in predicted  $R_{pg}$  that is of similar magnitude to annual anthropogenic C emissions (IPCC 2013). Given the wide range of  $R_{pg}$  values and the magnitude of the resultant C-fluxes, it is not surprising that parameterization of  $R_{pg}$  represents one of the greatest single uncertainties in TBM model predictions (Dietze et al. 2014). Quantifying variation in  $GRC_{ESM}$  thus represents a challenge that needs to be urgently addressed.

There are a number of reasons to suspect that the  $GRC_{ESM}$  might not be static across genotypes & environments. Firstly, given that tissue chemical compositions vary among environments (Dahlin et al. 2013; Asner et al. 2014; Niinemets et al. 2015) and species/PFTs (Poorter and Bergkotte 1992; Van Arendonk and Poorter 1994; Cornelissen et al. 1997; Wright et al. 2004), and that the energy costs of building tissues of contrasting chemical composition are variable (Nagel et al. 2002; Poorter et al. 2006; Villar et al. 2006; Díaz et al. 2016), it seems unlikely that  $GRC_{ESM}$  will be invariant. Secondly, factors such as developmental and/or environment-mediated increases in the engagement of non-phosphorylating pathways of mitochondrial electron transport (e.g. alternative oxidase, rotenone-insensitive NADH dehydrogenase, external NAD(P)H dehydrogenase), proton leakage through the inner mitochondrial membrane and proton flux via uncoupling proteins (PUMP) could all reduce the efficiency of ATP synthesis (Rasmusson et al. 2004; Sweetlove et al. 2006; Armstrong et al. 2008; Millar et al. 2011; Searle et al. 2011a; Kornfeld et al. 2012), which in turn could increase  $g_R$  and decrease  $Y_g$ , thus altering  $GRC_{ESM}$ . Given these issues, it seems extremely unlikely that  $GRC_{ESM}$  is universally constant amongst spe-

cies and environments. Only by understanding how  $GRC_{ESM}$  values – and thus  $g_R$  and  $Y_g$  – vary among PFTs and biomes can we predict the dynamic changes in growth respiration of terrestrial ecosystems across the Earth’s surface, and in doing so, predict future changes in the land carbon sink and future biogeography of land plants.

### III. Global Surveys of Leaf Respiration and Its Temperature Dependence

In earlier sections, we outlined how a range of TBMs represent variation in leaf respiration rates (Table 6.1) using previously reported relationships between respiration, photosynthesis and/or leaf nitrogen concentrations. Importantly, each TBM has had to rely on a relatively small data-set linking respiration to other traits (Farquhar et al. 1980; Collatz et al. 1991, 1992; Ryan 1991; Knorr 1997). Such data-sets have been used to predict variation in leaf  $R_d$  at a standard temperature (typically 20 or 25 °C). In the absence of global analyses of the temperature dependence of leaf  $R_d$ , assumptions have also been made about how to model rates of leaf  $R_d$  as leaves cool and warm over both short timescales (i.e. near-instantaneous variation in imposed micrometeorology, and over long periods which could include acclimation to anthropogenic-induced global warming). To address these deficiencies, two global databases are now available that provide equations that predict global variability in baseline values of leaf  $R_d$  [the ‘*GlobResp*’ database of  $R_d$  at 25°C and associated leaf traits (Atkin et al. 2015), that brings together new and previously reported data (Wright et al. 2006 and references cited therein)] and the short-term temperature dependence of leaf  $R_d$  (Heskel et al. 2016b). In this section, we describe

each data-set, and outline how those datasets can be incorporated into TBMs.

#### A. Global Dataset of Baseline Leaf Respiration Rates – ‘*GlobResp*’

‘*GlobResp*’ contains data on upper canopy leaf respiration and associated leaf traits (e.g. photosynthetic capacity, area:mass relationships, nitrogen/phosphorus concentrations) on 899 species from 100 sites distributed around the globe (arctic to equatorial tropics); it also provides climate information (Hijmans et al. 2005) for each site. Several woody and non-woody PFTs are represented in the dataset, with those PFTs covering a majority of the standard vegetation types used within TBMs (e.g.  $C_3$  grasses/herbs, shrubs, broad-leaf trees and needle-leaf trees). Both deciduous and evergreen vegetation types are represented within the dataset. Importantly, however, ‘*GlobResp*’ does not contain data on  $R_d$  of  $C_4$  grasses. Analysis of ‘*GlobResp*’ area-based rates of leaf  $R_d$  (at a standard temperature of 25 °C) revealed on average, three-fold higher rates of baseline respiration in the Arctic than the tropics (Fig. 6.4; Atkin et al. 2015), suggesting an acclimation effect. As a result of these global patterns in baseline  $R_d$  (Fig. 6.4), rates measured at the prevailing average daily growth temperature of each site were only two-fold higher in the hot tropics than the cold Arctic, despite a 20 °C difference in growth temperature (8–28 °C). Subsequent analysis by Vanderwel et al. (2015) has shown that the ‘*GlobResp*’ patterns of leaf  $R_d$  are consistent with thermal acclimation responses, whereby cold-grown plants exhibit higher rates of leaf respiration at a standard temperature than their warm grown counterparts (Atkin and Tjoelker 2003; Kruse et al. 2011; Slot and Kitajima 2015; Reich et al. 2016). Importantly, when mea-

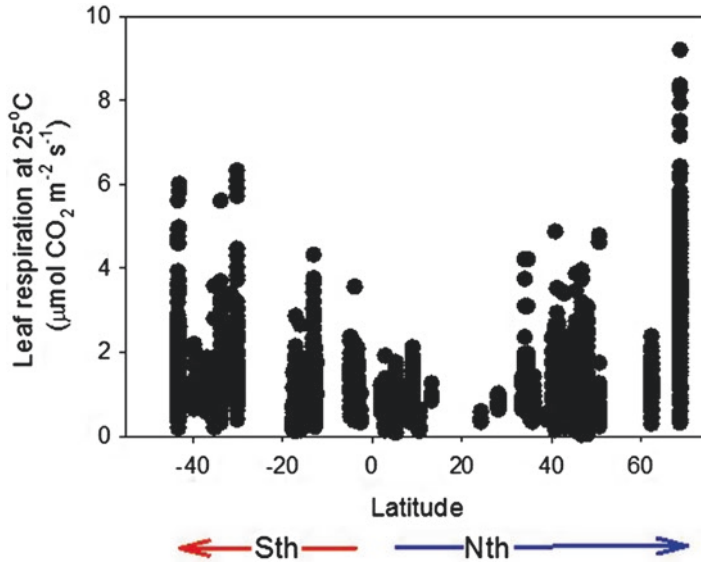


Fig. 6.4. Latitudinal variation in baseline leaf respiration measured in darkness, for area-based rates of leaf  $R_d$  normalized to a standard temperature of 25 °C. Data points are for individual measurements, with site:species means of the same dataset being reported in ‘GlobResp’ (Atkin et al. 2015)

sured at the standard temperature of 25 °C, species and PFTs at the cold sites exhibited higher  $R_d$  at a given photosynthetic capacity ( $V_{\text{cmax}}$ ) or leaf [N] than species from warmer sites. PFTs also differed in rates of  $R_d$  at a given  $V_{\text{cmax}}$  or leaf [N], being higher in  $C_3$  herbs than woody plants.

Using mixed-effects statistical models, Atkin et al. (2015) provided a set of PFT-specific equations that predicted mean rates of  $R_d$  across the globe. The equations captured a substantial amount of species variation across diverse sites, with the equations offering a reasonable first approximation for the purposes of modeling. Noting that TBMs often predict variation in leaf  $R_d$  via assumed relationships to leaf N (either directly, or via assumed leaf N- $V_{\text{cmax}}$ - $R_d$  relationships; Table 6.1), equations are available that link leaf  $R_d$  with leaf [N]. In a PFT-dependent matter, area-based rates of leaf  $R_d$  at 25°C

were found to vary with area-based values of leaf N concentration ( $n_{l,a}$  with units  $\text{gN} (\text{m}^2 \text{leaf})^{-1}$ ). Moreover, leaf  $R_d$  at 25 °C varied with the prevailing growth temperature ( $T_G$ ), in a consistent manner for all PFTs. The availability of equations for each PFT [Table 6.2 – assembled using ESM#3 in Table S4 of Atkin et al. (2015)] creates the opportunity to alter representation of leaf  $R_d$  at 25 °C from that assumed in the standard version of JULES to one which uses current, globally-relevant estimates of leaf  $R_d$  at 25 °C derived from ‘GlobResp’. Thus, the general form of the above equations is:

$$R_d \text{ at } 25^\circ\text{C} = [r_o + r_1 n_{l,a} - r_2 T_G] \quad (6.14)$$

Using equation (6.14) not only changes the scaling between leaf  $R_d$  at 25 °C and leaf [N] from that currently assumed in standard

Table 6.2. PFT-dependent parameters that enable leaf  $R_d$  at 25 °C to be predicted for four plant functional types (PFTs) for which data are available in the ‘*GlobResp*’ dataset (Atkin et al. 2015)

Plant functional type	Equation (6.14) parameter values and coefficients		
	$r_0$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$r_1$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} (\text{gN} (\text{m}^2 \text{ leaf})^{-1})^{-1}$ )	$r_2$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ }^\circ\text{C}^{-1}$ )
Broad-leaved trees	1.7560	0.2061	0.0402
Needle-leaf trees	1.4995	0.2061	0.0402
Shrubs	2.0749	0.2061	0.0402
C <sub>3</sub> herbs/grasses	2.1956	0.2061	0.0402

Note: no data for C<sub>4</sub> plants available in ‘*GlobResp*’. Values in the table are based on ESM#3 in Table S4 of Atkin et al. (2015), but using the recently reported PFT-specific equations with the continuous explanatory variables in absolute rather than centred form

runs of JULES, but also results in leaf  $R_d$  at 25 °C changing in response to changes in  $T_G$ , with rates of leaf  $R_d$  at 25 °C decreasing by  $\sim 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for every temporal 10 °C rise in  $T_G$ . That is, leaf  $R_d$  at 25 °C is allowed to acclimate to sustained changes in  $T_G$  at each site. This approach assumes that the global spatial patterns in leaf  $R_d$  at 25 °C are consistent with temporally-based adjustments in leaf  $R_d$  at 25 °C (i.e. acclimation). There is now strong support for this assumption (Slot and Kitajima 2015; Vanderwel et al. 2015). Importantly, any TBM runs made using equation (6.14) do not allow for adaptive changes in the baseline rate of respiration as the world warms over coming decades. Current data points to little adaptive difference in short-term temperature responses of respiration (Heskel et al. 2016b), while the work of Slot and Kitajima (2015) suggests that the ability to acclimate does not differ among biomes or plant functional types. Thus, assuming no adaptive changes in the temperature dependence (short or long term) is supported by available data. Of course, if PFT representation at any site changes in a future, warmer world, the basal rates of respiration could be altered at such sites, reflecting the PFT-dependent nature of leaf  $R_d$  at 25 °C (Atkin et al. 2015).

Fig. 6.5 illustrates the consequences of shifting from current PFT-specific estimates of leaf  $R_d$  at 25 °C in JULES (Cox et al. 1998; Cox 2001; Clark et al. 2011) to PFT-specific rates predicted from analysis of the ‘*GlobResp*’ dataset (Atkin et al. 2015). In the original version of JULES, rates of leaf  $R_d$  at 25 °C were assumed to remain constant irrespective of  $T_G$ , but vary among PFTs based on reported  $R_d-V_{\text{cmax}}-[\text{N}]$  relationships (Farquhar et al. 1980; Collatz et al. 1991; Schulze et al. 1994) and PFT-specific leaf [N]. By contrast, leaf  $R_d$  at 25 °C varies with  $T_G$  when applying equations from ‘*GlobResp*’ (Atkin et al. 2015), with rates normalised to 25 °C being greater in cold than warm habitats. Importantly, replacement of the existing JULES parameterization with ‘*GlobResp*’ (Atkin et al. 2015) results in marked increases in predicted leaf  $R_d$  at 25 °C for all of the four PFTs for which data are available (C<sub>3</sub> grasses, shrubs, broad-leaf trees and needle-leaf trees). As a result, model predictions of global leaf  $R_d$  are likely to be much higher when using ‘*GlobResp*’. Assessing the consequences of this for predicted global net primary productivity will be an important stimulus for developing the next generation of TBMs.

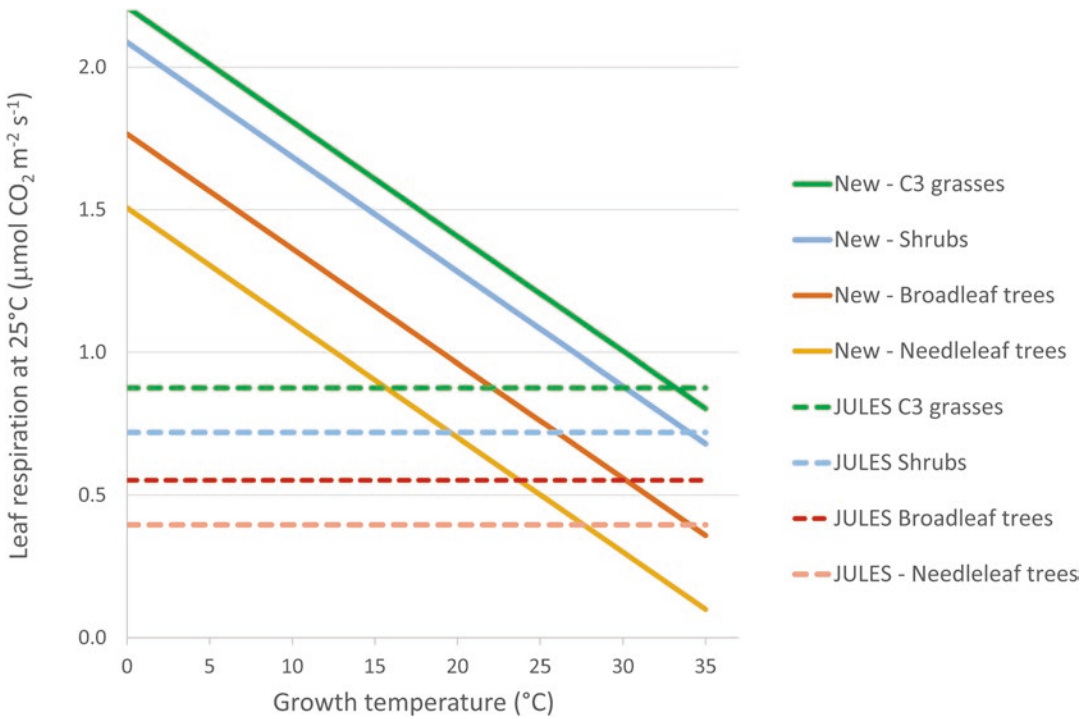


Fig. 6.5. Consequences of shifting from current estimates of leaf  $R_d$  at 25 °C in JULES (Cox et al. 1998; Cox 2001; Clark et al. 2011) to rates predicted from analysis of the ‘GlobResp’ dataset (Atkin et al. 2015). Shown are values for four plant functional types for which data are available in ‘GlobResp’. In the original version of JULES, rates of leaf  $R_d$  at 25 °C were assumed to remain constant irrespective of growth temperature, but vary among PFTs based on reported  $R_d-V_{\text{cmax}}-[N]$  relationships (Farquhar et al. 1980; Collatz et al. 1991; Schulze et al. 1994) and PFT-specific leaf  $[N]$ . By contrast, leaf  $R_d$  at 25 °C varies with growth temperature when applying equations from ‘GlobResp’ (Atkin et al. 2015), with rates at 25 °C being greater in cold than warm habitats. See equation (6.14) for details of how the new leaf  $R_d$  at 25 °C is calculated within each PFT

### B. Convergence in Temperature Response Curves of Leaf Respiration

As noted earlier, how leaf  $R_d$  responds to short-term variations in temperature will be crucial for TBM predictions, reflecting the importance of temperature-mediated changes in respiratory CO<sub>2</sub> efflux in determining future carbon storage in vegetation and atmospheric CO<sub>2</sub> concentrations (King et al. 2006; Atkin et al. 2008; Huntingford et al. 2013; Wythers et al. 2013; Lombardozzi et al. 2015; Heskell et al. 2016b). In several TBMs (Table 6.1), leaf  $R_d$  is assumed to increase with rising temperature such that respiration doubles for each 10 °C increase in temperature (i.e.  $Q_{10} = 2.0$ ). However, as

indicated above, the true  $Q_{10}$  is rarely a fixed value. Instead, the temperature coefficient of leaf  $R_d$  decreases as leaves warm. Reductions in the  $Q_{10}$  with increasing leaf temperature have been linked to substrate and/or adenylyate limitations at high measuring temperatures (Atkin and Tjoelker 2003).

It is thus important that TBMs be able to model the dynamic nature of the temperature response of leaf  $R_d$ . Acknowledging this, alternative models have been developed that allow for declines in the temperature sensitivity of leaf respiration as leaves warm. These model variants adopt modified Arrhenius formulations (Lloyd and Taylor 1994; Kruse and Adams 2008; Zaragoza-Castells et al. 2008; Noguchi et al. 2015),

universal temperature dependence (UTD) (UTD; Gillooly et al. 2001) and temperature-dependent  $Q_{10}$  functions (Tjoelker et al. 2001). Recently, high-resolution measurement of the temperature response of leaf  $R_d$  has enabled comparison of different model types, with three-parameter formulations (Kruse and Adams 2008; O’Sullivan et al. 2013; Adams et al. 2016; Heskell et al. 2016a, b) providing superior fits. Using this approach, Heskell et al. (2016b) analyzed 673 temperature responses of leaf  $R_d$  from 231 species across 18 globally distributed sites spanning 7 biomes that ranged from Arctic tundra to tropical rainforests. Their analysis confirmed that leaf  $R_d$  does not exhibit an exponential response to temperature. Tjoelker et al. (2001) reported similar findings, albeit using a smaller (minimal data from tropical ecosystems), lower resolution data set. Importantly, Heskell et al. (2016b) found convergence in the short-term temperature response of leaf  $R_d$  across biomes and PFTs, suggesting that a single empirical model can be used to predict the short-term temperature dependence of leaf  $R_d$  for global vegetation. The best such model describes this temperature dependence as log-polynomial rather than log-linear, with the  $Q_{10}$  continuously declining with increasing leaf temperature in a manner distinct from earlier observations (Tjoelker et al. 2001) and models (Lloyd and Taylor 1994; Gillooly et al. 2001), but similar to that reported by Kruse and Adams (2008). Discussion of the merits of the three-component models of Heskell et al. (2016b) and Kruse and Adams (2008) can be found in recent reports (Adams et al. 2016; Heskell et al. 2016a).

Heskell et al. (2016b) used a derivation of their global log-polynomial model (GPM) to predict values of leaf  $R_d$  at any given ambient temperature ( $T_a$ ), according to:

$$R_d = R_{d,25} \times e^{\left[ b(T_a - 25) + c(T_a^2 - 25^2) \right]} \quad (6.15)$$

where  $R_{d,25}$  is the rate of leaf  $R_d$  at a standard temperature of 25 °C, ‘ $b$ ’ is the slope of log  $R_d$  versus temperature curves at 0°C, and ‘ $c$ ’ describes how the slope of log  $R_d$  versus temperature curves declines with increasing temperature. Heskell et al. (2016b) found there were no significant differences in ‘ $b$ ’ or ‘ $c$ ’ parameters among biomes or PFTs, suggesting that temperature response curves of global vegetation can be modeled using a single polynomial function, where  $b = 0.1012$  and  $c = -0.0005$ . The convergence in the temperature sensitivity of leaf  $R_d$  suggests that there are universally applicable controls on the temperature response of leaf respiratory metabolism across the globe (Heskell et al. 2016b).

Fig. 6.6 shows how replacing a fixed  $Q_{10} = 2.0$  with the GPM (Heskell et al. 2016b) impacts on predicted rates of leaf  $R_d$  at any given temperature, using rates of leaf  $R_d$  at 25 °C as the reference point. Adopting the GPM results in reduced estimates of leaf  $R_d$  at low temperatures, with little change in rates at temperatures >25 °C. The consequences of shifting from a fixed  $Q_{10}$  to the GPM results in 28% lowering of predicted daily respiration in cold sites, such as those in the Arctic (Heskell et al. 2016b). Such changes are likely to impact predicted net primary productivity values of colder sites.

### C. Merging ‘GlobResp’ with the Global Polynomial Model

By merging equations derived from ‘GlobResp’ (Atkin et al. 2015) with those of the GPM (Heskell et al. 2016b), we suggest that TBMs will be able to predict variations in  $R_d$  in upper canopy leaves, taking into account: (i) PFT-specific baseline respiration rates at 25 °C; (ii) nitrogen-dependent variations in baseline respiration rates at 25 °C; (iii) growth-temperature variations in baseline respiration rates at 25 °C (i.e. thermal acclimation); (iv) responses of leaf  $R_d$  to short-term (e.g. diurnal) changes in tempera-



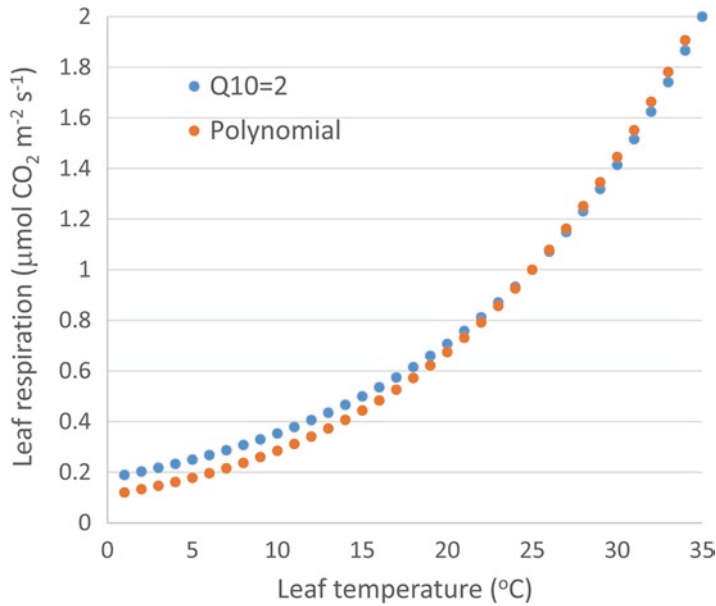


Fig. 6.6. Comparison of theoretical temperature responses curves of leaf respiration in darkness, calculated assuming rates of leaf  $R_d$  at 25 °C of  $1.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , with rates at other leaf temperatures predicted assuming a fixed  $Q_{10}$  (i.e. proportional change in leaf  $R_d$  per 10 °C change in temperature) value of 2.0 (i.e. a common  $Q_{10}$  assumed in TBMs; Table 6.1), and assuming that respiration varies with temperature according to that predicted by the global polynomial model (GPM; Heskell et al. 2016b). The structure of the GPM is similar that of the 3-component model approaches based on Arrhenius theory (Kruse and Adams 2008; Kruse et al. 2016). Adopting the GPM results in reduced estimates of leaf  $R_d$  at low temperatures, with little change in rates at temperatures  $>25$  °C

ture. An example of this integrative approach is shown in Fig. 6.7, where equations (6.14) and (6.15) are combined to model the temperature response of leaf  $R_d$  to short-term changes in temperature, for plants acclimated to growth temperatures of 15, 25 and 35 °C. Also shown is the temperature response curve of leaf  $R_d$  in the standard form of JULES, assuming no thermal acclimation and a fixed  $Q_{10}$  of 2.0 (Cox et al. 1998; Cox 2001; Clark et al. 2011). Adopting the ‘*GlobResp*’ approach allows for acclimation-dependent changes in baseline values of leaf  $R_d$ , resulting in higher rates at any given leaf temperature in cold-grown plants compared to their warm-grown counterparts. Importantly, ‘*GlobResp*’ predicts much higher rates at any given temperature than was previously assumed in the standard

form of JULES, particularly in cold habitats. When incorporated into TBMs, this is likely to result in significant increases in leaf  $R_d$  and overall plant  $R$  ( $R_p$ ) and reduced net primary productivity (NPP) at regional and global scales, depending on how future iterations of TBMs will model gross primary productivity (GPP), noting that  $\text{NPP} = \text{GPP} - R_p$ .

#### IV. Conclusions

Research into leaf  $R_d$  – both in terms of describing variability in rates among genotypes and environments – has advanced markedly over the past two decades, as manifested by a growing inventory of data that is providing new insights into how rates of leaf  $R_d$  vary. There are also advances being made

$$R_{dark,a} = \left[ r_0 + r_1 n_{l,a} - r_2 T_G \right] \times e^{[0.1012(T_a - 25) - 0.0005(T_a^2 - 25^2)]}$$

Globresp  $R_{dark}$  at 25°C    GPM – short-term response

Basal rate at 0°C    N-dependence    Growth T-dependence     $T_a =$  Ambient leaf T  
( $T_G =$  10-day mean temperature)

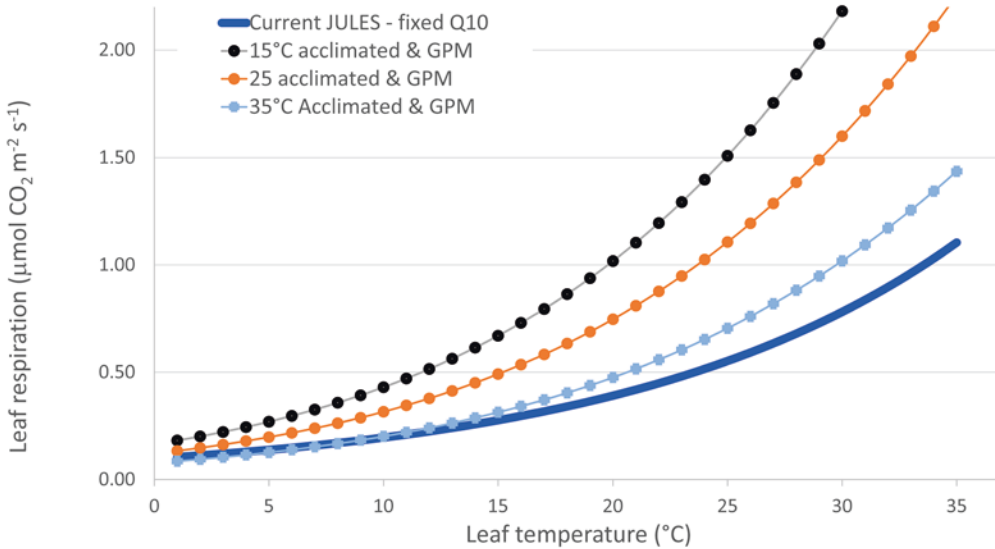


Fig. 6.7. Integration of equations emerging from the ‘GlobResp’ dataset (Atkin et al. 2015) and Global Polynomial Model (GPM) from Heskell et al. (2016b) to predict the shape of the temperature response curve of leaf  $R_d$  for broad-leaf trees, acclimated to three growth temperatures ( $T_a$ ; 15, 25 and 35 °C). Also shown is the temperature response curve of leaf  $R_d$  for broad-leaf

trees in the standard form of JULES, assuming no thermal acclimation and a fixed  $Q_{10}$  of 2.0 (Cox et al. 1998; Cox 2001; Clark et al. 2011). See equations (6.14) and (6.15) in the main text for descriptions of the components in the integrated equation shown above, and Table 6.2 for parameter constants for broad-leaf trees

to clarify individual and collective mechanistic controls of respiration (through models and experiments). Armed with these advances, the TBM community can now more accurately predict spatial and temporal variations in leaf respiratory  $\text{CO}_2$  release across the globe under current climatic conditions. Yet, we are not ‘there’ yet, since the research community continues to lack a process-based model to account for the complexity of taxa- and environment-driven variations in leaf  $R_d$ , thereby limiting the ability of TBMs to predict the impacts of

future climate regimes. Ideally, a truly mechanistic approach will emerge in the future that meets the TBM integration requirements of being parsimonious, scalable and spatially robust. Mechanistic models can be expected to have better predictive capability compared to those that are heavily parameterized, and that is important when trying to assess how the global carbon cycle will evolve within a climatic system perturbed through human burning of fossil fuels. Achieving a more mechanistically complete description will be a major challenge, requir-

ing new insights into the processes regulating energy metabolism of leaves, both during the day and night, in terrestrial ecosystems across the globe. We believe this is a challenge worth addressing, and especially if such models can be made applicable across spatial scales and thus appropriate for implementation in climate simulations, thereby characterizing leaf respiratory metabolism changes in the global carbon cycling.

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