Quantifying the temperature independent controls of nocturnal plant respiration

Submitted by Freya Newman to the University of Exeter
as a thesis for the degree of
Master of Science by Research in Geography
in May 2020

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: freyman Freya Newman (May 27, 2020) ……..

Table of Contents

List of Figures

List of Tables

List of Equations

List of Abbreviations

AOX	Alternative oxidase
CO_2	Carbon dioxide
DGVM	Dynamic global vegetation model
ESM	Earth system model
ETC	Electron transport chain
FPM	Flux partitioning model
GEP	Gross ecosystem productivity
GPP	Gross primary productivity
H_2O	Water
IRGA	Infra-red gas analyser
JULES	Joint UK Land Environment Simulator
LAI	Leaf area index
LEDR	Light enhanced dark respiration
LT	Local time
MODIS	MODerate-resolution Imaging Spectroradiometer
MOSES	Met Office Surface Exchange Scheme
MSE	Mean squared error
NEE	Net ecosystem exchange
NEE	Net ecosystem exchange
NPP	Net primary productivity
O_2	Oxygen
PAR	Photosynthetically active radiation
PFT	Plant functional type
PPFD	Photosynthetic photon flux density
RE	Ecosystem respiration
RMSE	Root mean squared error
SE	Standard error
SSE	Sum of squares error
TBM	Terrestrial biosphere model
TCA	Tri-carboxylic acid

Acknowledgements

Words cannot express how much I would like to thank my incredible supervisors, Lina Mercado and Dan Bruhn, for the opportunity to work with them on this project, their consistent support throughout, and their patience with me towards the rather prolonged end! I would like to thank Dan for his constant guidance and dependability, and Lina not only for the countless hours she has assisted me, but for making my masters a truly enjoyable and memorable experience. I would like to offer a special thank you to Zorayda Restrepo for helping make so much of this project possible, to Stephen Sitch and Iain Hartley for their continued support, and to collaborators Martijn Slot, Lasse Tarvainen and Göran Wallin for contributing data towards this project. I would also like to extend my gratitude to all staff and postgrads in the Geography department for creating a wonderful research community that I feel privileged to have been a part of.

Abstract

Autotrophic respiration is a critical determinant of plant, ecosystem and global carbon exchange, constituting a major control on the evolution of the contemporary carbon cycle with the potential to modulate the magnitude of future climate change. Due to an incomplete understanding of plant respiration and its underlying mechanisms, the process remains an important yet poorly quantified component of the global carbon cycle and currently dominates uncertainties in carbon cycle modelling. Plant respiration is currently represented by a fixed exponential temperature function in vegetation and earth system models. This rather simplistic description is inadequate to describe the co-regulation of respiration by endogenous mechanisms over longer timescales, such as the control exerted by substrate supply, product demand and the circadian clock. This study compiles the first comprehensive dataset of nocturnal leaf respiration to explore and quantify the temperature-independent control of leaf respiratory metabolism at night. A down-regulation in nocturnal respiration was observed to occur under constant temperature conditions which decreased the basal rate of respiration by ~40% of the initial rate at the onset of darkness, indicating the base rate of respiration cannot be considered constant as generally assumed in all modern field studies and models. An empirically derived term representing the non-temperature dependent component of leaf respiration at night was applied to the land surface component of an earth system model to describe nocturnal variation in endogenous metabolism in addition to the temperature dependency of respiration. Accounting for the non-temperature dependency of nocturnal respiration reduced annual rates of modelled plant respiration by up to 10% and increased annual net primary productivity by up to 16% across all tropical and temperate forest sites, suggesting that previous models have overestimated global respiration and underestimated net primary productivity, particularly in the tropics. The significant impact of the novel term presents important implications for land-atmosphere studies and estimates of global terrestrial carbon balance and storage. This study provides the foundation from which to advance research on endogenous rhythms in plant metabolism to develop a more comprehensive understanding and description of plant respiration for modelling frameworks, ultimately to increase the realism of vegetation models for greater confidence in simulations of the current and future terrestrial and global carbon cycle.

1. Introduction and Literature Review

1.1. The Carbon Cycle

Carbon is a finite resource that cycles the earth in the form of a vast number of organic compounds, serving as a common element of all life on the planet. In the form of carbon dioxide (CO_2) it is one of the principal mediums in the biochemical processes of photosynthesis, respiration and organic decomposition (Schimel *et al.*, 2005). The global carbon cycle describes this series of processes by which carbon compounds are interconverted in the environment and exchanged between four major reservoirs: the atmosphere, land, oceans and fossil fuels (Figure 1.1; Houghton, 2003). Anthropogenic CO_2 emissions from the combustion of fossil fuels and land-use change have exerted a significant influence on the natural carbon cycle since the industrial revolution, constituting the most consequential of human impacts on the environment (Malhi *et al.*, 1999). Since the start of the industrial era, atmospheric CO_2 concentration has increased from approximately 227ppm in 1750 (Joos and Spahni, 2008) to 407 ± 0.1 ppm in 2018 (Dlugokencky and Tans, 2019) and is now the highest in at least 650,000 years (IPCC, 2007). Only an estimated 45% of global anthropogenic emissions remain in the atmosphere, with approximately 29% sequestered by land and 24% by oceans (Friedlingstein *et al.*, 2019). The remaining 2%, referred to as the carbon budget imbalance, is a measure of imperfect data and understanding of the contemporary carbon cycle. CO_2 is a greenhouse gas, defined as a constituent of the atmosphere that absorbs and emits infra-red radiation emitted by the earth's surface, clouds and the atmosphere itself, ultimately reducing net radiation emitted to space and resulting in an energy imbalance at the top of the atmosphere known as radiative forcing (Allwood *et al.*, 2014). This property results in the greenhouse effect by which surface temperature and the troposphere warm in response to the radiative forcing. An increase in the concentration of greenhouse gases increases the magnitude of this effect, widely described as global warming. Uptake by the terrestrial and ocean carbon sinks therefore decelerates global warming and climate change, however the capacity of these ecosystems to sequester elevated CO_2 is not yet fully understood and appears to be saturating (Lambers *et al.*, 2008). Atmospheric CO_2 records indicate that the land surface has acted as an increasingly strong carbon sink over the past five decades (Ballantyne *et al.,* 2012), however the first signs of saturation in the carbon sink of some forests are already becoming apparent (Nabuurs *et al.,* 2013; Brienen *et al.,* 2015; Hubau *et al.*, 2020).

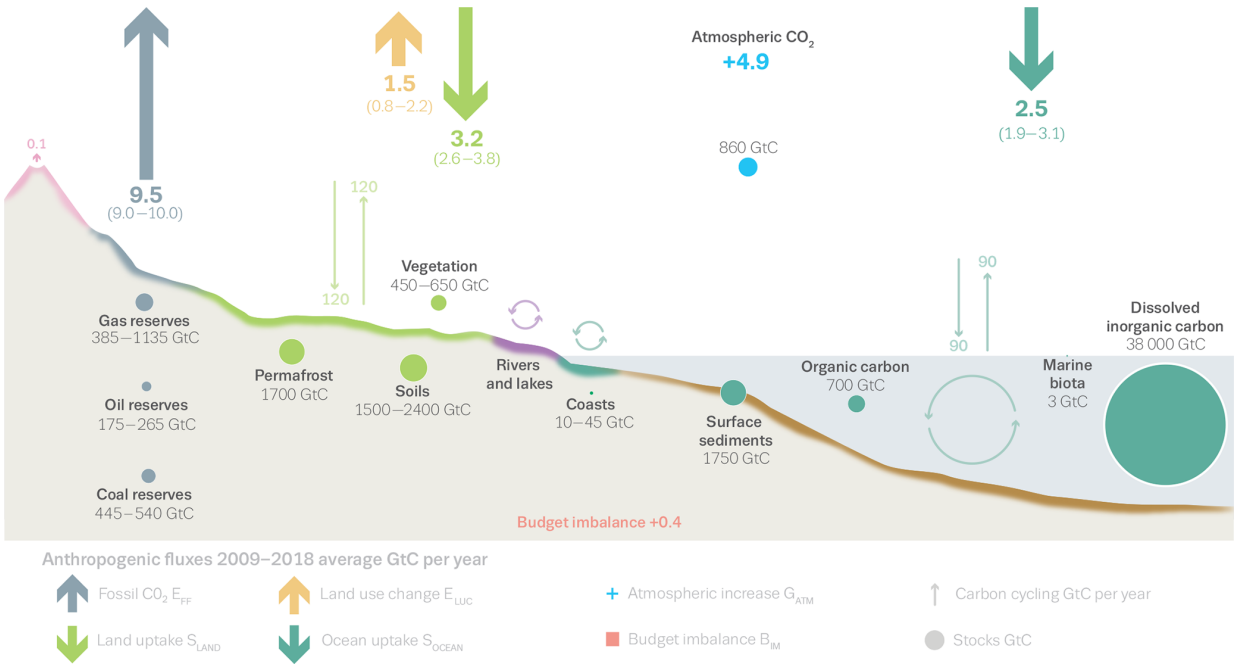


Figure 1.1. Schematic of the global carbon cycle and anthropogenic perturbation averaged globally for the decade 2009-2018, taken from Friedlingstein *et al*. (2019). Carbon stocks in coasts taken from a literature review of coastal marine sediments (Price and Warren, 2016). All other fluxes and stocks statistics are taken from Ciais *et al*. (2013), with the ocean gross fluxes updated to 90 GtC yr^{-1} to account for the increase in atmospheric CO_2 since publication.

The continued increase in atmospheric CO_2 is one of the most certain projections in environmental sciences (Figure 1.2; Faitichi *et al.*, 2018), therefore the contemporary carbon cycle, its integral processes and the capacity of natural sinks have gained a new political prominence and become an increasingly focal topic of research.

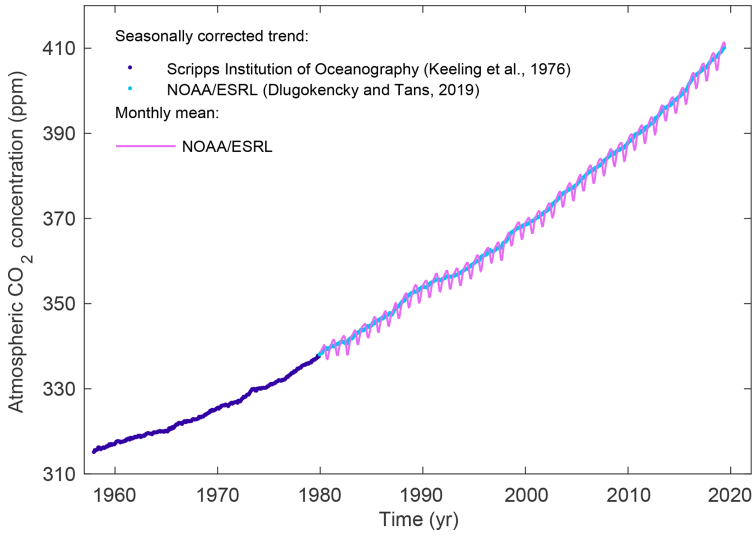


Figure 1.2. Surface average atmospheric CO_2 concentration (ppm), taken from Friedlingstein *et al*. (2019). The 1958-1979 monthly data are from the Scripps Institution of Oceanography, based on an average of direct atmospheric CO_2 measurements from the Mauna Loa and South Pole stations (Keeling *et al*., 1976). The 1980-2018 monthly data are from NOAA ESRL (Dlugokencky and Tans, 2019), based on an average of direct atmospheric CO_2 measurements from multiple stations (Masarie and Tans, 1995).

The terrestrial biosphere constitutes a valuable component of the carbon cycle, removing an estimated 3.2 ± 0.7 Gt C yr^{-1} from the atmosphere over the past decade, equating to a third of anthropogenic emissions (Friedlingstein *et al*., 2019). Future climate change has been projected to rapidly alter the structure and functioning of terrestrial ecosystems with inconclusive effects on the complex ecology and physiology that underlies land-atmosphere CO_2 fluxes (Figure 1.3; IPCC, 2013). Photosynthesis and respiration, autotrophic and heterotrophic, are the primary biological processes that regulate the land-atmosphere exchange of CO_2 (Griffin e*t al.,* 2002), and it is the delicate equilibrium between these fluxes that defines the carbon balance of an ecosystem and determines whether the system acts as a net source or sink of carbon (Valentini *et al*., 2000). The terrestrial biosphere currently acts as a strong net sink of carbon due to uptake by photosynthesis for primary production exceeding release through respiration, thereby reducing the climate impact of anthropogenic emissions (Schimel *et al*., 2014). Current projections suggest that the terrestrial sink may transition to a net source of carbon during the 21st century as climate-driven losses exceed gains, resulting in a positive carbon cycle-climate feedback that would accelerate global warming and significantly alter the carbon balance and storage of terrestrial ecosystems (Friedlingstein *et al*., 2014; Anderegg *et al*., 2015). Considerable progress has been made in understanding the processes of photosynthesis and heterotrophic soil respiration, however a general understanding of autotrophic respiration dynamics is still lacking (Collalti *et al*., 2019).

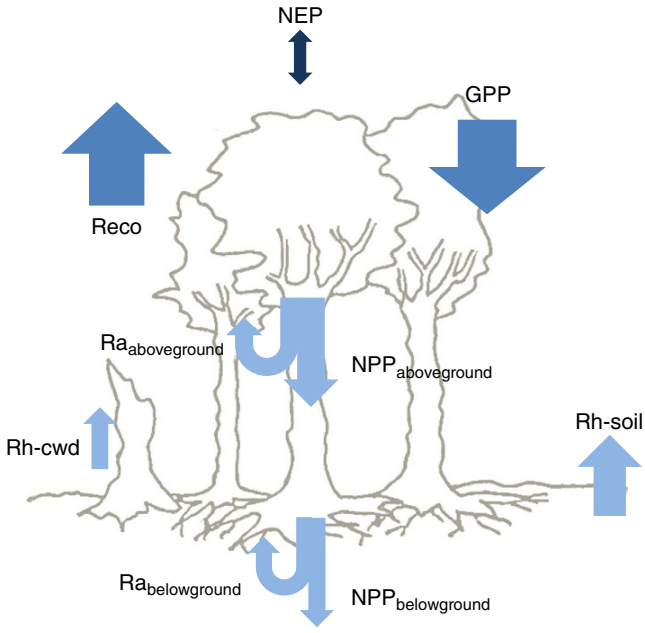


Figure 1.3. Schematic of the major components of the forest carbon cycle, taken from Campioli *et al.* (2016). $Ra_{aboveground}$ and $Ra_{belowground}$ represent above and below ground autotrophic respiration respectively; Rh-soil and Rh-cwd represent heterotrophic respiration from soil and coarse woody debris respectively; $NPP_{aboveground}$ and $NPP_{belowground}$ represent above and below ground net primary production respectively; Reco is ecosystem respiration (Reco = Ra + Rh); GPP is gross primary production (GPP = NPP + Ra); and NEP is net ecosystem production (NEP = GPP – Reco = NPP – Rh).

Autotrophic respiration plays a fundamental role in carbon exchange at plant, ecosystem and global scales, postulated to be the main determinant of the carbon balance of terrestrial systems (Valentini *et al.*, 2000). At ecosystem level, plant respiration contributes up to 65% of the total CO_2 efflux, with the remaining released by heterotrophic soil respiration (Xu *et al*., 2001; Reichstein *et al*., 2002). Globally, plant respiration releases ~60 Gt C yr^{-1} into the atmosphere, constituting a substantial carbon flux that is estimated to be six to eight times that emitted by anthropogenic activity (Canadell *et al*., 2007; IPCC, 2013). Leaf respiration comprises half of this autotrophic respiratory flux (Atkin *et al.,* 2007), indicating that fractional changes in leaf respiration could potentially modulate climate on the scale of anthropogenic forcing (Heskel *et al*., 2016). Plant respiration, and leaf respiration in particular, is predicted to increase as a consequence of future warming with the ability to generate positive feedback mechanisms and partly define the magnitude of future climate change (King *et al*., 2006). Leaf respiration is therefore a crucial process for ecosystem functioning with global implications, yet remains poorly quantified (Atkin *et al*., 2015), contributing to uncertainty in estimates of the terrestrial carbon sink which remains the least constrained component of the contemporary carbon cycle (Le Quéré *et al*., 2018).

1.2. Plant Respiration

Plant respiration has a major influence on the carbon cycle and global climate and is a fundamental physiological process at organism and cellular scales, essential for myriad energy-dependent metabolic processes in plants (Scafaro *et al.*, 2017). Both photosynthesis and respiration are required to produce ATP and NADPH to meet demands for plant growth, maintenance and active transport (Lambers *et al*., 2008). Occurring in the cytosol and mitochondria, plant respiration comprises a suite of metabolic pathways and biochemical reactions, including glycolysis, the tri-carboxylic acid (TCA) cycle, and the electron transport chain (ETC; Lambers *et al.,* 2005). Mitochondrial respiration occurs under both light and dark conditions yet is often referred to as ‘dark respiration’ to differentiate the respiratory flux that reflects plant metabolic activity from the release of CO_2 by photorespiration in photosynthesis (Wright *et al*., 2006). Occurring in chloroplasts, photosynthesis uses light energy and water to convert CO_2 from the atmosphere into carbon rich compounds such as carbohydrates (Barnes, 1893). A large proportion of carbohydrates assimilated by photosynthesis serve as respiratory substrate and are subsequently expended by respiration, mediating the link between the two processes (Whitehead *et al*., 2004). Dark respiration

oxidises these compounds to liberate ATP and carbon skeletons necessary for cellular maintenance and biosynthesis, releasing CO_2 as a by-product (Atkin *et al*., 2000a). Approximately 30-80% of daily photosynthetic carbon fixation is released back into the atmosphere by respiration (Loveys *et al.,* 2002). Dark respiration relies upon the supply of photosynthates to serve as respiratory substrate at all times, however photosynthetic carbon fixation only occurs in the light (Feugier and Satake, 2014). Glycine is the main primary photosynthetic product used as respiratory substrate during the day (Ellsworth and Reich, 1996; Hurry *et al.,* 1996). Darkness eliminates the production of primary carbon products such as this, causing respiration to rely entirely upon the degradation of transitory starch reserves in leaves (Smith and Stitt, 2007). Starch is stored inside the chloroplasts during daily photosynthesis and subsequently broken down in a linear manner at night, enabling a continuous supply of carbon to support nocturnal metabolism and growth (Graff and Smith, 2011). The biochemistry of leaf respiratory metabolism therefore differs significantly between light and dark, and day and night (Kromer, 1995).

The process of respiration is typically partitioned into two components, growth respiration (Rpg) and maintenance respiration (Rpm) (Amthor, 1989; Ryan, 1991), to help conceptualise the different use of metabolic energy for biosynthesis in growing versus full-grown tissues (Thornley, 1970; 2011). However, respiratory processes for growth and maintenance are not biochemically distinct, and growing organs also contain mature tissues whose respiration is limited to a maintenance component (Lavigne *et al.,* 1997). Furthermore, Lambers *et al.* (1998) suggested inclusion of a third category is necessary to describe the energy required to fuel active transport processes. Despite these limitations, the simple growth-maintenance paradigm has formed the most widely used approach for interpreting and modelling the complex process of respiration for over 40 years.

1.3. Controls of Plant Respiration

Respiratory CO_2 release is the net effect of many constituent processes, therefore, compared to a relatively comprehensive understanding of photosynthetic metabolism, understanding the factors that regulate respiratory fluxes remains incomplete (Atkin *et al*., 2014).

1.3.1. Exogenous Controls

Temperature is one of the predominant environmental factors that regulates the rate of biological processes (Davidson and Janssens, 2006). The high temperature sensitivity of plant respiration has long been recognised and studied (Dehérain and Moissan, 1874; James, 1953; Forward, 1960; Berry and Raison, 1981) and is therefore considered the most well understood variable affecting rates of respiration (Griffin *et al*., 2002). The short-term temperature sensitivity of leaf respiration is regulated by the temperature-dependence of enzymatic reactions that are involved in a variety of respiratory pathways (King *et al*., 2006), causing the rate of metabolic processes to generally increase with increasing temperature. An increase in the activity of respiratory enzymes at high temperatures facilitates greater rates of growth, maintenance and active transport, resulting in an augmented respiratory flux that reflects an increased demand for energy (Lambers *et al.,* 2008). Predicted global warming and the widely established temperature dependency of respiratory processes highlights the importance of accurately quantifying plant respiration and its temperature sensitivity (Griffin *et al*., 2002).

Respiratory metabolism is continuous, occurring under both light and dark conditions, however leaf level studies have long suggested the inhibition of leaf respiration in the light, exerting an exogenous control on rates of daytime respiration (Tcherkez *et al*., 2017a). Irradiance induced inhibition of mitochondrial respiration was first described in unicellular algae by Kok (1948) and has since been observed in numerous plant species (Tcherkez *et al*., 2017b). Light inhibition has been found to cause a 25-100% reduction in respiratory rate at leaf level, with many studies reporting a mean inhibition of ~30% (Budde and Randall 1990; Buckley and Adams 2011; Heskel *et al*. 2013; Kroner and Way 2016; Tcherkez *et al*. 2005; 2009; 2012; 2017*b*). The extent of light inhibition, its effect on ecosystem scale fluxes, and the mechanisms involved remain heavily contested (Loreto *et al*., 2001; Buckley *et al*., 2017; Farquhar and Busch, 2017; Tcherkez *et al*., 2017a; 2017b; Keenan *et al*., 2019). Consequently, this study exclusively examines leaf respiration at night due to significant differences in the process of respiration under light conditions, the complexities of which are beyond the scope of this investigation.

1.3.2. Endogenous Controls

In addition to environmental controls, plant respiration is generally limited by respiratory substrate availability, energy demand, and the capacity of respiratory enzymes (Lambers *et al*., 2005; Covey-Crump *et al*., 2007). These fundamental endogenous mechanisms co-regulate respiratory rates across varying environmental conditions and thermal environments, potentially responsible for a large proportion of diurnal variation in the rate autotrophic respiration.

Whether the rate of plant respiration is limited by substrate supply or product demand is a long-standing question (Farrar and William, 1991; Amthor, 1994; Noguchi, 2005). In the 'demand-centric' model, rates of respiration are determined by the activity of growth, maintenance and transport processes that consume respiratory products such as ATP, NADPH and carbon skeletons (O'Leary *et al.,* 2019). Changes in respiratory fluxes over the very short-term are largely driven by fluctuations in the turnover of these products. The turnover of ATP is also influenced by diurnal variation in the relative engagement of alternative oxidase (AOX), an enzyme that forms part of the ETC and dramatically reduces the ATP yield of respiration (Vanlerberghe, 2013), which could impact CO_2 production and further drive diurnal changes in the rate of respiration. Alternatively, respiration rate in the 'supply-centric' model is regulated by carbohydrate supply (O'Leary *et al.,* 2019). During darkness leaf concentrations of non-structural carbohydrates typically decrease (Fondy and Geiger, 1982; Grimmer and Komor, 1999), reflected by the respiratory rate of mature leaves (Noguchi, 2005). Substrate supply has received less attention as a key control of autotrophic respiratory flux, partly due to the difficulties involved in measuring cellular substrate concentrations (Davidson *et al*., 2006). However, it is becoming increasingly apparent that temporal and spatial variation in substrate availability may explain a large proportion of the observed variation in autotrophic respiration (Davidson *et al*., 2006). Ultimately, the question of supply versus demand controlling the rate of plant respiration is problematic because they are not independent forces. Rather, the supply-demand relationship is highly coordinated, with respiratory activity correlating with both substrate supply and product demand across plant and ecosystem scales. In the long-term, at whole-plant scale the ratio of photosynthesis to respiration is relatively consistent across species from different habitats (Atkin *et al*., 2007), and in a range of species under differing growth stages and thermal environments (Gifford, 1994). At ecosystem scale, respiration is believed to have a positive linear

relationship with both photosynthetic carbon fixation and biomass production (DeLucia *et al*., 2007; Litton *et al*., 2007). It is often changes to the supply and demand components of respiration that constitutes the response of respiration to exogenous environmental change. Variation in the capacity of respiratory enzymes is a further endogenous factor that may limit rates of respiration by influencing the maximum flux able to be attained through the respiratory apparatus (O'Leary *et al*., 2019). Due to the temperature dependence of enzyme activity, capacity limitations may only occur above and below certain thermal thresholds (O'Leary *et al*., 2019).

How respiratory processes are integrated diurnally with photosynthesis and changes in the external environment and regulated to meet fluctuating cellular demands is at the core of understanding plant carbon metabolism. What remains unclear is how the discussed factors alone combine to account for the often-reported variation in rates of leaf respiration in both field studies and controlled environments (Atkin *et al*., 2015).

1.4. The Circadian Clock

1.4.1. The Circadian Mechanism

The respiratory metabolism network is known to be directly operated by a number of established mechanisms: substrate supply, product demand, respiratory capacity and the environment, however the circadian clock may also contribute to diel variation in rates of plant respiration. The daily rotation of the Earth on its axis causes regular alterations in the physical environment, resulting in diurnal cycles of light, temperature and humidity (Harmer, 2009). This 24-hour periodicity in the geophysical world is reflected in the daily behaviour and physiology of most organisms due to the circadian clock mechanism (Harmer, 2009). The circadian clock is an internal biochemical oscillator that synchronises physiological processes with the external environment, providing organisms with the innate ability to anticipate the onset of dawn and dusk and adjust their biology accordingly (McClung, 2006).

Plant circadian rhythms are described in writings dating back to the fourth century BC (Bretzl, 1903), however the scientific literature began in the 18th century when de Mairan (1729) reported daily leaf movements of *Mimosa pudica* to persist in constant darkness, demonstrating their endogenous origin. Almost a century later, the period length of these

movements were accurately measured and determined to be ~24 hours, taking the form of sinusoidal waves (McClung, 2006). Further research by de Candolle (1832) revealed that the rhythm could be inverted by reversing the alternation of light and dark periods. Observations of leaf movement rhythms were repeated and expanded throughout the 19th and 20th centuries, helping explicate the three fundamental characteristics that now define the circadian clock, outlined by Harmer (2009). First, circadian rhythms persist with an approximate 24-hour periodicity when deprived of exogenous cues in constant environmental conditions. Second, the onset of circadian rhythms can be reset by appropriate environmental cues such as light and temperature. Third, circadian rhythms occur within approximately the same periodicity across a range of temperatures.

Powerful approaches in genetic analysis to identify the molecular components of the cellular circadian clock began in the 1970s and has led to rapid progress in understanding the mechanism in higher plants and other organisms (Dunlap, 1999). Circadian rhythms arise from the circadian oscillator, a complex gene autoregulatory network comprised of interlocked transcriptional-translational feedback loops (Harmer, 2009), found to regulate 30-90% of all transcriptions in the model species *Arabidopsis thaliana* (Covington *et al*., 2008; Michael *et al*., 2008). The circadian clock mechanism has been identified in all eukaryotes studied to date (Dunlap *et al*., 2004) and thousands of genes are now determined to be under circadian control (Harmer *et al.,* 2000).

Circadian clocks are cell-autonomous systems, therefore multiple clocks exist within a single organism and are coordinated by a process termed entrainment (Harmer, 2009). Entrainment by external cues such as temperature and light are used to set the circadian clock, creating a synchrony between internal physiology and the rhythmicity of the environment (Müller et al., 2014). The availability of light changes the most rapidly and predictably over a diurnal cycle, therefore light received through the photoreceptors of plant cells is the predominant signal that synchronises the circadian clock with day-night cycles (Harmer, 2009). Temperature cycles are less well defined, however steps as small as 0.5°C have been observed to entrain circadian rhythms in the absence of any significant changes in light intensity (Rensing and Ruoff, 2002), demonstrating the exquisite sensitivity of the circadian system.

Circadian clocks now appear almost ubiquitous among higher organisms, having evolved to be in phase with the Earth's rotation and conferring a selective advantage. The circadian clock has been conserved for at least *c*. 450 million years of plant evolution (Rensing *et al*., 2008), believed to have evolved towards a more complex and robust architecture (Rand *et al*., 2004; Tsai *et al*., 2008). The coordination of physiological functions with the 24-hour clock provides an adaptive advantage by allowing plants to balance energy needs and resources with respect to the changing environment. Optimal tuning of the mechanism to light-dark cycles enhances chlorophyll accumulation, carbon fixation, biomass production, water-use efficiency and growth, thus increasing competitive advantage and survival (Dodd *et al*., 2005). Consequently, plants with clocks that are dissonant from the environment are likely to be disadvantaged by poor growth, out-competition and increased mortality.

1.4.2. Circadian Rhythms in Plant Respiration

The circadian clock and its underlying molecular mechanisms are now well established and have been described extensively in plants since the discovery of leaf movement rhythms. Further rhythms in stomatal conductance were first reported by the pioneering work of Francis Darwin (1898) and the circadian clock is now recognised to drive diurnal oscillations in photosynthesis, growth, flowering and other leaf-level physiological processes (Gessler *et al*., 2017; Greenham and McClung, 2015). Despite establishing circadian rhythms in many significant plant processes, the potential role of the circadian clock in regulating leaf respiratory metabolism has received a surprising lack of attention. Circadian rhythms in dark respiration were hypothesised by Chia-Looi and Cumming (1972) and have since been reported to reduce respiration at night for a number of plants measured in controlled environments (Pallas *et al.*, 1974; Hew *et al*., 1978; 1994; Lee and Akita, 2000). Furthermore, at the molecular level, Harmer *et al*. (2000) found six genes involved in glycolysis and the TCA cycle to be under circadian control, in addition to a cluster of genes encoding enzymes implicated in starch metabolism. Despite this compelling evidence for the existence of circadian rhythms in respiration, few subsequent studies have attempted to examine the significance of these rhythms in field settings and quantify their impact on plant and ecosystem scale fluxes.

Doughty *et al.* (2006) conducted the most extensive study to date to determine whether the circadian clock regulates diurnal patterns of leaf gas exchange in field settings at Tapajós

National Forest, a tropical rainforest site in the Brazilian Amazon. The gas exchange of six *Micropholis sp.* leaves exposed to darkness and constant environmental conditions were monitored for 20-48 hours. The rate of respiration began to decline after 13:00 Local Time (LT) and recovered around 06:00 LT, indicating a down-regulation of respiratory metabolism at night. The authors concluded the endogenous circadian clock to be the only established mechanism able to account for the observed rhythms in respiration when deprived of exogenous environmental cues. A second field experiment conducted by Bruhn *et al*. (2008) investigated the temperature response of two cold climate species, *Eucalyptus pauciflora* and *Pringlea antiscorbutica,* on a short timescale using temperature manipulations and a longer timescale using natural variation in ambient temperatures over a 24-hour period. The authors calculated Q_{10} values, which denote the proportional change in respiration in response to a temperature increase of 10°C (Kruse *et al*., 2011), to describe the temperature response of respiration over the two different timescales. The resulting Q_{10} values were 0.3-1 units lower when calculated from short-term temperature manipulations than measurements taken as ambient temperatures varied over the diurnal cycle. This consistent discrepancy led to the conclusion that factors other than temperature contribute to diel variation in both rates of respiration and Q_{10} values. This study supports the conclusions of Doughty *et al.* (2006), suggesting that the circadian clock and other endogenous mechanisms play a role in co-regulating leaf respiration in field settings across contrasting biomes. The findings of Bruhn *et al*. (2008) also present implications for the modelling of plant respiration that currently relies upon a fixed Q_{10} temperature coefficient over the 24-hour cycle.

1.5. Representation of Plant Respiration in Vegetation Models

1.5.1. Modelling Plant Physiological Processes

Current international political concerns regarding the management of the terrestrial biosphere and reduction of greenhouse gas emissions have highlighted the importance of measuring and modelling CO_2 fluxes of terrestrial ecosystems (Gifford, 2003). Models are essential prediction tools for understanding carbon-climate cycle feedbacks, evaluating the potential impacts of climate change and ultimately informing climate policies and management decisions (Harper *et al*., 2016). Carbon, water and energy cycles are intimately linked therefore Earth System Models (ESMs) require a realistic representation of the land surface

and plant physiological processes, with a robust description of atmospheric CO_2 capture by photosynthesis and release by plant and soil respiration (Blyth *et al*., 2011; Booth *et al.,* 2012; Huntingford *et al*., 2017). The representation of plant physiological processes currently dominates uncertainties in carbon cycle modelling due to an incomplete understanding of the underlying biophysical mechanisms (Huntingford *et al.,* 2013; Friedlingstein *et al.,* 2014). Variations in leaf and plant respiration are particularly poorly understood and inadequately represented, restricting progress in modelling the carbon balance of terrestrial ecosystems at regional and global scales (Gifford, 2003).

Research on the cycling of carbon between the biosphere and the atmosphere has predominantly focused on understanding and modelling the process of photosynthesis. The establishment of a robust, physiologically based and mathematically tractable framework for modelling leaf-level carbon assimilation in response to radiation, temperature and interior CO_2 concentration by Farquhar *et al.* (1980) subsequently enabled the development of large-scale models of photosynthesis and its climate-dependency. Contrary to existing biochemical models of photosynthesis, the description of plant respiration is often simplistic. The considerable complexity of plant respiratory metabolism, its interaction with other endogenous processes and its sensitivity to exogenous variables are a significant impediment to the development of a mechanistic framework, in addition to a previous lack of data to constrain estimates of leaf and plant respiration (Gifford, 2003; Kruse and Adams, 2008; Atkin *et al*., 2015). Minor differences in the modelled rate of respiration can significantly impact simulations of ecosystem carbon balance, therefore accounting for spatial and temporal variation in leaf respiratory CO_2 release is crucial (King *et al.,* 2006; Wythers *et al*., 2013). It has become increasingly apparent that respiration is inadequately represented in global vegetation models and ESMs, resulting in substantial uncertainty in projections of climate and carbon cycling (Booth *et al*., 2012; Huntingford *et al*., 2013; Smith and Dukes, 2013) and the increasingly urgent need to improve the representation of leaf and plant respiration in these models (Atkin *et al*., 2010).

1.5.2. Temperature Dependency of Plant Respiration in Models

The high sensitivity of respiration to short-term changes in temperature is well established, with many studies assuming rates of plant respiration to increase as an approximate exponential function of temperature (Atkin and Tjoelker, 2003). Therefore, the description of

respiration in a majority of vegetation, land surface and earth system models assumes the tight control of respiration by temperature due to its direct effect on respiratory enzyme activity and the rate of respiratory processes (Piao *et al.,* 2010). The temperature response of respiration and many biochemical reactions are typically represented by equations established in the 19th century by Arrhenius (1889) and van't Hoff (1898). Leaf and plant respiration are commonly described by a Q_{10} function which denotes the factor by which respiration is multiplied when temperature increases by 10°C (Davidson *et al.,* 2006).

$$Q_{10} = \left(\frac{R}{R_0}\right)^{[10/(T-T_0)]} \qquad (1)$$

So described, Q_{10} values are calculated using the rate of respiration (R) at any given temperature (T), and the base rate of respiration (R_0) at an arbitrarily set temperature (T_0) which is currently considered to be constant (Eq. 1). Correspondingly, a rearrangement of the formula provides an equation to estimate respiration at a given temperature using a predetermined Q_{10} value:

$$R = R_0 Q_{10}{}^{0.1(T-T_0)} \qquad (2)$$

Diel variation in plant respiration is thus predicted from only three parameters: the base rate of respiration at an arbitrarily set temperature, the inherent temperature sensitivity of respiration, and variation in leaf tissue temperature. The global vegetation modelling community places considerable trust in this comparatively simple function that assumes an exponential relationship between respiration and temperature, scarcely modified since its 19th century origin. The Q_{10} of plant respiration is presently derived from the instantaneous response of respiration to short-term artificial temperature manipulations applied to dark-adapted leaves at varying times during the day, documented by Tjoelker *et al*. (2001) to range from 1.1 to 4.2 across plant species and biomes with a mean Q_{10} of 2.5 that accords with values reported in wider studies (Ryan *et al*., 1997; Atkin *et al*., 2005a; Luyssaert *et al*., 2007; Piao *et al*., 2010). The use of a constant Q_{10} of 2 that describes the inherent temperature sensitivity of respiration on the timescale of minutes has since gained wide acceptance in modelling leaf, plant and ecosystem scale respiration, with respiratory rate doubling for every 10°C increase in temperature. This Q_{10} value of 2, founded upon data collected during the

day, is assumed to be characteristic of nocturnal respiration and is also used to model variation in rates of leaf respiration at night. However, this Q_{10} function describes only the control exerted by the kinetic effects of temperature on respiratory enzymes, representing the 'inherent' temperature-sensitivity of plant respiration that can be derived from the artificial manipulation of temperature over the timescale of minutes (Bruhn *et al*., 2008). It fails to consider the additional temperature-independent control of respiration exerted by the circadian clock and temporal variation in the availability of respiratory substrate and demand for respiratory products, representing the 'apparent' temperature-sensitivity of plant respiration estimated over longer timescales of hours to days (Bruhn *et al*., 2008). Furthermore, the short-term temperature response of many biological processes, including plant respiration, often fail to accurately fit an exponential function (Belehradek, 1930; Lloyd and Taylor, 1994) and it has long been recognised that the Q_{10} of plant respiratory CO_2 efflux is not constant, nor a value of 2 except over a limited range of temperatures (Wager, 1941; James, 1953). Despite increasing acceptance of the variability and insufficiency of a fixed Q_{10} function to describe plant respiration, attempts to resolve the inadequacies of a constant Q_{10} and improve the description of plant respiration in models are limited.

The Arrhenius equation was also developed to describe the temperature-dependence of chemical reactions, found to accurately represent the behaviour of rather complex biological processes (Laidler, 1972). A modification of the original Arrhenius equation by Lloyd and Taylor (1994), where the activation energy of respiratory processes varies inversely with temperature, was found to produce an unbiased estimate of respiration over a wide range of temperatures:

$$R = R_0 \times e^{\frac{E_0}{r} \times \left[\frac{T - T_0}{T \times T_0}\right]} \qquad (3)$$

The formula uses the overall activation energy of respiratory processes (E_0) and base rates of respiration (R_0) and temperature (T_0) to predict respiration at any given temperature (T). Most Dynamic Global Vegetation Models (DGVMs) use the Q_{10} function, however this alternative temperature response function has also been widely applied to model the temperature sensitivity of respiration (Sitch *et al*., 2003; Turnball *et al*., 2003; Shapiro *et al*., 2004; Xu and Griffin, 2006), yet the additional temperature-independent control of respiration remains unaccounted for.

1.5.3. The Joint UK Land Environment Simulator

The Joint UK Land Environment Simulator (JULES) forms the land surface component of the earth system modelling framework of the UK Met Office Hadley Centre Earth System Model, simulating fluxes of carbon, water, momentum and energy between the land surface and the atmosphere (Best *et al*., 2011; Clark *et al*., 2011; Harper *et al*., 2016). JULES is a process-based model, founded upon a theoretical understanding and description of key ecological processes at leaf-level that can be upscaled to represent the canopy. Mechanistic models such as this offer significant advantages in extrapolating beyond known conditions and exploring the effects of global change compared to purely statistical or rule-based models (Cuddington *et al*., 2013). JULES is based on the Met Office Surface Exchange Scheme (MOSES; Cox *et al*., 1999; Essery *et al*., 2003) and the TRIFFID DGVM (Cox, 2001) and consolidates improved representations of relevant ecological processes gained from numerous studies (Cox *et al.,* 2000; Gedney *et al*., 2004; Jones *et al*., 2005; Sitch *et al*., 2008; Mercado *et al*., 2009a: Harper *et al*., 2016; 2018). JULES can also be coupled to the IMOGEN system (Huntingford *et al*., 2010), thereby linking terrestrial carbon cycling to climate and providing the opportunity to assess how the biogeochemical processes in JULES may respond and feedback to a changing environment.

Leaf dark respiration is parameterised in JULES at a reference leaf-level temperature of 25°C (R_{d25}). The model assumes R_{d25} to be proportional to carboxylation capacity of the enzyme Rubisco at 25°C (V_{cmax25}) that is predicted from the leaf nitrogen concentration of nine Plant Functional Types (PFTs), a system used to classify plants according to their physical, phenological and phylogenetic characteristics for modelling purposes (Harper *et al.,* 2016). Maintenance respiration is thus calculated as a function of photosynthetic capacity, temperature and a linear function of leaf nitrogen concentration due to links between the TCA pathway and nitrogen metabolism (Crous *et al*., 2012), with growth respiration obtained as a constant fraction of the residual between Gross Primary Productivity (GPP) and maintenance respiration. Remaining plant respiration components, root and stem, are estimated as a proportion of leaf respiration based on the relationships between tissue nitrogen content and respiration. Diurnal variation in leaf and plant respiration is calculated in JULES according to diel changes in temperature alone, estimated for the entire 24-hour period using the inherent temperature-sensitivity and a fixed base rate of respiration. This description does not consider

temporal variation in endogenous metabolic status that may also contribute significantly to variation in rates of leaf and plant respiration and its apparent temperature-sensitivity over a diurnal cycle.

1.5.4. Recent Advances in Plant Respiration Modelling

The development of JULES is ongoing, with revised and novel representations of several key earth system processes constantly under consideration. Since the initial development of JULES, a better understanding of plant respiration has become available, facilitating the development of alternative models, some of which attempt to address the aforementioned shortcomings of the Q_{10} approach.

In process-based models such as JULES, the upscaling of processes observed at leaf-level to represent gas exchange for the entire canopy is challenging due to complex environmental and physiological gradients that exist within a canopy (Lambers *et al*., 2008). JULES previously relied upon the big leaf approach in which radiation attenuation through the canopy is described by Beer's law (Monsi and Saeki, 1953). This method simulates an exponential decline in leaf nitrogen, photosynthesis and respiration through the canopy that is assumed to vary proportionally with the vertical distribution of irradiance (Sellers *et al*., 1992). However, numerous studies have found that the distribution of photosynthetic capacity within canopies does not vary proportionally with radiation (Carswell *et al*., 2000; Meir *et al*., 2002), thereby disputing the assumptions upon which the big leaf approach is founded and discrediting the scaling method. This led to the development of the JULES multi-layer scaling method that follows the 'two-stream' approach (Sellers, 1985), accounting for the absorption of direct and diffuse radiation from light interception at different canopy levels (Mercado *et al.,* 2007). Studies by Jogireedy *et al*. (2006) and Mercado *et al*. (2007; 2009b) demonstrated the superior performance of the multi-layer scaling approach that compared more closely to observations than the big leaf approach, therefore providing a more realistic representation of the canopy in JULES.

JULES originally represented only five PFTs: broadleaf trees, needle-leaf trees, C_3 and C_4 grasses, and shrubs. Harper *et al*. (2016) improved the PFT parameterisation by separating trees and shrubs into deciduous and evergreen to more appropriately represent the range of leaf life spans and metabolic capacities that exist in nature and a further distinction was made

between tropical and temperate broadleaf evergreen trees. This resulted in a new set of nine PFTs: tropical broadleaf evergreen trees (BET-Tr), temperate broadleaf evergreen trees (BET-Te), broadleaf deciduous trees (BDT), needle-leaf evergreen trees (NET), needle-leaf deciduous trees (NDT), C_3 grass, C_4 grass, evergreen shrubs (ESh), and deciduous shrubs (DSh). The authors also used information from the TRY plant trait database (Kattge *et al*., 2011) to update the relationship between leaf nitrogen and V_{cmax} and leaf turnover and growth rates. These modifications were found to improve the simulation of GPP and Net Primary Productivity (NPP) for almost all biomes when compared to eddy covariance data and NPP estimates from MODIS-based measurements (MODerate-resolution Imaging Spectroradiometer satellite), ultimately increasing the realism of JULES and confidence in the simulation of vegetation dynamics and carbon exchange and storage.

A long history of earth science research has focused on constraining rates of photosynthesis (Hollinger *et al*., 1994; Jones, 1998), resulting in a previous lack of data to constrain estimates of respiration (Gifford, 2003; Kruse and Adams, 2008). Atkin *et al*. (2015) recently compiled the most comprehensive global dataset for leaf respiration (GlobResp) from previously unpublished data, recent publications, field campaigns and the TRY plant trait database (Kattge *et al*., 2011). GlobResp combines measurements of upper canopy leaf respiration derived from dark-adapted leaves during the daytime, parametrised at a reference leaf-level temperature of 25°C. GlobResp comprises data for 899 species from one hundred sites, from 43°S in the tropics to 69°N in the arctic, extending from sea level to an elevation of 4350m above sea level. The database represents a wide range of biomes and a majority of the PFTs categorised in JULES, providing a new framework for improving the representation of respiration in JULES and other Terrestrial Biosphere Models (TBMs) and associated land surface components of ESMs.

The Q_{10} of plant respiration is commonly modelled using a constant value of 2, however Q_{10} has been reported to decline predictably with increasing temperature across biomes and diverse plant taxa (Lambers *et al*., 2008). This declining Q_{10} indicates that the temperature-sensitivity of respiration is reduced with increasing measurement temperature, implying that Q_{10} itself is temperature-dependent (Tjoelker *et al*., 2001). The predominant factor responsible for the temperature-dependence of Q_{10} is the effect of measurement temperature on the control exerted by enzyme capacity on respiratory processes (Atkin *et al*., 2002). A

synthesis of published data corroborates the finding, providing ample evidence that Q_{10} typically declines with increasing measurement temperature regardless of thermal environment or species (Wager, 1941; James, 1953; Ivanova *et al*., 1989; Gillooly *et al*., 2001; Bruhn *et al.,* 2002; Covey-Crump *et al*. 2002; Atkin and Tjoelker, 2003). The potential existence of a temperature-dependent Q_{10} renders models using a constant Q_{10} of 2 as biased, in theory leading to the over-prediction of respiration with warming at high temperatures and the under-prediction of increases in respiration with warming at low temperatures (Tjoelker *et al*., 2001). This challenges the widespread use of a constant Q_{10} and calls into question the accuracy of current global estimates and predictions of terrestrial carbon balance, prompting Tjoelker *et al*. (2001) to propose a temperature-corrected Q_{10} for modelling purposes. Using data for 56 species from 23 studies, the authors found the mean temperature-dependence of Q_{10} could be adequately described by a simple, empirically-derived linear function (R^2 = 0.45, $p<0.0001$):

$$\text{Temperature dependent } Q_{10} = 3.22 - 0.046T \qquad (4)$$

Additional modelling studies are required to accurately determine the impact of incorporating a temperature-dependent Q_{10} such as this (Eq. 4) into the land-surface component of ESMs in direct replacement of the fixed Q_{10} currently used to describe the short-term temperature response of leaf respiration.

In an attempt to address the shortcomings of a fixed Q_{10} function, Heskel *et al*. (2016) developed a new model for the temperature response of leaf respiration by evaluating a novel and comprehensive set of 673 high-resolution short-term temperature response curves derived in the daytime from the dark-adapted leaves of 231 species across 18 sites. The authors found a second-order log-polynomial model best characterised the global temperature response of respiration, enabling the authors to develop a novel formulation to predict values of leaf respiration (R_T) at a desired temperature (T):

$$R_T = R_{Tref} \times e^{\left[0.1012\left(T - T_{ref}\right) - 0.0005\left(T^2 - T_{ref}^2\right)\right]} \qquad (5)$$

The new model for respiration (Eq. 5) shows the temperature-sensitivity of leaf respiration to decrease with increasing temperature, in accordance with the findings of Tjoelker *et al*.

(2001). When implemented in JULES for a variety of geographic regions, the new formulation significantly reduced annual rates of leaf respiration in temperate, boreal, arctic and alpine cold climate ecosystems when compared to the commonly applied constant Q_{10} function, generating a 28% decrease in respiration at Toolik Lake, Alaska, and a 10-20% decrease at other temperate sites, with little impact on calculated rates of respiration for tropical forests (Heskel *et al*., 2016). The authors argue application of this new function will have important consequences for predicted rates of carbon exchange and storage and future atmospheric CO_2 concentration.

The potential acclimation of plant respiration to sustained changes in prevailing ambient growth temperature also challenges the fixed and exponential characteristics of the standard Q_{10} function. Studies have demonstrated that the initial response of plant respiration to a change in temperature is largely transient due to the ability of plants to acclimate metabolic rates and Q_{10} to the prevailing ambient temperature (Atkin *et al*., 2005b; King *et al*., 2006). Respiratory thermal acclimation is defined as the subsequent adjustment in respiratory rate to compensate for a sustained change in temperature, decreasing upon acclimation to a warmer climate and increasing upon acclimation to a colder climate (Atkin *et al*., 2000b), thereby reducing the long-term temperature-sensitivity of respiration to changes in thermal environment (Lambers *et al*., 2008). The plant thermal acclimation mechanism has been established in many species (Billings *et al*., 1971; Larigauderie and Korner, 1995; Collier, 1996; Fitter *et al*., 1998; Tjoelker *et al*., 1999a; 1999b; Atkin *et al*., 2000b; 2000c; Slot *et al*., 2014; Vanderwel *et al*., 2015), found to occur over a period of up to ten days following ambient temperature change (Atkin *et al*., 2000c; Covey-Crump *et al*., 2002; Campbell *et al*., 2007). Thermal acclimation results in a tendency towards respiratory homeostasis, such that cold-acclimated and warm-acclimated plants exhibit similar rates of respiration when measured at their respective growth temperatures (Lambers *et al*., 2008). However, many published results of the acclimation of plant respiration to long-term changes in temperature are contradictory (Griffin *et al*., 2002; Loveys *et al*., 2003; Zha *et al*., 2003), and the nature of acclimation remains a contentious issue. Bruhn *et al*. (2007) hypothesise that one source of apparent contradiction arises from the way that temperature response functions of respiration are typically expressed. Additionally, the response of respiration to long-term temperature change is commonly examined independent of mechanistic context, failing to consider the impact of temperature change on other confounding factors such as substrate supply and product demand (Bruhn *et al*., 2007). Despite these apparent contradictions, the potential

acclimation of respiration to elevated temperature would have major implications for predictions of plant respiration in a future warmer world; reduced temperature sensitivity could play an important role in weakening the magnitude of positive feedback between climate and the carbon cycle. When accounting for thermal acclimation, King *et al*. (2006) found simulated rates of leaf respiration at the end of the 21st century to be significantly reduced with more carbon stored in plants and soils, corresponding to a reduction in the amount of carbon released into the atmosphere and a subsequent weakening of the positive climate-carbon cycle feedback, ultimately resulting in a weaker amplification of additional warming. The authors determined the influence of including leaf respiratory thermal acclimation to be significant, concluding that the mechanism should be permanently incorporated into vegetation and earth system models.

1.5.5. Simulations Incorporating Most Recent Advances in Plant Respiration

Huntingford *et al*. (2017) incorporated the modelling advances previously discussed in *1.5.4.* to assess how these developments revise estimates of leaf and plant respiration for a number of temperate and tropical forests using JULES. First, the authors used GlobResp, the most comprehensive dataset for leaf respiration (Atkin *et al.,* 2015), to derive a new parametrisation for leaf respiration at 25°C (R_{d25}) that scales linearly with leaf nitrogen content in a PFT-dependent manner. Second, the authors implemented the temperature sensitivity function developed by Heskel *et al*. (2016) to account for the temperature sensitivity of respiration that declines with increasing temperature. Finally, using GlobResp, Huntingford *et al*. (2017) determined a linear temperature-dependent perturbation of R_{d25} to be the most robust procedure to account for the long-term thermal acclimation of leaf respiration in the new description of respiration in JULES, with values of b=0.1012 °C^{-1} and c=-0.0005 °C^{-2}:

$$R_{d25} = [r_o + r_1 n_{1,a}\, r_2 - r_2 T_G] \times e^{[b(T_1-25)+c(T_1^2-25^2)]} \quad (6)$$

Huntingford *et al*. (2017) employed the new R_{d25}, temperature sensitivity function and thermal acclimation response in JULES using a stepwise approach to investigate how each of these new components of the function uniquely influenced simulations of respiration at leaf, whole plant and canopy scales under pre-industrial climate forcings (280ppm). First,

assimilating the new R_{d25} with JULES caused the model to yield plant respiration rates considerably larger than current estimates across all geographical regions. The increase in respiration was most significant in the tropics where rates of respiration in the Amazon, central Africa and Indo-Pacific increased by 800-1000 gC m^{-2} yr^{-1}. This increase is equivalent to the size of tropical forest NPP under present conditions with ramifications for parameterisations at canopy and plant scales. The new R_{d25} also increased rates of respiration across Europe and northern mid-latitudes by 150-350 gC m^{-2} yr^{-1}. Inclusion of a temperature sensitivity function further enhanced plant respiration in the Amazon by up to 10 gC m^{-2} yr^{-2}, however supressed rates of respiration by 10-60 gC m^{-2} yr^{-1} in mid-latitudes. Introduction of a thermal acclimation response generally increased rates of plant respiration across mid latitudes by up to 50-120 gC m^{-2} yr^{-1} in Europe and eastern USA, whereas acclimation to higher temperatures in the tropics lowered rates of respiration by up to 100 gC m^{-2} yr^{-1} in the Amazon, central Africa and Indo-Pacific region. The novel R_{d25} derived from the GlobResp database significantly increased respiration unanimously across the globe, both with and without the inclusion of the temperature sensitivity function and thermal acclimation, resulting in large reductions in simulated NPP that were found to be considerably lower than NPP estimates from MODIS-based measurements across the eight biomes used in the study. Furthermore, the authors employed the JULES big leaf approach to scale respiration from leaf to canopy level. As outlined previously, the big leaf approach can induce significant error when averaging gradients of light and photosynthetic capacity (Lambers *et al.,* 2008) and employment of the superior multi-layer scaling approach is preferential, providing a more accurate representation of the canopy (Mercado *et al*., 2007; 2009b). When the new processes from Huntingford *et al*. (2017) were tested using the multi-layer scaling approach, they revealed even greater rates of whole plant respiration than the big leaf approach which in some instances exceeded simulated GPP (Mercado, L 2018, pers. comm., 12 March). This result stemmed from higher canopy nitrogen represented in the multi-layer approach and the linear scaling between leaf and whole plant respiration in JULES. In summary, JULES significantly overestimates plant respiration when assimilating the most extensive dataset for leaf respiration (Huntingford *et al*., 2017) and employing a state-of-the-art multi-layer scaling approach, despite the inclusion of a dynamic temperature sensitivity function and thermal acclimation response, imposing a negative and unrealistic impact on modelled NPP.

The evaluation of model performance against field observation data is central to the successful development and validation of climate and carbon cycle projections. The global eddy covariance network, FLUXNET, is arguably one of the most comprehensive terrestrial ecosystem datasets presently available (Baldocchi *et al*., 2001). Blyth *et al*. (2011) designed a set of benchmark tests to quantify the performance of JULES without the aforementioned advances and assess the ability of the model to reproduce observed fluxes of CO_2 and water at ten FLUXNET sites covering the major global biomes. The metric chosen to evaluate model performance against the benchmark data was RMSE (Root Mean Square Errors) of the mean monthly fluxes of CO_2. Blyth *et al*. (2011) found JULES to overestimate respiration for all wetlands and tropical and temperate forests by 1.6μmol m^{-2} (RMSE). FLUXNET measurements are derived at ecosystem level, therefore it is impossible to clearly distinguish between autotrophic and heterotrophic sources and differentiate the individual roles of plant and soil respiration in these overestimates. However, considering the major contribution of plants to overall ecosystem CO_2 efflux (Xu *et al*., 2001), the description of plant respiration in JULES may be partly responsible.

The comprehensive modelling study by Huntingford *et al*. (2017) reveals the inadequacies that continue to persist in the modelling of plant respiration despite a number of pivotal advances, further evident in the results of model validation conducted by Blyth *et al.* (2011). It has been acknowledged that failure to appropriately account for variability in the rate of respiration and Q_{10} values is likely to result in the overestimation of respiratory CO_2 release (Atkin *et al*., 2000b; Wythers *et al*., 2005), such as that exhibited by both Huntingford *et al.* (2017) and Blyth *et al*. (2011). The GlobResp database compiled by Atkin *et al*. (2015), the dataset employed by Heskel *et al*. (2016) to develop a new model for respiration, and the dataset used by Tjoelker *et al*. (2001) to develop a temperature-dependent Q_{10} are all comprised of measurements acquired from dark-adapted leaves during the daytime that may not appropriately characterise leaf respiration at night. The datasets do not specify when measurements were obtained during the diurnal cycle, thereby failing to recognise the potential significance of temporal variation in endogenous metabolic status over the 24-hour period and the influence this may exert on the apparent temperature sensitivity and base rate of respiration. The extent to which daytime measurements of dark respiration differ from fluxes measured at night and the impact this may have on modelled rates of respiration is currently undetermined (Atkin *et al*., 2015). Thus, there remains the need to quantify

variability in rates of nocturnal respiration to better understand leaf carbon metabolism and develop a more realistic description of plant respiration in models that will ultimately provide more accurate and reliable projections of climate and carbon cycling.

1.6. Project Rationale

It is increasingly recognised that the description of leaf respiration in models by a fixed exponential temperature function is inadequate, resulting in substantial uncertainty in projections of climate and carbon cycling (Huntingford *et al*., 2013; Smith and Dukes, 2013). Furthermore, no extensive measurement of nocturnal leaf respiratory flux presently exists (O'Leary *et al*., 2017), therefore the current parametrisation of leaf respiration in models is founded entirely upon measurements collected during the day, despite evidence that leaf respiratory metabolism differs significantly between the day and night (Kromer *et al*., 1995). This study aims to compile a comprehensive dataset of nocturnal leaf respiration in field settings in combination with data derived from the existing literature that accounts for the temperature-independent control of leaf respiratory metabolism by endogenous mechanisms which may cause the down-regulation of leaf respiration at night (Doughty *et al*., 2006; Bruhn *et al*., 2008). This novel dataset will be used to develop a new model of leaf respiration that describes the temporal variation of respiration in response to both temperature fluctuations and nocturnal variation in endogenous metabolic status, moving beyond the modelling of respiration according to temperature control alone. The new model for leaf respiration, which better accounts for nocturnal variation in respiratory CO_2 release, may offer an improvement to the modelling of plant and terrestrial ecosystem respiration that is currently overestimated (Blyth *et al*., 2011; Huntingford *et al*., 2017) and has been identified as a major source of uncertainty in constraining and modelling the global carbon cycle (Atkin *et al*., 2014).

1.6.1. Hypotheses

The following hypotheses will be addressed in this investigation:

1. Decline in the rate of leaf respiration at night is a result of both temperature and non-temperature controls.

2. The non-temperature dependency of nocturnal leaf respiration can be quantified using measurements of leaf gas exchange under constant temperature conditions, allowing for a mathematical formulation to be derived and applied to vegetation and earth system models.
3. Implementation of the new non-temperature dependent term for leaf respiration at temperate and tropical forest sites will reduce the simulation of plant respiration and increase NPP.

1.6.2. Aims and Objectives

To address the hypotheses of this study, the following aims and objectives will be met:

- Collect nocturnal leaf respiration measurements under constant temperature conditions in the field and from existing publications to quantify the temperature-independent contribution to the decline in leaf respiration at night.
- Based on the collected dataset, derive an equation describing the temperature-independent component of nocturnal respiration.
- Develop a new function for leaf respiration that includes a temperature-dependent and non-temperature dependent term that can be incorporated into vegetation and earth system models.
- Evaluate the novel leaf respiration formulation using leaf level measurements of nocturnal respiration under ambient conditions.
- Implement the novel formulation for leaf and plant respiration into the JULES land-surface model to improve the simulation of respiration for tropical and temperate forests.
- Apply the new model at existing FLUXNET sites from different biomes and evaluate performance of the novel plant respiration formulation.

2. Methodology

2.1. Field Techniques

2.1.1. Gas Exchange Analyser

Photosynthesis and respiration both result in the exchange of CO_2 and oxygen (O_2); the net rate at which these gases are produced and consumed forms the basis of most methods for measuring the two processes (Hunt, 2002). In this study, leaf respiratory gas exchange is measured in the dark as the rate of CO_2 release in the absence of photorespiration using a portable LI-COR 6400XT infra-red gas analyser (IRGA; LI-COR, Lincoln, Nebraska, USA). IRGAs are commonly used to measure rates of plant respiratory CO_2 efflux due to the infra-red absorption properties of CO_2 and other hetero-atomic molecules such as water (H_2O; Scafaro *et al.*, 2017). The rate of leaf respiration is measured in an enclosed cuvette that uses IRGAs to determine differences in the CO_2 and H_2O concentration of an air stream as it flows through the leaf chamber between incoming reference and outgoing sample cells (Figure 2.1; Atkin *et al.*, 2005a). The high sensitivity of the IRGAs enables even minor changes in concentration to be detected. The simultaneous measurement of CO_2 exchange, temperature, pressure and humidity enables changes in leaf dynamics to be measured in real time and instantaneous measurements of leaf respiration to be obtained. The open system also allows for the independent regulation of environmental conditions within the chamber, enabling temperature, light, humidity and CO_2 concentration to be controlled at the leaf surface.

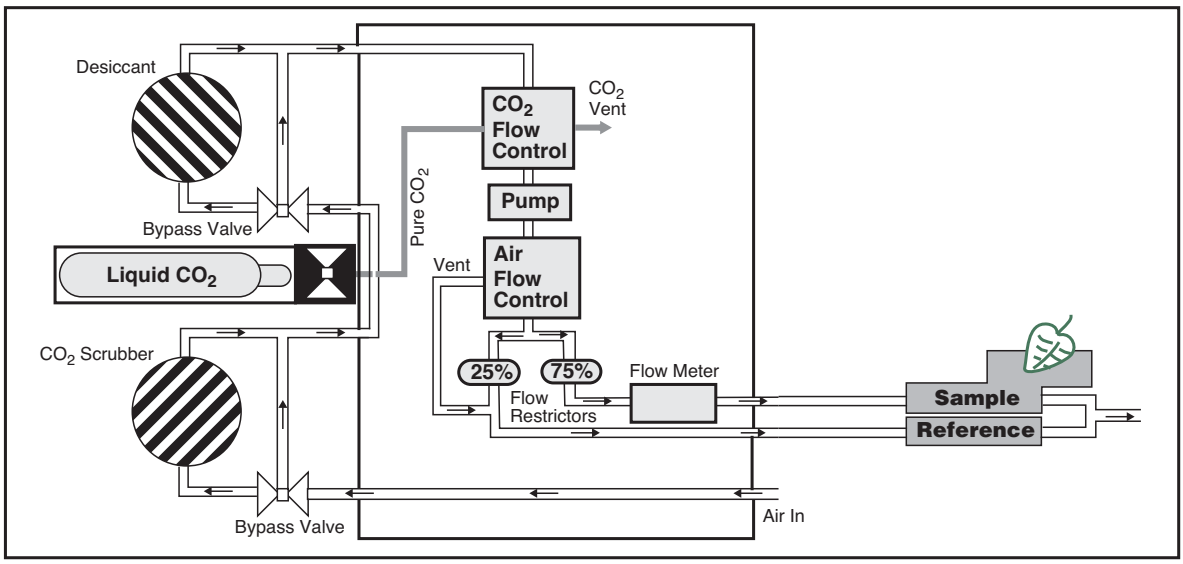


Figure 2.1. Flow schematic of the LI-6400XT Portable Photosynthesis System with CO_2 mixer, taken from LI-COR (2011).

2.1.2. Experimental Setup and Conditions

A number of prerequisites were set for data collection to approximately match the leaf chamber environment to ambient atmospheric conditions. Chemical tubes of soda lime and drierite are used to remove CO_2 and H_2O from the air stream, facilitating the control of chamber CO_2 concentration and humidity respectively. The drierite desiccant was set to maintain a relative humidity of ~65% and allow the rapid, automatic control of chamber humidity under fluctuating rates of transpiration. Ambient atmospheric CO_2 concentrations (~410ppm) were emulated in the cuvette through the use of the CO_2 mixer. The soda lime desiccant was set to remove all CO_2 from the incoming air stream that was subsequently injected with the desired reference CO_2 concentration of 410µml mol^{-1} from the controlled flow of CO_2 from a canister. Flow rate was set to 300µmol s^{-1} to control the speed of the air stream through the cuvette, helping regulate and maintain constant environmental conditions in the chamber. Since respiratory CO_2 efflux rates can be small, a low flow rate such as this is necessary to detect minor yet significant changes in gas concentration and respiratory CO_2 release. Finally, assuming the leaves are hypostomatous, with stomata only on the abaxial surface, the stomata ratio was set to 0. Maintaining these constant environmental conditions within the chamber helped isolate the effects of temperature and endogenous controls on the rate of nocturnal leaf respiration.

Care must be taken during experimental setup to minimise any gas leaks that may occur where the chamber gaskets contact the plant tissues (Bruhn *et al.*, 2002), therefore the neoprene gaskets were checked and kept in good condition and leak tests were performed prior to every measurement to ensure the leaf chamber was tightly sealed. Leaks were detected by exhaling near the chamber gaskets and checking for fluctuations in the outgoing sample CO_2 concentration; increases greater than 1-2mmol mol^{-1} are indicative of a leak.

2.1.3. Measurements to Determine Q_{10}

Field measurements were collected for eight deciduous broadleaf species (Table 2.1) at the University of Exeter campus, UK, to further investigate nocturnal variation in respiration rate. A set of leaf respiration measurements were taken from dark-adapted leaves under ambient temperature conditions after sunset, approximately between 21:30LT and 23:00LT during the summer. Mature, attached leaves positioned in the sunlight throughout the day

were chosen for the investigation and covered in foil for at least 30 minutes prior to measurements to dark-adapt the leaves and account for Light-Enhanced Dark Respiration (LEDR). LEDR is the enhancement of the respiratory CO_2 flux after transferring a light-acclimated leaf to darkness (Azcón-Bieto and Osmond, 1983), occurring naturally in the field during day-night transitions (Barbour *et al*., 2011). Data was logged for 3 minutes at 15 second intervals. A second set of leaf respiration measurements were obtained from the same leaf following artificial manipulation of block temperature within the chamber, lowering the temperature by ~5°C. Since relative humidity increases with decreasing temperature, the drierite desiccant was used to maintain relative humidity levels within 10% of previous measurements at ambient temperature. These two sets of measurements illustrate the instantaneous response of leaf respiration to short-term artificial temperature manipulations. This method is commonly employed to calculate Q_{10} values (Eq. 1) that describe the intrinsic temperature sensitivity of respiration over the timescale of minutes; for the purpose of this study, these Q_{10} values will be termed 'inherent Q_{10}' (Q_{10inh}). A further set of measurements were collected under ambient temperature conditions before the following sunrise, approximately between 3:30LT and 05:00LT. These measurements form the basis of an 'apparent Q_{10}' (Q_{10app}) that describes variation in nocturnal respiratory metabolism owing to both temperature control and temporal variation in endogenous metabolic status. The observed values of leaf respiration under ambient temperature conditions at the start and end of the night also provide a framework for model evaluation.

Unpublished data to calculate and examine Q_{10inh} and Q_{10app} has also been provided for this study by co-supervisor Dan Bruhn (Aalborg University, Denmark) for two species, *Solanum lycopersicum* and *Musa acuminata*, measured in a growth cabinet. Published field data for *Eucalyptus pauciflora* and *Pringlea antiscorbutica* from Bruhn *et al*. (2007; 2008) is also included in this analysis (Table 2.1).

Table 2.1. Species used in this study for the calculation of inherent and apparent Q_{10} values and estimation of the temperature control of nocturnal respiration.

Species	Growth Condition	Replicates	Study
Acer pseudoplatanus	Field	1	UK – this study
Betula pendula	Field	6	UK – this study
Eucalyptus pauciflora (autumn)	Field	5	Bruhn *et al*. (2007)
Eucalyptus pauciflora (spring)	Field	3	Bruhn *et al*. (2008)
Eucalyptus pauciflora (summer)	Field	3	Bruhn *et al*. (2008)
Fagus sylvatica f. purpurea	Field	1	UK – this study
Musa acuminata	Growth cabinet	5	Denmark – this study
Platinus x hispanica	Field	4	UK – this study
Pringlea antiscorbutica	Field	4	Bruhn *et al*. (2008)
Prunus padus	Field	4	UK – this study
Solanum lycopersicum	Growth cabinet	5	Denmark – this study
Tilia x europaea	Field	5	UK – this study

2.1.4. Nocturnal Variation in R_{To}

According to the current description of respiration (Eq. 2), the base rate of respiration (R_{To}) under constant temperature conditions should remain constant. To investigate this, nocturnal leaf respiration data was collected in the field under constant temperature conditions for three tropical species near Manaus in the Amazon rainforest, Brazil, and three tropical montane species near Medellin in the Colombian Andes (Table 2.2.). Block temperature within the chamber was set to mean ambient night-time temperature and maintained throughout the night. At constant temperature, measurements of nocturnal leaf respiration were logged at regular 10-minute intervals over the course of 12 hours, from sunset (18:00LT) to sunrise (06:00LT), to capture and quantify any variation in the rate of nocturnal respiration that occurs independent of temperature.

Unpublished field data has been provided for this study by Dan Bruhn (Aalborg University, Denmark) and collaborators Stephen Sitch (University of Exeter, UK) and Martijn Slot (Smithsonian Tropical Research Institute, Panama) to add to the existing dataset of nocturnal leaf respiration in field settings. Field measurements of nocturnal leaf respiration under constant temperature conditions, following the protocol outlined previously, were collected

for the temperate species *Hedera helix* and *Forsythia* by Dan Bruhn, Denmark, and Stephen Sitch, UK, respectively. Following a similar procedure, data collected by Martijn Slot for five tropical species in Panama and Florida are also used in this study (Table 2.2.). Martijn Slot's measurements of leaf respiration were derived at constant temperature throughout the night at 1.5-minute intervals under ambient CO_2 conditions. The leaves were not pre-darkened prior to data collection, therefore the first hour of measurements were removed to eliminate any variation in the rate of respiration caused by LEDR from the analysis.

Secondary data collected under constant temperature conditions using similar protocols have also been derived from the published literature with the help of Dan Bruhn, providing nocturnal leaf respiration data for a total of 75 leaves from 19 different temperate and tropical species (Table 2.2.). Leaves were dark-adapted for ~30 minutes prior to data collection in a majority of these studies and was accounted for in the remaining studies by starting data extraction ~30 minutes into the plot of the original paper. These additional studies present data for diverse species from contrasting biomes under a range of temperatures in both field and laboratory environments, helping elucidate whether a trend in the rate of nocturnal respiration exists across PFTs and experimental conditions.

Table 2.2. Data used in this to study to examine nocturnal leaf respiration under constant temperature conditions.

Species	Location	Experimental Conditions	Temperature (ºC)	PAR (μmol m^{-2} s^{-1})	Biome	Replicates	Reference
Alocasia macrorrhiza		Lab	25	320, 160, 40	Tropical	3	Noguchi *et al*. (1996)
Alocasia odora		Lab	20	400 330	Tropical	1 1	Noguchi & Terashima (1997) Noguchi *et al*. (2001)
Amaranthus hypochondriacus		Lab	20, 25, 30, 35	1000	Tropical	6	Bunce (2007)
Arabidopsis thaliana		Lab	17 20 23	150 100 115	Temperate	2 2 2	O'Leary *et al*. (2017) Trethewey & ap Rees (1994) Watanabe *et al*. (2014)
Astronium graveolens	Gamboa, Panama	Field	25		Tropical	3	Slot (unpublished)
Beta vulgaris		Lab		350	Temperate	1	Fondy & Geiger (1982)
Bistorta bistortoides	Colorado, USA	Field	5, 15	106-1120	Temperate	16	McCutchan & Monson (2001)
Campanula rotundifolia	Colorado, USA	Field	5, 15	314-1449	Temperate	8	McCutchan & Monson (2001)
Castilla elastica	Gamboa, Panama	Field	25		Tropical	4	Slot (unpublished)
Cecropia longipes	Gamboa, Panama	Field	25		Tropical	6	Slot (unpublished)
Chrysophyllum cainito	Gamboa, Panama	Field	25		Tropical	9	Slot (unpublished)
Eucalyptus camaldulensis		Lab	21.5	800	Temperate	1	Scafaro *et al*. (2017)
Flaveria linearis		Lab	25	200	Tropical	1	Leonardos *et al*. (2006)
Forsythia	London, UK	Field	16-19		Temperate	6	Sitch (unpublished)
Glycine max		Lab	20, 25, 30, 35	1000	Tropical	6	Bunce (2007)
Gossypium		Lab	19	500	Temperate	1	Gessler *et al*. (2017)
Halimium halimifolium		Lab	15	400	Temperate	1	Lehmann *et al*. (2016)

Hedera helix	Denmark	Field	18, 20		Temperate	2	Bruhn (unpublished)
Heliconia	Manaus, Brazil	Field	24		Tropical	3	Newman (unpublished)
Hordeum distichum		Lab	18	720	Temperate	1	Farrar & Farrar (1985)
Hordeum vulgare		Lab	20	530	Temperate	1	Baysdorfer *et al*. (1987)
Inga villosissima	Antioquia, Colombia	Field	18, 22, 23		Tropical	8	Newman (unpublished)
Luehea seemannii	Gamboa, Panama Florida, USA	Field	25		Tropical	5 9	Slot (unpublished)
Miconia	Manaus, Brazil	Field	25		Tropical	2	Newman (unpublished)
Musa	Manaus, Brazil	Field	25		Tropical	5	Newman (unpublished)
Oryza sativa		Lab	30	600	Temperate	1	Giuliani *et al*. (2019)
Phaseolus vulgaris		Lab	19 20	500 330	Temperate	1 1	Gessler *et al*. (2017) Noguchi *et al*. (2001)
Pisum sativum		Lab	21	650	Temperate	1	Azcon-Bieto *et al*. (1983)
Quercus humboldtii	Antioquia, Colombia	Field	18, 22		Tropical	3	Newman (unpublished)
Spinacia oleracea		Lab	21 25 20	650 500, 320, 160 400	Temperate	1 3 1	Azcon-Bieto *et al*. (1983) Noguchi *et al*. (1996) Noguchi & Terashima (1997)
Tabebuia rosea	Antioquia, Colombia	Field	23		Tropical	1	Newman (unpublished)
Triticum aestivum		Lab	21 21.5 25 13.5, 20, 24, 27, 30	650 800 190, 470 550	Temperate	1 1 4 5	Azcon-Bieto *et al*. (1983) Scafaro et al. (2017) Averill & ap Rees (1995) Azcon-Bieto & Osmond (1983)
Unidentified	Manaus, Brazil	Field	25		Tropical	1	Newman (unpublished)

2.2. Data Analysis

2.2.1. The Q_{10} Approach

The Q_{10} approach (Eq.1) was employed to calculate inherent and apparent Q_{10} values of leaf respiration. Statistical analyses to test for a significant difference between the two groups of Q_{10inh} and Q_{10app} values were completed in IBM SPSS 25 using $p<0.05$ as the critical threshold for statistical significance. The Shapiro-Wilk test for normality determined the Q_{10inh} ($p=0.52$) and Q_{10app} ($p=0.24$) datasets to be normally distributed, allowing for a paired samples t-test to be performed to test for a statistically significant difference between groups.

2.2.2. Temperature Control of Respiration

The temperature control of nocturnal respiration is estimated using the following equation (Bruhn, D 2017, pers. comm., 13 June):

$$\mathrm{TC} = \alpha/(\alpha + \beta) \qquad (7)$$

Here, α represents the decline in leaf respiration in response to artificial temperature change alone, whereas β describes additional variation in the rate of nocturnal respiration owing to rhythms in leaf metabolism that may result in a further decrease in the rate of respiration at night, demonstrated in Figure 2.2. Data collected in Exeter was used to calculate Q_{10inh} and Q_{10app}. The decrease in respiration achieved by artificially manipulating temperature constitutes α, and β represents the further decline in respiration at the same temperature due to natural cooling during the night. Application of α and β values to Eq. (7) estimates the relative temperature control of nocturnal respiration versus the control of nocturnal respiration by temperature-independent factors.

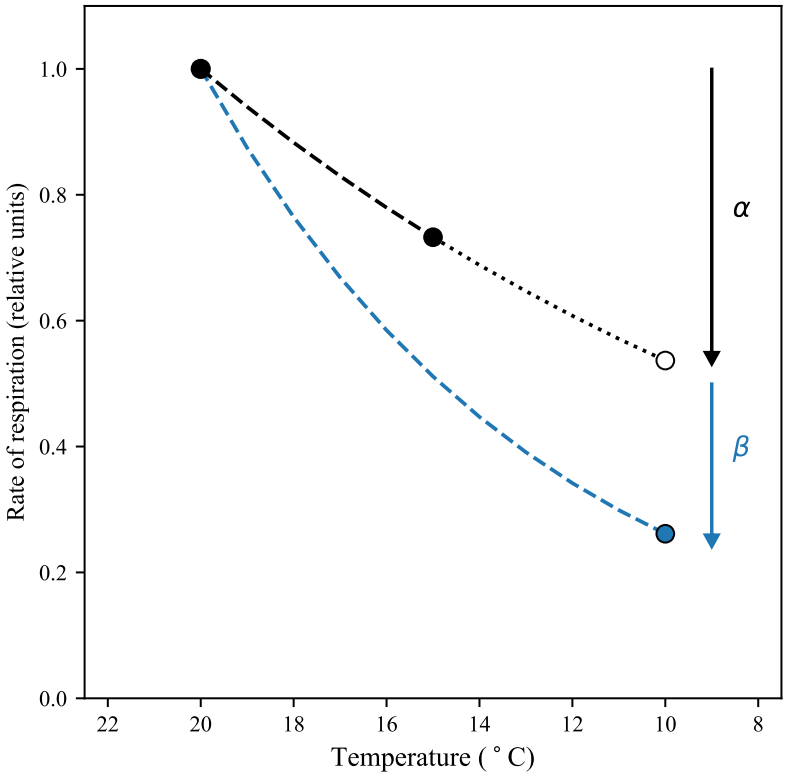


Figure 2.2. Conceptual illustration of the different temperature responses of respiration, where α represents the decline in leaf respiration in response to rapid artificial temperature manipulation, and β represents additional variation in the rate of nocturnal respiration owing to its non-temperature dependency.

2.3. Model Development

2.3.1. Quantifying the Non-Temperature Dependency of Respiration

Assuming that leaf respiration is entirely temperature dependent, as suggested by the exponential characteristic of the Q_{10} temperature function, the data collected under constant temperature conditions should exhibit a constant rate of respiration throughout the night from sunset to sunrise. To investigate this, leaf respiration values (R_{To}) were divided by the initial rate of respiration ($R_{To\text{-}initial}$) at the start of each night. Values deviating from 1 reveal proportional changes in the rate of respiration owing to mechanisms other than temperature. Significant noise in the measurement of dark respiration is typical of data collected using gas exchange systems. This measurement noise is increased by the high frequency of measurements and absence of CO_2 control in the data collected by Martijn Slot. Therefore, hourly means of $R_{To}/R_{To\text{-}initial}$ were calculated for each leaf replicate to remove measurement noise and reduce bias due to the measurement of some species at more frequent intervals

throughout the night. For species with multiple leaf replicates, these hourly means of $R_{To}/R_{To\text{-}initial}$ were then combined to create hourly averages of $R_{To}/R_{To\text{-}initial}$ at species level. For each species, these values were plotted as a function of time using Python to demonstrate how $R_{To}/R_{To\text{-}initial}$ decreases with time since the onset of darkness, from sunset until sunrise.

2.3.2. Functions and Statistical Analyses

To model the relationship between $R_{To}/R_{To\text{-}initial}$ and hours in darkness, plots of $R_{To}/R_{To\text{-}initial}$ against time were fitted with various functions to determine which model best described the data. Power and exponential functions were fitted and a linear function was fitted following a natural log transformation to normalise the distribution of the data, often valuable for making patterns in the data more interpretable. The hourly means calculated for respiration enabled the various functions to be fitted more effectively to a simplified trend. Regression analysis was employed as a statistical method to assess the fit of the different models to the data. The coefficient of determination (R^2) was used as a statistical measure to determine the goodness of fit of the data to the regression line, representing the percentage of the variability in the data able to be explained by the model. To further determine which type of function best fit the data, Mean Squared Error (MSE) was calculated to measure the average squared difference between the values estimated by the model and the actual observed values. This analysis of the field data was undertaken at both individual leaf and species level, whereas the data extracted from the literature was only analysed at species level due to a smaller number of replicates and data points. Datasets were also combined to determine which function best described the decline in nocturnal respiration for species in tropical biomes, temperate biomes, field settings and controlled laboratory environments. Following these statistical analyses, the model with the highest R^2 and lowest MSE values across replicates (Appendix B), species (Appendix C), biomes and experimental conditions (Appendix D) was selected as the most suitable function and fitted across all of the data.

One-way ANOVA was carried out to determine whether one function could be fitted to the entire dataset to derive a single equation for modelling. For each replicate, a natural log transformation was applied to $R_{To}/R_{To\text{-}initial}$ and plotted as a function of time. Linear functions forced to pass through the origin were fitted to the data and regression analysis was employed to derive slope values. Comparison of slopes between species, plant type, biomes, and

experimental conditions using one-way ANOVA tested for a statistically significant difference between groups to determine whether one equation was adequate for modelling.

2.3.3. Novel Model Formulation

Ultimately, all measurements of nocturnal leaf respiration under constant temperature conditions (n=141, 33 species) were collated into a single plot and fitted with the chosen function. Regression analysis of the final plot and fitted model was employed to derive a universal equation that predicts respiration at any time of night as a fraction of the initial respiration rate as a function of time in darkness. This represents the non-temperature dependent component of leaf respiration at night. The resulting equation from regression analysis that couples respiration to time of night was combined with the Q_{10} temperature function (Eq. 2) currently used in many TBMs and ESMs, resulting in a new formulation to calculate leaf and plant respiration at night. The new equation includes both a non-temperature dependent and temperature-dependent term, thereby accounting for nocturnal variation in endogenous metabolism in addition to the temperature dependency of respiration. Implementation of this novel formulation in JULES to simulate plant respiration will reveal the impact of accounting for the non-temperature dependency of nocturnal respiration.

The novel formulation was also used to investigate variation in nocturnal respiration in response to temperature decrease during the night, both including and excluding the effect of temperature-independent controls. First, standard respiration was modelled according to Eq. (2) with a constant R_{To} of 2.5 and a standard Q_{10} of 2. Second, a rearrangement of the novel equation acquired in this study, that predicts $R_{To}/R_{To\text{-}initial}$ as a function of time throughout the night, produces an equation to calculate R_{To} values that decrease with time in darkness, representing endogenous rhythms in leaf metabolism. Respiration was predicted using each of these formulations in response to two different speeds of cooling, 0.5°C/h and 1.25°C/h. The area beneath each of the four curves was calculated using integration and used to determine the cumulative difference in nocturnal respiration due to the inclusion of non-temperature controls over the eight-hour period for each speed of cooling.

2.4. Modelling

2.4.1. Model Setup

JULES version 5.2 was used to assess the impact of the new model on simulations of plant respiration and NPP. The current description of the temperature response of leaf dark respiration (R_{d25}) in JULES uses the Q_{10} function (Eq. 2) with a value of 2, modified by suppression at high and low temperatures from the temperature response of V_{cmax} as presented in Table 2.3. (Clark *et al*., 2011); relevant parameters for the different PFTs in JULES are presented in Table 2.4. (Harper *et al*., 2016).

Table 2.3. Equations used in JULES to calculate leaf and whole plant respiration, taken from Clark *et al.* (2011).

	Description	**Equation**
$f_T(T_c)$	Q_{10} temperature dependence function	$Q_{10\_leaf}^{0.1(T_c-25)}$
V_{cmax}	Maximum rate of carboxylation of Rubisco	$\frac{V_{cmax25} f_T(T_c)}{\left[1+e^{0.3(T_c-T_{upp})}\right]\left[1+e^{0.3(T_{low}-T_c)}\right]}$
R_d	Leaf dark respiration	$f_{dr} V_{cmax}$
R_{dc}	Canopy respiration: the big leaf approach	$R_d \frac{\left[1-e^{-kL_c}\right]}{k}$
R_{di}	Canopy layer respiration	$R_d d L_c$
R_{dc}	Canopy respiration: multi-layer scaling approach	$\sum_{i=1}^{n} R_{di}$
N_l	Leaf nitrogen content	$n_m \sigma_l L_c$
N_r	Root nitrogen content	$\mu_{rl} n_m \mathcal{R}$
N_s	Stem nitrogen content	$\mu_{sl} n_m S$
$\mathcal{L}$	Carbon content of leaves	$\sigma_l L_c$
$\mathcal{R}$	Carbon content of roots	$\mathcal{L}$
S	Carbon content of respiring stem	$\eta_{sl} h L_c$
R_{pm}	Maintenance respiration	$0.012 R_{dc}\left(\beta + \frac{N_r + N_s}{N_l}\right)$
R_{pg}	Growth respiration	$r_g(\Pi_G - R_{pm})$
R_p	Plant respiration	$R_{pm} + R_{pg}$

Table 2.4. PFT-specific parameters used in JULES to model leaf and plant respiration for tropical broadleaf evergreen trees (BET-Tr), temperate broadleaf evergreen trees (BET-Te), broadleaf deciduous trees (BDT), needle-leaf evergreen trees (NET), and needle-leaf deciduous trees (NDT), taken from Harper *et al.* (2016).

	Description	**BET-Tr**	**BET-Te**	**BDT**	**NET**	**NDT**
a_{wl}	Allometric coefficient	0.65	0.65	0.65	0.65	0.75
D_{crit}	Critical humidity deficit	0.09	0.09	0.09	0.06	0.041
d_T	Rate of change of leaf turnover with temperature	9	9	9	9	9
f_0	Stomatal conductance parameter	0.875	0.892	0.875	0.875	0.936
f_{dr}	Leaf dark respiration coefficient	0.01	0.01	0.01	0.015	0.015
i_{v}	Intercept for relationship between N_a and $Vcmax_{25}$	7.21	3.90	5.73	6.32	6.32
L_{max}	Maximum LAI	9	7	7	7	6
L_{min}	Minimum LAI	1	1	1	1	1
LMA	Leaf mass per unit area	0.1039	0.1403	0.0823	0.2263	0.1006
N_{a}	Leaf nitrogen per unit area	1.76	2.02	1.74	2.61	1.87
n_{m}	Top-leaf nitrogen concentration	0.017	0.0144	0.021	0.0115	0.0186
rootd	*e*-folding root depth	3	2	2	1.8	2
s_{v}	Slope between N_a and $Vcmax_{25}$	19.22	28.40	29.81	18.15	23.79
T_{low}	Lower temperature parameter for Vcmax	13	13	5	5	-5
T_{off}	Threshold temperature for phenology	0	-40	5	-40	5
T_{opt}	Optimal temperature Vcmax	39	39	39	33	34
T_{upp}	Upper temperature parameter for Vcmax	43	43	43	37	36
V_{cmax25}	Maximum rate of carboxylation of Rubisco at 25ºC	41.16	61.28	57.25	53.55	50.83
a	Quantum efficiency	0.08	0.06	0.08	0.08	0.10
γ_0	Minimum leaf turnover rate	0.25	0.50	0.25	0.25	0.25
γ_p	Leaf growth rate	15	15	20	15	20
μ_{rl}	Ratio of nitrogen concentrations in root and leaves	0.67	0.67	0.67	0.67	0.67
μ_{sl}	Ratio of nitrogen concentrations in stem and leaves	0.1	0.1	0.1	0.1	0.1

For the purpose of this study, the temperature response of leaf and plant respiration will be represented using the standard Q_{10} function (Eq. 2) and a value of 2, forming the standard JULES simulations in this study (S1). The equation for a temperature-dependent Q_{10} (Eq. 4) proposed by Tjoelker *et al.* (2001) was implemented into JULES and simulations were run with the temperature-dependent Q_{10} in direct replacement of the standard Q_{10} to further investigate the consequences of using a fixed versus temperature-dependent function (S2). The novel term describing the non-temperature dependency of nocturnal respiration acquired in this study was also implemented in the JULES code and run with the standard Q_{10} function to determine the impact of accounting for endogenous rhythms in nocturnal metabolism (S3). The non-temperature dependent term from this study was also combined with the temperature-dependent Q_{10}, creating an additional new formulation for respiration that incorporates both proposed model developments (S4). These different equations for respiration were implemented in JULES to simulate leaf and plant respiration and enable model comparison. The equation for respiration developed by Heskel *et al.* (2016) (Eq. 5) was excluded from this analysis due to close similarity with the standard Q_{10} function over a large range of temperatures (Figure 2.3.).

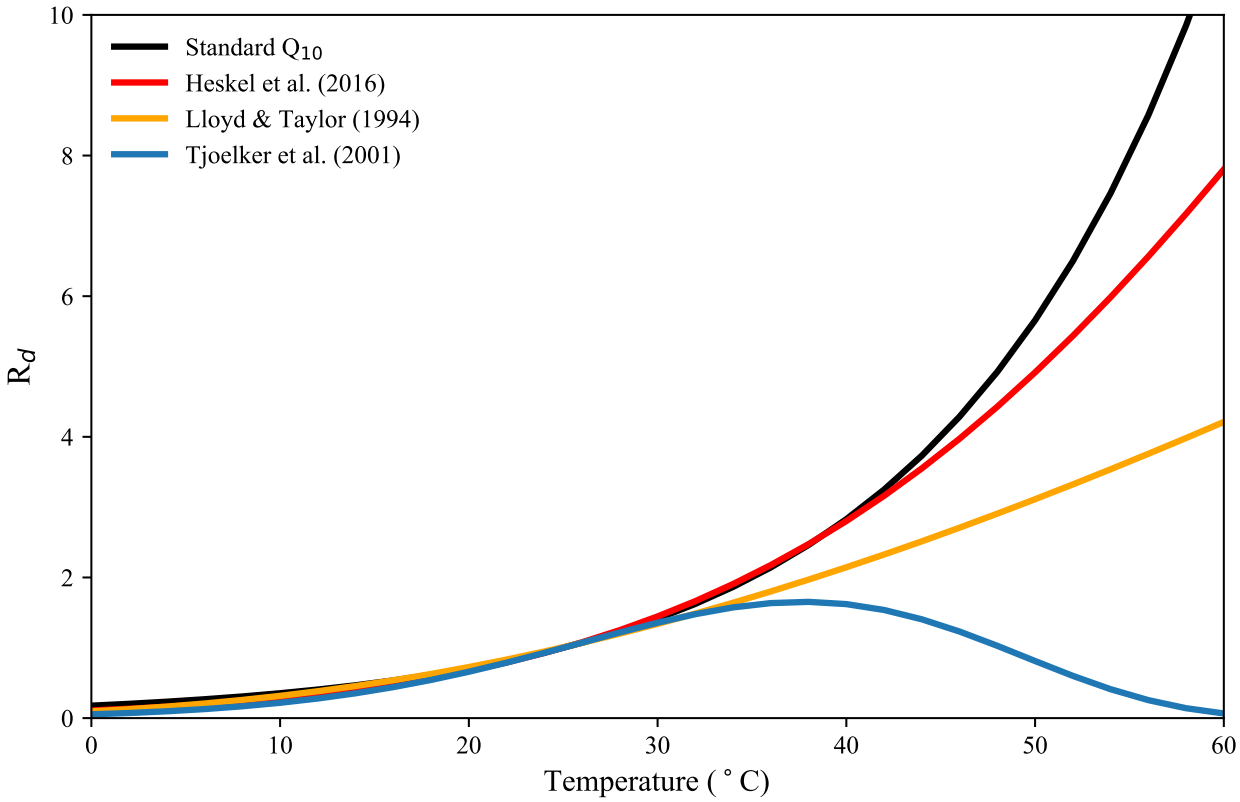


Figure 2.3. Temperature response of leaf respiration according to the standard Q_{10} temperature function, formula for respiration from Heskel *et al.* (2016), Arrhenius type equation from Lloyd and Taylor (1994) with a reference temperature of 25ºC as implemented in Lloyd *et al.* (1995), and temperature-dependent Q_{10} function from Tjoelker *et al.* (2001).

Two different methods were employed to scale leaf respiration to canopy level (R_{dc}) in JULES. The simple big-leaf approach was used to simulate an exponential decline in leaf respiration through the canopy with a light extinction coefficient (k) of 0.5 and dependency on Leaf Area Index (LAI). The more advanced multi-layer scaling approach was also employed to divide the canopy into a number of layers of equal leaf area increments (Mercado *et al*., 2007; 2009), with canopy-scale fluxes estimated as the sum of leaf-level fluxes in each layer, scaled by leaf area (Clark *et al*., 2011). This scaling method incorporates sunlit and shaded leaves in each layer, sunfleck penetration, direct and diffuse radiation, and the inhibition of leaf respiration in the light, ultimately providing a more sophisticated description of light interception. The two scaling approaches therefore produce different representations of the canopy with distinct leaf nitrogen concentrations upon which the estimated rate of leaf and plant respiration depends. Three additional components of plant respiration are those of roots, stem, and growth. Root and stem respiration are dependent on PFT-specific nitrogen concentrations and combine with canopy respiration to give overall whole-plant maintenance respiration (Clark *et al*., 2011). The original JULES description assumes growth respiration (R_{pg}) to be a fixed fraction of GPP (Π_G) minus maintenance respiration (R_{pm}), multiplied by the growth respiration coefficient (r_g) of 0.25:

$$R_{pg} = r_g(\Pi_G - R_{pm}) \qquad (8)$$

The calculation of growth respiration in JULES was modified for this study to avoid erroneous negative values of respiration at night:

$$R_{pg} = r_g \Pi_G \qquad (9)$$

Whole plant respiration (R_p) is represented as the sum of maintenance and growth respiration (Table 2.3.). Hence, changes to the description of leaf dark respiration influences all respiratory components that combine to give R_p.

2.4.2. Model Simulations

Five simulations with different descriptions of leaf respiration (Table 2.5.), outlined in *2.5.1.*, were run in JULES and the impact of a temperature-dependent Q_{10} and the non-temperature dependent term on annual rates of plant respiration and NPP were calculated as the percentage difference between simulations (Table 2.6.).

Table 2.5. Modelling protocol and description of leaf respiration used for each simulation.

Simulation	Description	Equation
S1	Standard JULES function	$R_{25}Q_{10}^{0.1(T-T_{25})}$
S2	Standard JULES function with temperature-dependent Q_{10}	$R_{25}TDQ_{10}^{0.1(T-T_{25})}$
S3	Standard JULES function with night-time temperature independent control	$R_{sunset}Q_{10}^{0.1(T-T_{sunset})} * (1 - 0.12hour^{0.46})$
S4	Standard JULES function with night-time temperature independent control and temperature-dependent Q_{10}	$R_{sunset}TDQ_{10}^{0.1(T-T_{sunset})} * (1 - 0.12hour^{0.46})$
S5	Standard JULES function with night-time temperature independent control and temperature-dependent Q_{10} at night-time only	$R_{sunset}TDQ_{10}^{0.1(T-T_{sunset})} * (1 - 0.12hour^{0.46})$

Table 2.6. Calculation of the effect of the temperature-dependent Q_{10} and non-temperature dependent term on annual rates of plant respiration and NPP.

Calculation	Effect
S1-S3	Inclusion of the non-temperature dependency of nocturnal respiration with standard Q_{10}
S2-S4	Inclusion of the non-temperature dependency of nocturnal respiration with temperature-dependent Q_{10}
S1-S5	Inclusion of the non-temperature dependency of nocturnal respiration with temperature-dependent Q_{10} at night-time only

The modelling protocol was applied using JULES at eleven existing FLUXNET eddy covariance sites (Table 2.7.) for a variety of land cover classifications and forest types (Table 2.8.). Sites in both temperate and tropical biomes were chosen to explore how varying temperatures, night lengths and speeds of cooling influence the simulation of respiration for each model. First, standard JULES was run with fixed fractional coverage with a spin-up period of ten years for a maximum of four spin-up cycles, allowing the simulated soil moisture to reach equilibrium. At each site, simulations were then run from the spin-up

output, enabling each simulation to run from the same initial conditions. This protocol was repeated using the big leaf and multi-layer scaling approaches for each simulation in Table 2.5. The Shapiro-Wilk test confirmed both datasets to be normally distributed, allowing for a parametric independent samples t-test to be performed to test for a statistically significant difference between the effects of the non-temperature dependent term on respiration and NPP for tropical and temperate forests (Table 2.6).

Table 2.7. Eddy covariance FLUXNET sites used in this study, taken from Fluxdata (2019).

Country	Site	Year	Latitude	Longitude	Mean Annual Temperature (ºC)	Mean Annual Precipitation (mm)	Elevation (m)	Forest Type
Brazil	Manaus	2003	-2.60900	-60.20910	26.7	2100	130	EBF
Brazil	Tapajos	2002	-2.85700	-54.95900	25.3	1920	130	EBF
Belgium	Vielsalm	2005	50.30496	5.99808	7.8	1062	493	MF
Canada	Saskatchewan	2005	53.62889	-106.19779	0.34	428.53	530	DBF
China	Dinghushan	2003	23.1733	112.5361	19.64	1618.1	-	EBF
Finland	Hyytiala	2005	61.84741	24.29477	3.8	709	181	ENF
France	Puechabon	2007	43.7413	3.5957	13.5	883	270	EBF
French Guiana	Guyaflux	2007	5.27877	-52.92486	25.7	3041	48	EBF
Germany	Tharandt	2003	50.96235	13.56516	8.2	843	385	ENF
Italy	Castelporziano	2014	41.70427	12.35729	15.2	805	19	EBF
USA	Harvard	2005	42.5378	-72.1715	6.62	1071	340	DBF

Table 2.8. International Geosphere-Biosphere Programme (IGBP) descriptions of land cover classifications for the eddy covariance FLUXNET sites used in this study, taken from Fluxdata (2019).

Land Cover Classification	Forest Type	Description
EBF	Evergreen broadleaf forest	Lands dominated by woody vegetation with a percent cover >60% and height exceeding 2 meters. Almost all trees and shrubs remain green year round. Canopy is never without green foliage.
ENF	Evergreen needleleaf forest	Lands dominated by woody vegetation with a percent cover >60% and height exceeding 2 meters. Almost all trees remain green all year. Canopy is never without green foliage.
DBF	Deciduous broadleaf forest	Lands dominated by woody vegetation with a percent cover >60% and height exceeding 2 meters. Consists of broadleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
MF	Mixed forest	Lands dominated by trees with a percent cover >60% and height exceeding 2 meters. Consists of tree communities with interspersed mixtures or mosaics of the other four forest types. None of the forest types exceeds 60% of the landscape.

2.4.3. Model Evaluation

Projections of the terrestrial carbon cycle and its feedback to climate change largely depend upon model output, thus it is critical to evaluate model performance against observation data and identify uncertainties in prediction to enable further model development. Terrestrial model evaluation is typically carried out with *in situ* field observations (Prentice *et al*., 2001), therefore two datasets comprising field measurements of nocturnal leaf respiration under ambient temperature conditions have been used in this study to evaluate the ability of each model presented in Table 2.5. to predict the rate of respiration throughout the night. The first dataset includes variation across six species with a different replicate for each night of measurement. The second dataset includes continuous measurements of different shoots of the same tree at a high temporal resolution.

Field measurements of leaf respiration under ambient temperature conditions were collected at sunset and sunrise for six temperate broadleaf species (n=24, 1 leaf per tree) in Exeter, outlined in *2.1.3.,* forming a framework for model evaluation. Sunset measurements of respiration and ambient temperature were applied to the formulations in Table 2.5. as the base rate of respiration at a given temperature. The rate of respiration at the end of the night was then predicted from these base values and the ambient temperature recorded at sunrise. Predicted values of leaf respiration at sunrise (R_T) were divided by the initial rate of respiration observed at sunset ($R_{T\text{-initial}}$) and compared to $R_T/R_{T\text{-initial}}$ values calculated using the observed rate of respiration at sunrise to evaluate model performance.

Data for model evaluation has also been provided by Lasse Tarvainen and Göran Wallin (University of Gothenburg, Sweden) for this study from the Skogaryd research site in Sweden (58°23'N, 12°09'W, 60m above sea level). *Picea abies* planted in 1951 account for 82% of the basal area of the forest, whilst *Pinus sylvestris* account for 13% and *Betula pendula* comprise 5% (Taravainen *et al*., 2013; 2015). The mixed coniferous stand grows on well-drained peat with agricultural history (Klemedtsson *et al*., 2010). Three dominant *Picea abies* in the centre of the stand, between 55-60 years old and 22-25m tall, were selected for study. The LAI of these Norway spruce varies seasonally between 5.8 and 6.5m^2 m^{-2}. Continuous gas exchange measurements under ambient conditions were taken on 1-year-old shoots at three different positions within the canopy: top, middle and bottom. Data was collected every

30 minutes using a LI-COR 6400 Portable Photosynthesis System with a conifer chamber, providing continuous measurements of CO_2 flux throughout growing season from May-September (n=26, 42 nights). Photosynthetically Active Radiation (PAR) values of less than 0 were used to delineate night-time values of respiration. Nocturnal respiration was modelled from sunset to sunrise using the different formulations (Table 2.5.) and changes in measured leaf temperature throughout the night. Hourly averages of $R_T/R_{T\text{-initial}}$ were calculated using the observed values of respiration and predicted values of respiration to compare and assess the ability of each model to accurately estimate respiration as a function of time throughout the night.

To further evaluate the models, all 614 predicted values of respiration from model evaluation were plotted in the abscissas (x-axis) against observed values in the ordinates (y-axis), in accordance with the findings of Piñeiro *et al*. (2008), and fitted with a linear regression. Analysis of R^2 shows the proportion of the total variance explained by the regression models and comparison of the slope and intercept parameters against the 1:1 line is indicative of consistency and model bias respectively (Smith and Rose, 1995; Mesple *et al*., 1996.) To conduct a residual analysis, standardised residuals were calculated and plotted in the ordinates against predicted values of respiration, leaf temperature, and time in darkness in the abscissas to subjectively detect biases and compare the non-linearity, heteroscedasticity, and outliers of the different models for respiration.

3. Results

3.1. The Q_{10} Function and Temperature Control

The mean inherent and apparent temperature responses of leaf respiration are shown in Figure 3.1. The range of inherent Q_{10} values (Q_{10inh}) derived from the short-term artificial manipulation of temperature over the timescale of minutes is relatively narrow, with a mean Q_{10inh} of 1.94 ± 0.09 SE (n=46). The range of apparent Q_{10} values (Q_{10app}) obtained from measurements of respiration in response to natural cooling during the night are twice as high as Q_{10inh} and exemplify a greater range, with a mean Q_{10app} of 4.15 ± 0.5 SE (n=46). A paired samples t-test determined a statistically significant difference between datasets of Q_{10inh} and Q_{10app} presented in Table 3.1., significant at the 99.9% confidence level ($t(11)=5.065$, $p<0.001$).

Mean temperature control of leaf respiration at night is estimated to be 0.46 ± 0.05 SE (n=21), calculated from values of α and β (Figure 3.1).

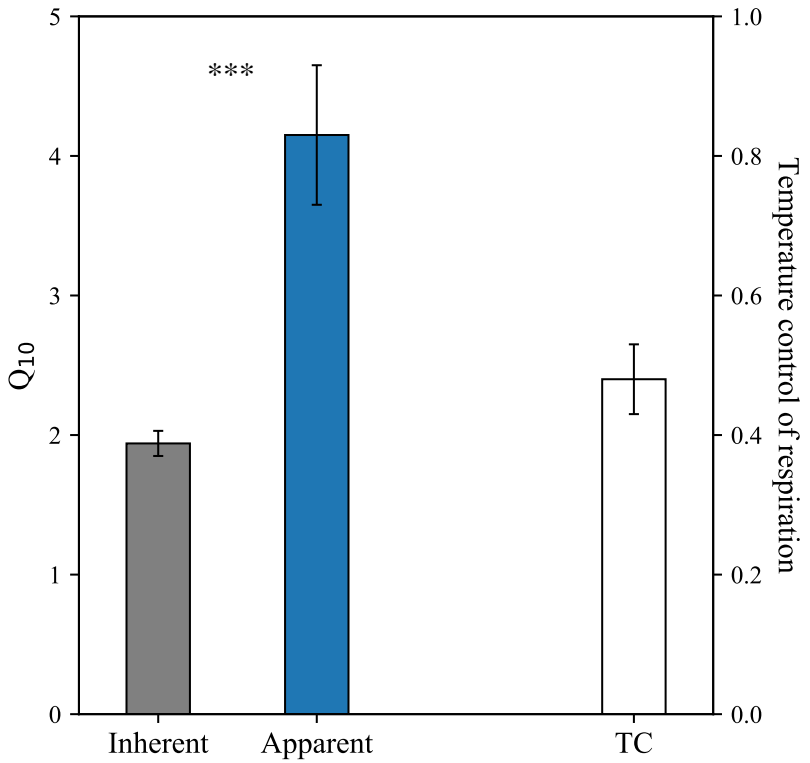


Figure 3.1. Mean inherent and apparent Q_{10} values (n=46) and temperature control (n=21) of nocturnal respiration, error bars are standard error. Results from an independent samples t-test is presented, ***p<0.001.

Table 3.1. Mean inherent and apparent Q_{10} values per species and estimated temperature control of respiration.

Species	Inherent Q_{10}	Apparent Q_{10}	Temperature Control
Acer pseudoplatanus	1.8	3	0.57
Betula pendula	2	6.5	0.43
Eucalyptus pauciflora (autumn)	1.7	4.2	-
Eucalyptus pauciflora (spring)	2	2.8	-
Eucalyptus pauciflora (summer)	2	2.7	-
Fagus sylvatica f. purpurea	2.6	7.9	-
Musa acuminata	1.5	3.5	-
Platinus x hispanica	1.7	3	0.49
Pringlea antiscorbutica	1.6	2	-
Prunus padus	2.4	5	0.65
Solanum lycopersicum	2.1	4.3	-
Tilia x europaea	1.9	4.9	0.41
Mean	1.94	4.15	0.48
SE	0.09	0.5	0.05

3.2. Novel Representation of Nocturnal Plant Respiration

A universal decline in $R_{To}/R_{To\text{-}initial}$ as a function of time in darkness was found to occur consistently across almost all species, measurement conditions and biomes considered in this study (Figure 3.2). The basal rate of nocturnal respiration decreased by ~40% of the initial rate at the onset of darkness under constant temperature conditions. Overall, the power function produced the highest R^2 values and lowest MSE values at both replicate and species level across biomes and experimental conditions, deeming it the most suitable model to describe the data across all species. At species level, the chosen power function was fitted across the entire dataset (Figure 3.2.). The results from one-way ANOVA found the slope only varied significantly between species ($F(32,990)=2.359$, $p=0.001$), and did not vary significantly between biomes ($F(1,130=0.149$, $p=0.700$), experimental conditions ($F(1,130)=0.210$, $p=0.647$), or plant type ($F(3,128)=2.573$, $p=0.057$), allowing the entire dataset to be collated and a single universal equation to be derived for modelling which could be applied and tested for all plant functional types, representative of all groups.

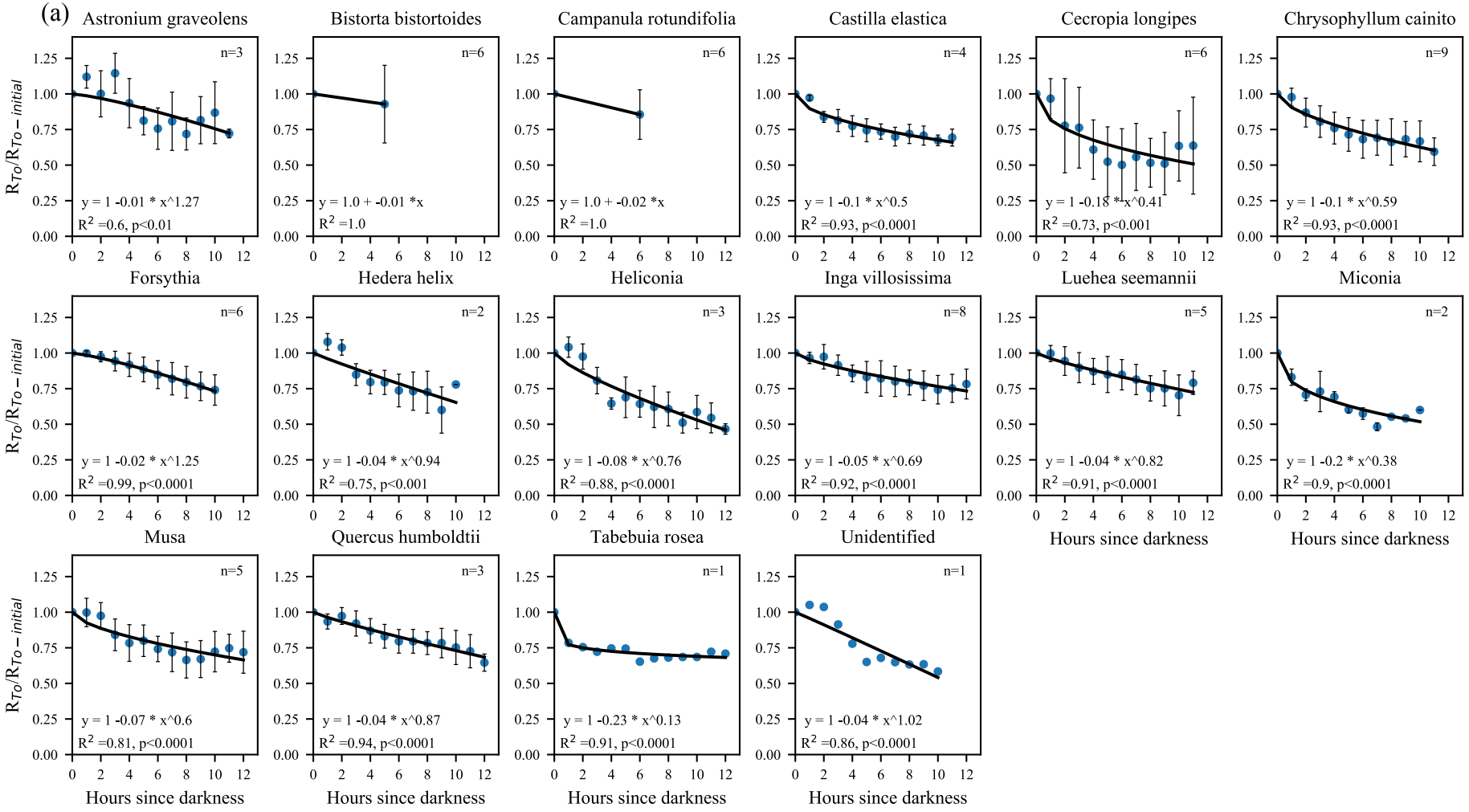
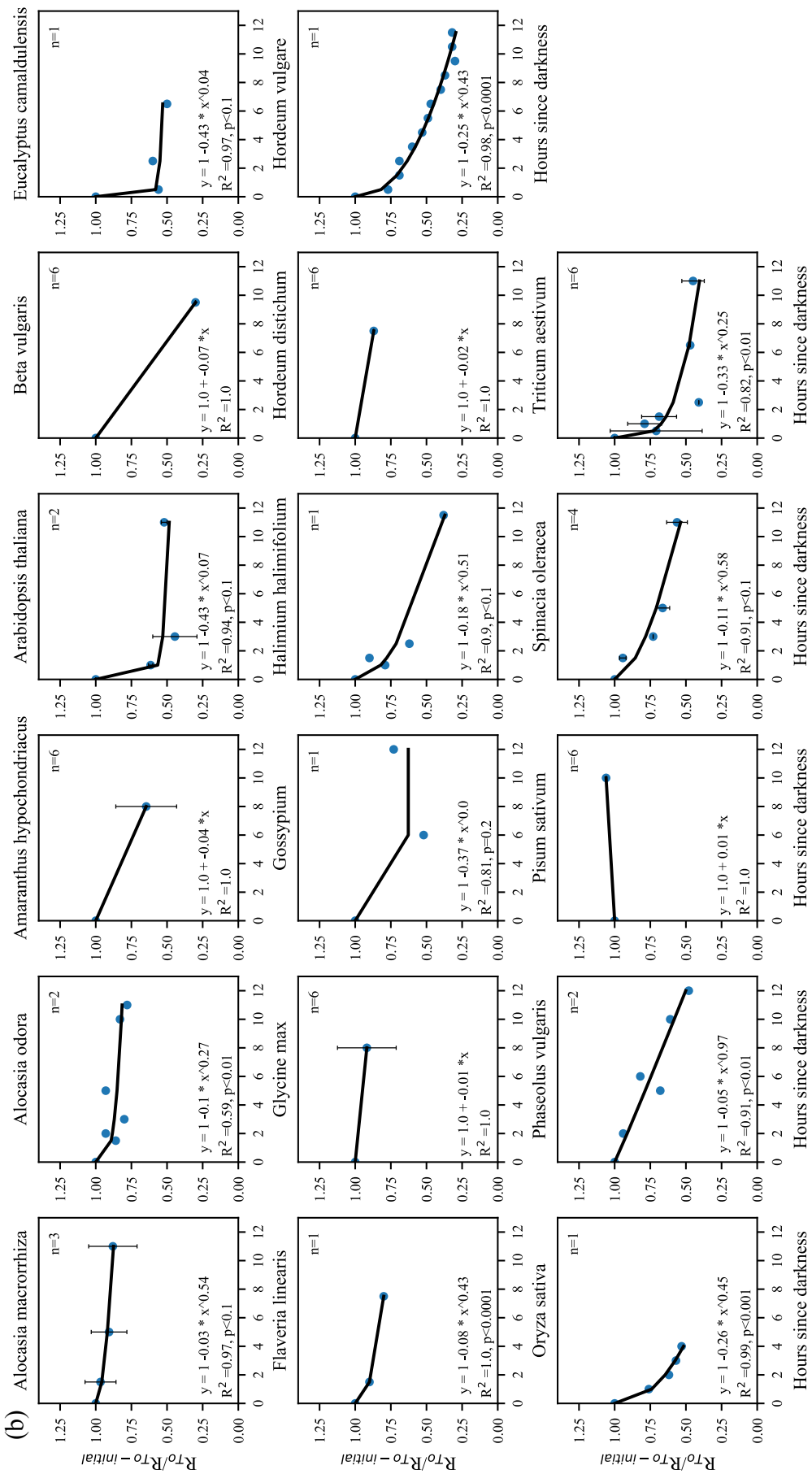


Figure 3.2. Hourly means of $R_{To}/R_{To\text{-}initial}$ as a function of time in darkness for each species used in this study measured under (a) field conditions and (b) laboratory conditions, fitted with a power function. Error bars are standard deviation.


(b)
Alocasia macrorrhiza
Alocasia odora
Amaranthus hypochondriacus
Arabidopsis thaliana
Beta vulgaris
Eucalyptus camaldulensis
Flaveria linearis
Glycine max
Gossypium
Halimium halimifolium
Hordeum distichum
Hordeum vulgare
Oryza sativa
Phaseolus vulgaris
Pisum sativum
Spinacia oleracea
Triticum aestivum
Hours since darkness
RTo/RTo − initial

All measurements of $R_{To}/R_{To\text{-}initial}$ for the 33 species and 141 leaves in this study were fitted with the chosen power function (Figure 3.3), demonstrating the rate of respiration to decrease in the night by ~40% of the initial rate of respiration at the onset of darkness. Regression analysis of the final plot derives a universal equation that predicts respiration at any time of night as a fraction of the initial respiration rate at the start of the night as a function of time in darkness. Under the assumptions of the Q_{10} function, $R_{To}/R_{To\text{-}initial}$ should remain constant throughout the night, producing a slope of 0 in regression analysis. Here, the null hypothesis that the slope coefficient is equal to 0 is rejected at the 99.9% confidence level ($p<0.0001$) and the R^2 of 0.46 indicates an adequate fit of the model to the data.

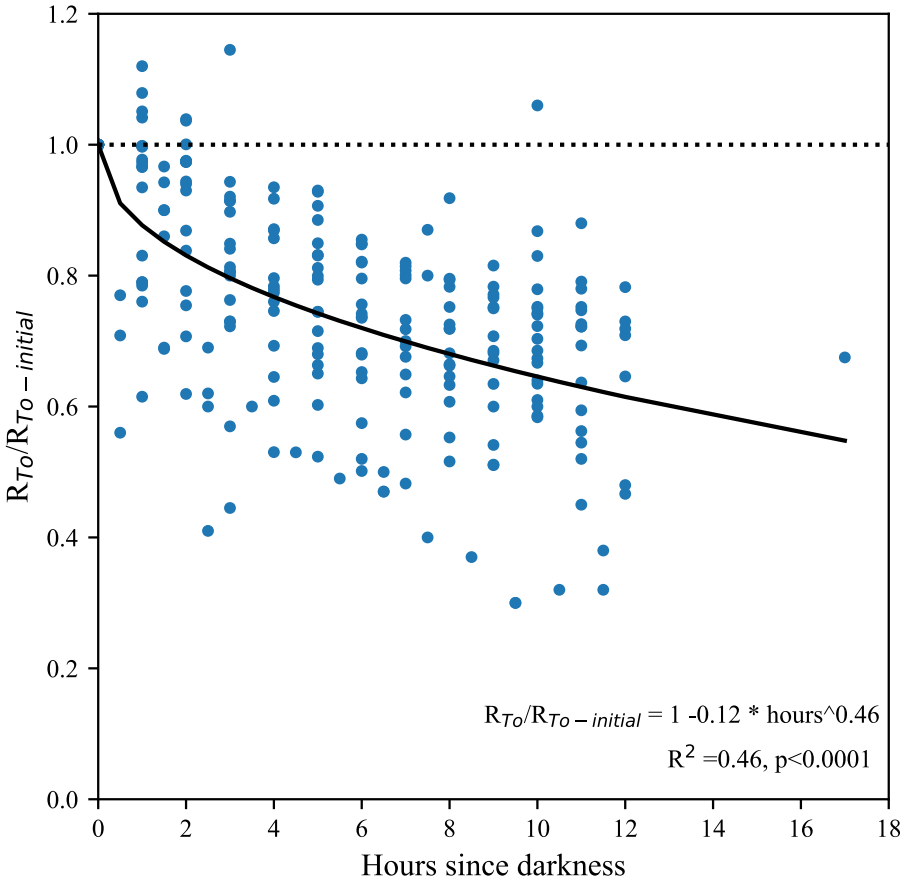


Figure 3.3. $R_{To}/R_{To\text{-}initial}$ as a function of time in darkness for all species used in this study (n=33), fitted with a power function. Equation from regression analysis forms the novel non-temperature dependent term for modelling.

The novel equation derived from Figure 3.3. describes the non-temperature dependency of nocturnal respiration and couples respiration to time of night after sunset:

$$R_{To}/R_{To-initial} = 1 - 0.12hour^{0.46} \qquad (10)$$

The resulting equation was combined with the description of respiration currently used in JULES with a standard Q_{10} of 2 (Eq. 2) to develop a new function for nocturnal leaf respiration that includes both a temperature-dependent and non-temperature dependent term:

$$R = R_{sunset} Q_{10}^{0.1(T-T_{sunset})} * (1 - 0.12^{*}hour^{0.46}) \qquad (11)$$

This equation predicts respiration at night from base values of respiration (R_{sunset}) and temperature at sunset (T_{sunset}) according to changes in temperature (T) and time in darkness (hour), thereby accounting for the temperature-independent controls of nocturnal respiratory metabolism in addition to the temperature-dependency of the process. This novel description of leaf respiration (Eq. 11) was also adapted to include the temperature-dependent Q_{10} (Eq. 4) proposed by Tjoelker *et al*. (2001):

$$R = R_{sunset}(3.22 - 0.046T)^{0.1(T-T_{sunset})} * (1 - 0.12^{*}hour^{0.46}) \qquad (12)$$

The standard function used in JULES (Eq. 2) was also adapted to include the temperature-dependent Q_{10} in direct replacement of the standard Q_{10}:

$$R = R_0(3.22 - 0.046T)^{0.1(T-T_0)} \qquad (13)$$

These final equations (Eq. 11-13) were implemented in JULES to explore the impact of each description of nocturnal leaf respiration on simulations of plant respiration and NPP for tropical and temperate forest sites.

3.3. Sensitivity of Nocturnal Decline in Respiration to Temperature Decrease

To investigate the effect of temperature decrease, a sensitivity test was conducted to quantify the impact of speed of cooling and length of night on simulated plant respiration (Figure 3.4). Open symbols represent simulations with a constant R_{To} (Eq. 2), whereas closed symbols represent simulations with the new variable R_{To} that decreases with time in darkness (Eq. 10). Circle and triangle symbols represent speeds of cooling of of 0.5°C/h and 1.25°C/h respectively. The blue area is the cumulative difference in nocturnal respiration due to the inclusion of non-temperature controls over an eight-hour period with a temperature decrease

of 0.5°C/h (3.64 arbitrary units of respiration). The dashed area highlights the cumulative difference over an eight-hour period with a temperature decrease of 1.25°C/h (2.88 arbitrary units of respiration). Figure 3.4. depicts the cumulative difference in respiration due to the inclusion of non-temperature controls to increase with length of night for both speeds of cooling. However, the cumulative difference over the eight-hour period is 0.76 arbitrary units of respiration greater when the speed of cooling is slower (0.5°C/h), compared to when temperate decreases rapidly and control by temperature is greater (1.25°C/h). This shows $R_{To}/R_{To\text{-}initial}$ is not constant throughout the night, and it is increasingly apparent the longer the night and the slower the natural cooling.

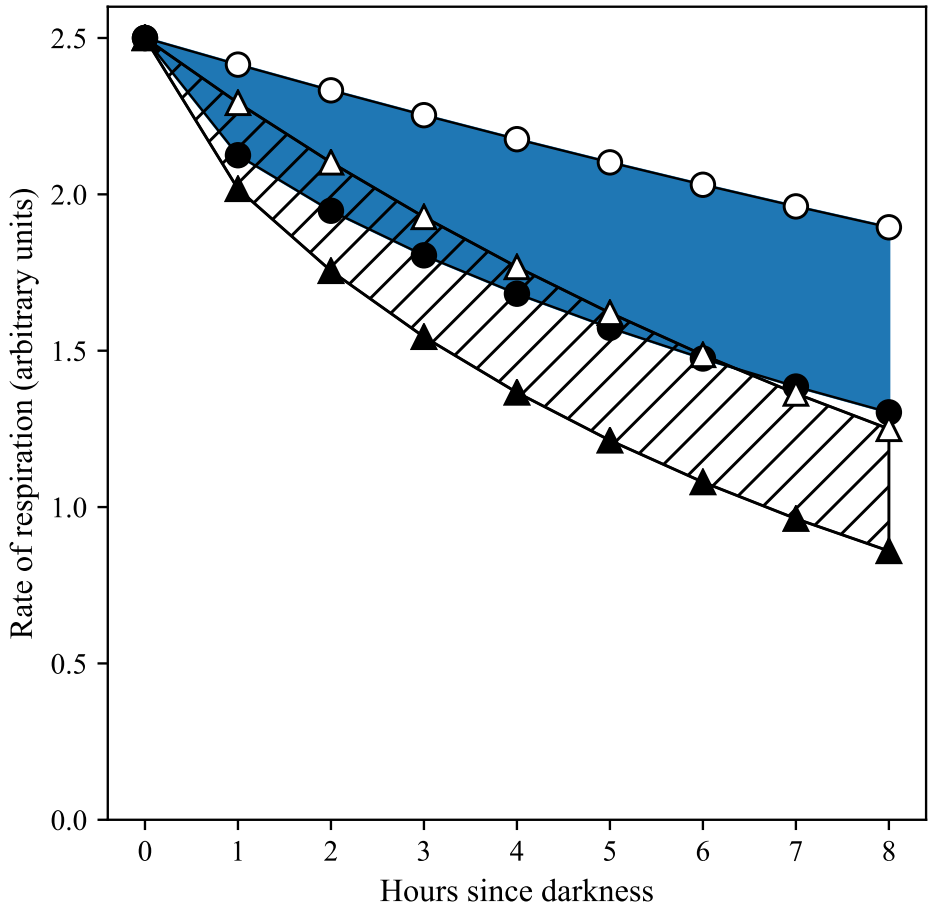


Figure 3.4. Modelling of nocturnal variation in the rate of respiration in response to temperature decrease during the night. Circle symbols represent a temperature decrease of 0.5°C, triangle symbols represent a temperature decrease of 1.25°C. Open symbols represent a constant R_{To}, closed symbols represent the new R_{To} that decreases with time in darkness.

3.4. Evaluation of Novel Formulation

Evaluation of the standard Q_{10} equation (Eq. 2) and the novel formulation developed in this study (Eq. 12) against leaf level observations demonstrates that the standard equation (S1) consistently overpredicts the rate of respiration compared to observations and significantly overestimates $R_T/R_{T\text{-initial}}$ at the end of the night by up to 0.3 for all temperate broadleaf species measured in Exeter (Figure 3.5). Implementation of the temperature-dependent Q_{10} (S2) reduces predicted $R_T/R_{T\text{-initial}}$ by between 0.05 and 0.09. Application of the new term for the non-temperature dependency of nocturnal respiration (S3) reduces $R_T/R_{T\text{-initial}}$ by 0.20 to 0.23 across all species. Overall, S1 (0.77) and S2 (0.71) overestimate $R_T/R_{T\text{-initial}}$ and S4 (0.51) underestimates $R_T/R_{T\text{-initial}}$ at the end of the night compared to observations (0.54) (Figure 3.6). It is the non-temperature dependent term from this study that has the largest impact on modelled nocturnal respiration and most accurately predicts $R_T/R_{T\text{-initial}}$ at the end of the night (0.56) in Figure 3.6.

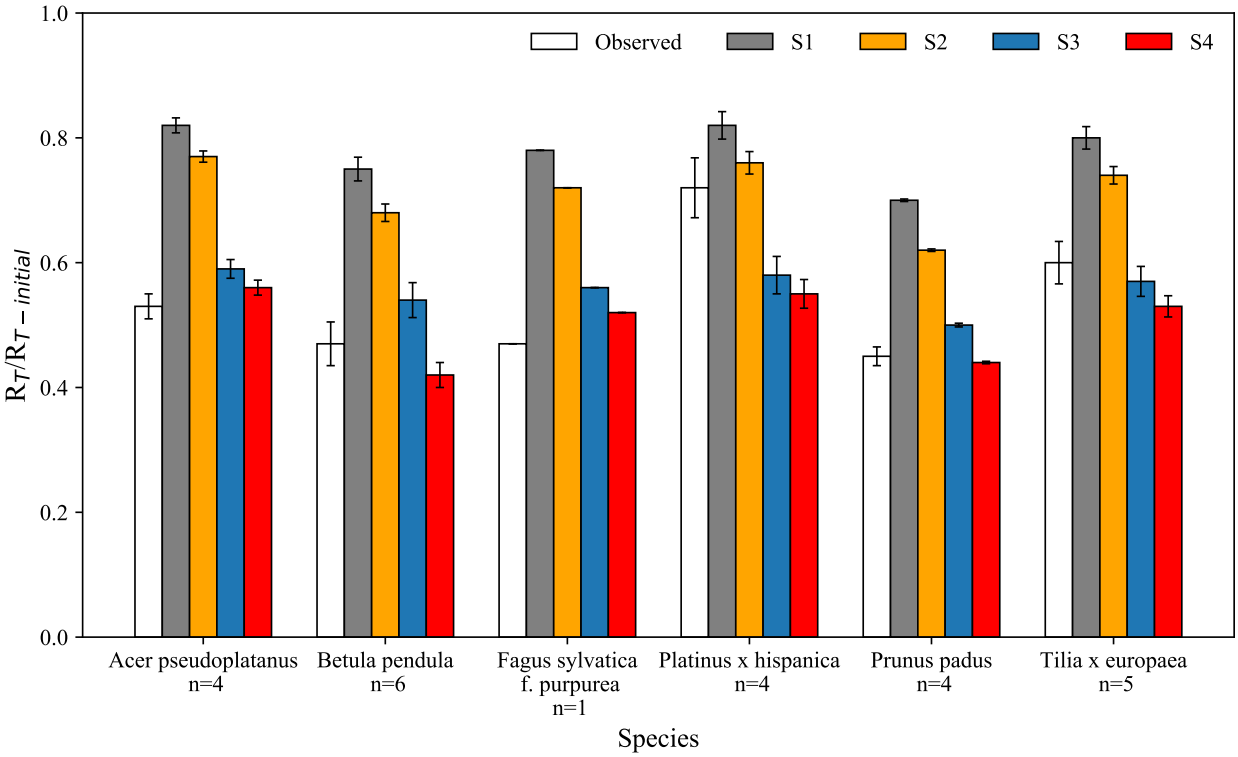


Figure 3.5. Mean observed and predicted rates of respiration as a fraction of the initial respiration rate at the start of the night for each broadleaf species in Exeter using standard Q_{10} (S1), temperature-dependent Q_{10} (S2), standard Q_{10} with non-temperature dependent term (S3), and temperature-dependent Q_{10} with non-temperature dependent term (S4). Error bars are standard deviation.

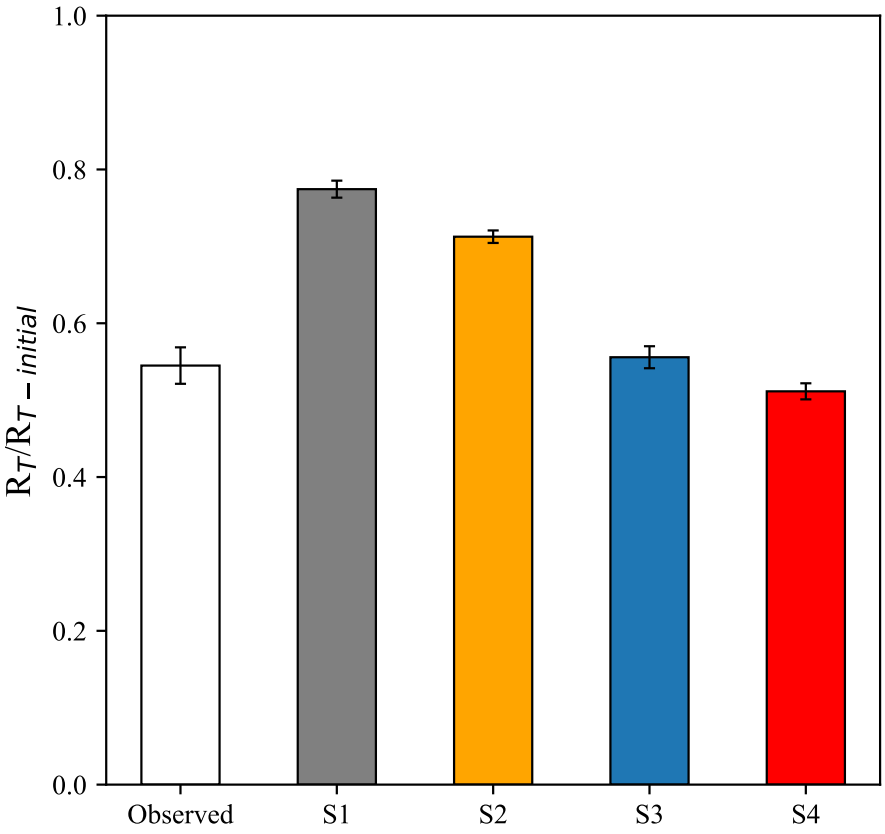


Figure 3.6. Mean observed and predicted rates of respiration as a fraction of the initial respiration rate at the start of the night across all species (n=6) and replicates (n=24) measured in Exeter using standard Q_{10} (S1), temperature-dependent Q_{10} (S2), standard Q_{10} with non-temperature dependent term (S3), and temperature-dependent Q_{10} with non-temperature dependent term (S4). Error bars are standard deviation.

Similar results were obtained when the models were evaluated against a continuous dataset of needleleaf *Picea abies* shoots in Sweden. The standard Q_{10} formulation consistently overestimates changes in $R_T/R_{T\text{-initial}}$ throughout the night for most months over growing season (Figure 3.7). Application of the temperature-dependent Q_{10} offers a small improvement to the prediction of respiration throughout the night, however $R_T/R_{T\text{-initial}}$ at the end of the night is still overestimated for the months of June, July, August and September. Inclusion of the non-temperature dependent term with a standard Q_{10} best predicts changes with $R_T/R_{T\text{-initial}}$ as a function of time for these summer months. Overall, S1 (0.59) and S2 (0.47) overestimate $R_T/R_{T\text{-initial}}$ at the end of the night and S4 (0.31) results in an underestimate compared to observations (0.38) in Figure 3.8. The model with a standard Q_{10} and the novel non-temperature dependent term (S3) best simulates the temporal decline in $R_T/R_{T\text{-initial}}$ throughout the night and most accurately predicts $R_T/R_{T\text{-initial}}$ at the end of the night (0.38) for all measurements combined (Figure 3.8).

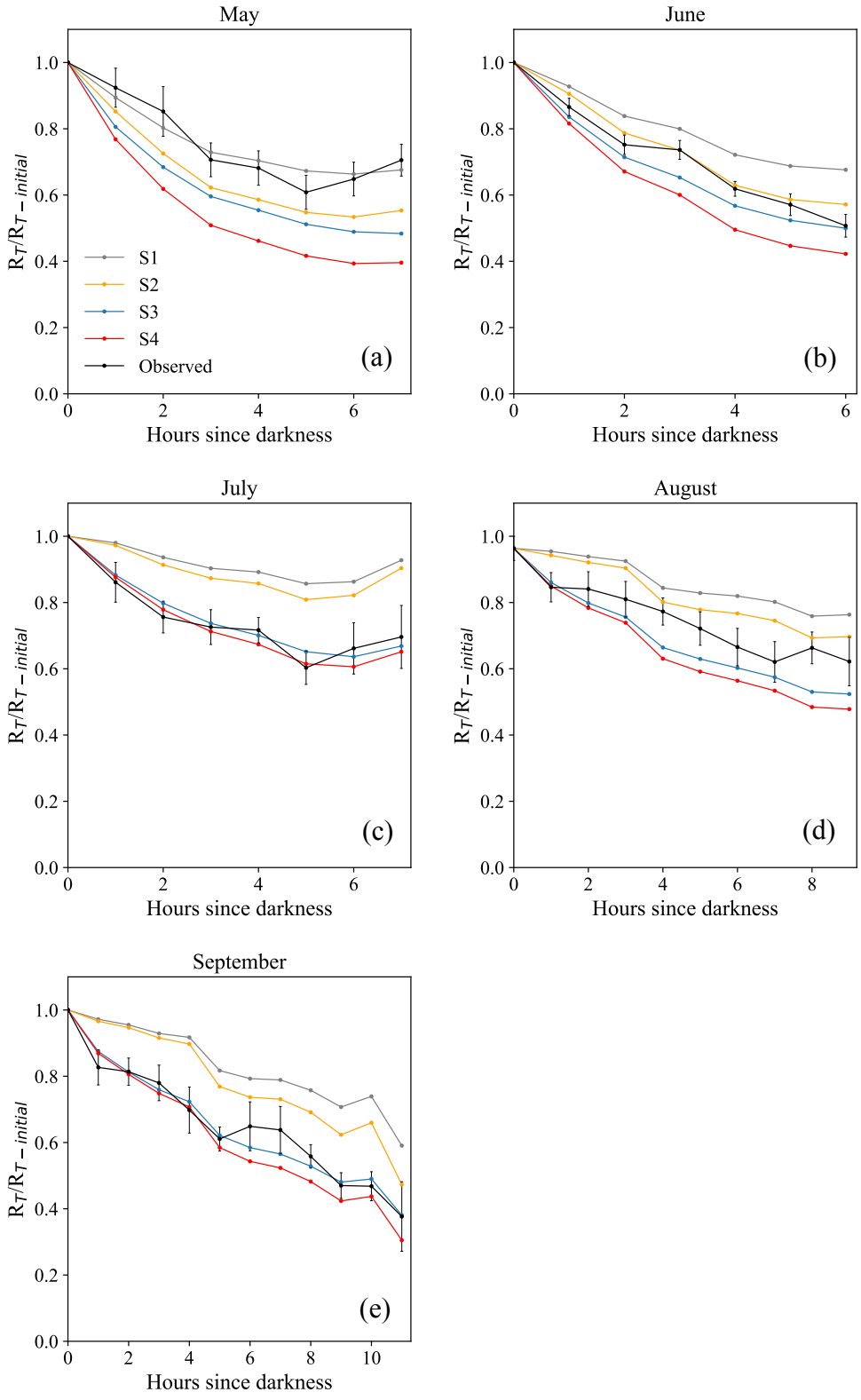


Fig 3.7. Mean observed and predicted rates of respiration throughout the night as a fraction of the initial respiration rate at the start of the night for *Picea abies,* Sweden, in (a) May (n=10, 10 nights), (b) June (n=11, 14 nights), (c) July (n=6, 6 nights), (d) August (n=5, 7 nights), and (e) September (n=2, 4 nights) using standard Q_{10} (S1), temperature-dependent Q_{10} (S2), standard Q_{10} with non-temperature dependent term (S3), and temperature-dependent Q_{10} with non-temperature dependent term (S4). Error bars are standard error.

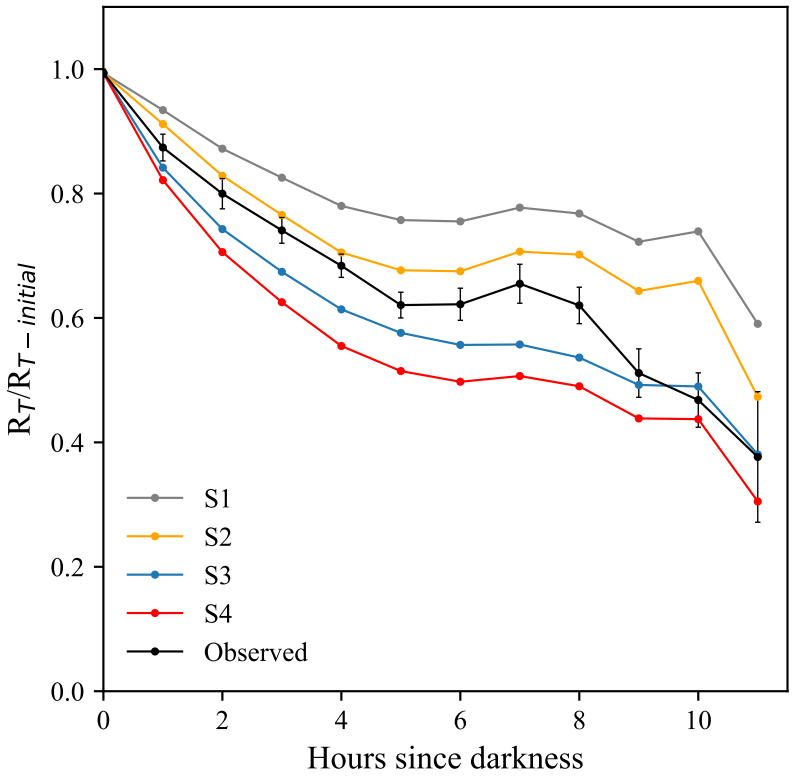


Figure 3.8. Mean observed and predicted rates of respiration throughout the night as a fraction of the initial respiration rate at the start of the night for all measurements of *Picea abies* in Sweden (n=34, 41 nights) using standard Q_{10} (S1), temperature-dependent Q_{10} (S2), standard Q_{10} with non-temperature dependent term (S3), and temperature-dependent Q_{10} with non-temperature dependent term (S4). Error bars are standard error.

For a perfect model, regressing the 614 observed values against predicted values should form a straight line with a slope (a) of 1 that passes through the origin with a y-intercept (b) of 0, and the scatter of points around the regression line should be small generating a low Sum of Squares Error (SSE). The two models that fail to account for temperature-independent controls of respiration have notably lower slope values of $a = 0.81$ and $a = 0.82$ and $b > 0$, indicating they overpredict the rate of respiration proportionally to their value, regardless of whether the standard (S1; Figure 3.9a) or temperature-dependent Q_{10} (S2; Figure 3.9b) is employed. Conversely, the models incorporating the novel temperature-independent term have improved slope values of $a = 0.99$ and $a = 0.98$ with a standard (S3; Figure 3.9c) and temperature-dependent Q_{10} (S4; Figure 3.9d) respectively, however b > 0 signifies the models still overestimate, on average, the observations. Overall, the model combining the novel temperature-independent term with the standard Q_{10} function (Figure 3.9c) appears the most appropriate when compared to the 1:1 line and has the greatest coefficient of determination (R^2=0.75), helping further discriminate among simulations and indicate the preferred model.

A high proportion of the standardised residuals for S1 and S2 are negative, implying that both formulations generally overestimate respiration (Figure 3.10). The standardised residuals for S1 and S2 are also skewed below the zero line when plotted against leaf temperature (Figure 3.11.) and hours in darkness (Figure 3.12.), indicating the models are biased and consistently overpredict nocturnal leaf respiration. The residuals are more symmetrically distributed around the zero line for models S3 and S4 indicating the models that include the novel non-temperature dependent term have fewer biases and an improved predictive capacity.

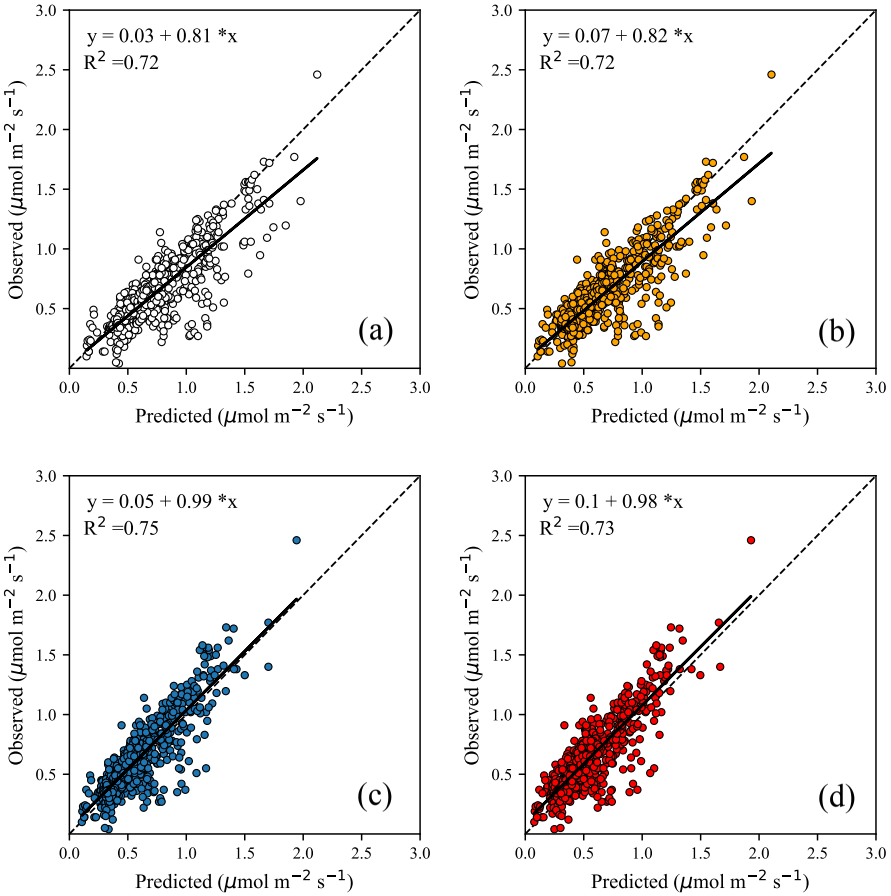


Figure 3.9. Observed versus predicted rates of nocturnal leaf respiration using the ambient data from Sweden and Exeter for (a) S1 using a standard Q_{10}, (b) S2 using a temperature-dependent Q_{10}, (c) S3 using a standard Q_{10} and non temperature-dependent term, and (d) S4 using a temperature-dependent Q_{10} and non-temperature dependent term (n=50, 66 nights).

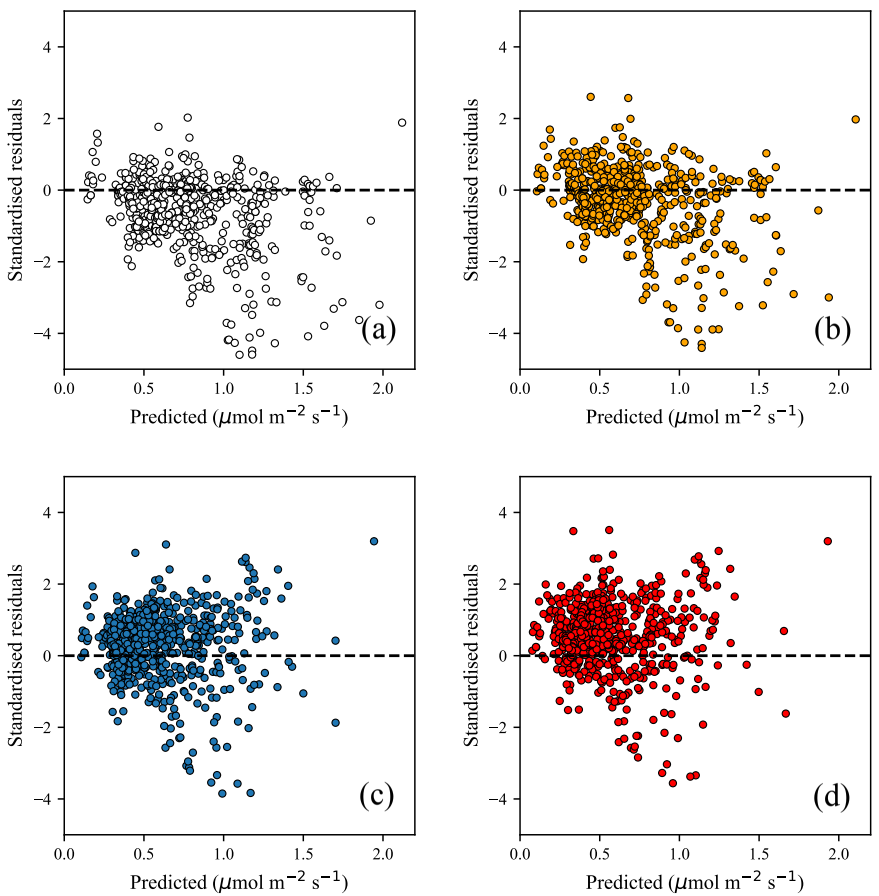


Figure 3.10. Standardised residuals versus predicted rates of nocturnal leaf respiration using the ambient data from Sweden and Exeter for (a) S1 using a standard Q_{10}, (b) S2 using a temperature-dependent Q_{10}, (c) S3 using a standard Q_{10} and non temperature-dependent term, and (d) S4 using a temperature-dependent Q_{10} and non-temperature dependent term (n=50, 66 nights).

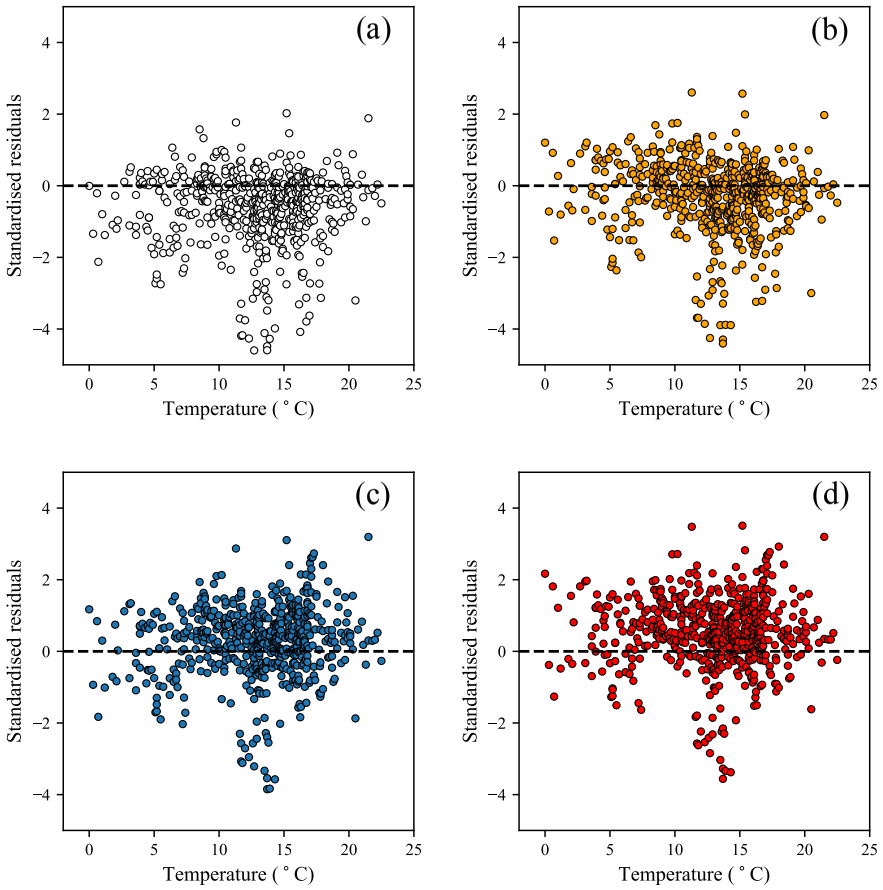


Figure 3.11. Standardised residuals versus leaf temperature using the ambient data from Sweden and Exeter for (a) S1 using a standard Q_{10}, (b) S2 using a temperature-dependent Q_{10}, (c) S3 using a standard Q_{10} and non temperature-dependent term, and (d) S4 using a temperature-dependent Q_{10} and non-temperature dependent term (n=50, 66 nights).

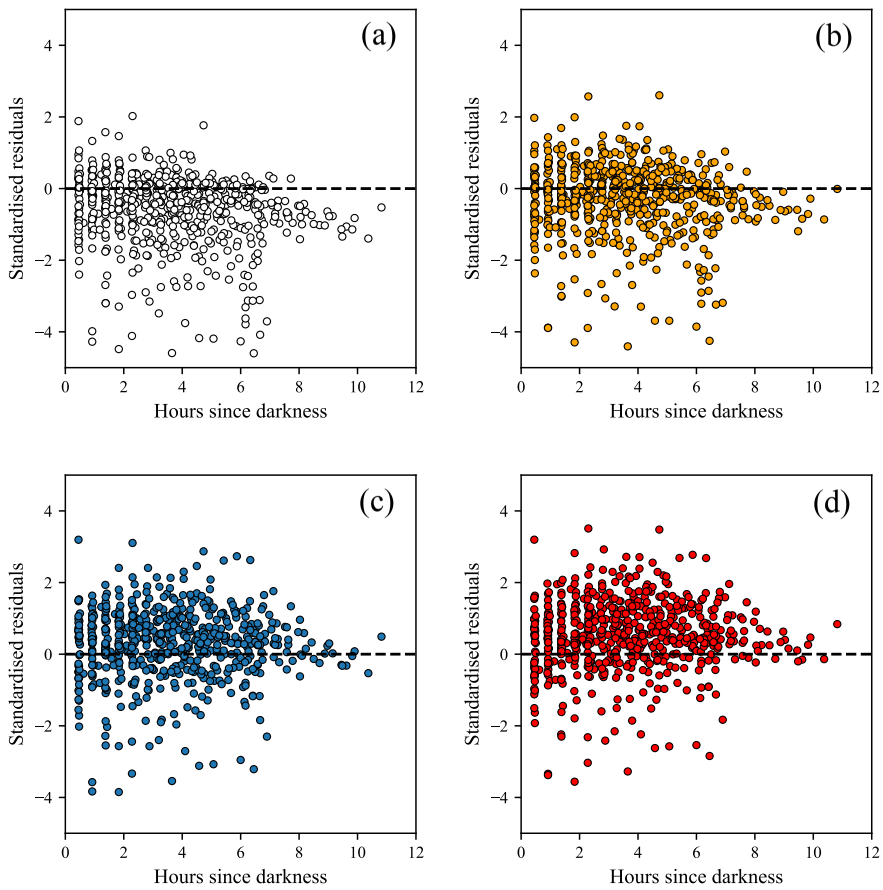


Figure 3.12. Standardised residuals versus hours in darkness using the ambient data from Sweden and Exeter for (a) S1 using a standard Q_{10}, (b) S2 using a temperature-dependent Q_{10}, (c) S3 using a standard Q_{10} and non temperature-dependent term, and (d) S4 using a temperature-dependent Q_{10} and non-temperature dependent term (n=50, 66 nights).

3.5. Site Level Application Using JULES

Site level simulations with JULES (Figure 3.13) demonstrate that, overall, the novel non-temperature dependent term for modelling nocturnal respiration decreases the simulation of annual plant respiration and increases annual NPP unanimously across all simulation scenarios in JULES. Application of the non-temperature dependent term reduces plant respiration and increases NPP for all forest sites when the simple big leaf approach is employed to scale from leaf to canopy level, ultimately simulating a canopy with a low nitrogen content (Figure 3.13a and 3.13c). However, the effect of the non-temperature dependent term on modelled respiration and NPP is notably greater when the advanced multi-layer scaling approach is employed which accounts for light interception at different canopy levels, ultimately providing a more realistic representation of the canopy with a higher nitrogen content (Mercado *et al*., 2007; 2009b). Therefore, the simulations resulting from the multi-layer scaling approach (Figure 3.13b and 3.13d) should be considered as more realistic and accurate when evaluating the overall effect of the non-temperature dependent term on simulated rates of plant respiration and NPP.

The new non-temperature dependent term reduces annual rates of respiration by up to ~6% at temperate forest sites and ~10% at tropical sites, leading to an increase in annual rates of NPP of up to ~13% and ~16% respectively. The novel term has a larger impact at tropical sites (Manaus, Tapajos, China and French Guiana) and a markedly smaller effect on temperate and cold climate sites, resulting in a statistically significant difference between the effect of the new term on the simulation of respiration ($t(64)=3.584$, $p=0.001$) and NPP ($t(64)=4.223$, $p<0.0001$) for tropical and temperate forests. Broadleaf evergreen tropical sites, such as French Guiana and China, experience longer nights of ~12 hours and a relatively constant temperature throughout the night, producing the greatest decrease in the simulation of nocturnal respiration when including the non-temperature dependent term (Figure 3.14. and 3.15). The effect of the non-temperature dependent term is less significant for broadleaf evergreen temperate sites, France and Italy, which experience shorter nights of ~10 hours and more than a ~10°C drop in night-time temperatures. The effect is further reduced at broadleaf deciduous temperate sites, Canada and USA, that typically experience lower growth temperatures and shorter nights of ~8 hours. This disparity between the effect of the non-temperature dependent term on tropical and temperate sites is evident when employing both a

standard Q_{10} (S1-S3; Figure 3.14.) and a temperature-dependent Q_{10} (S2-S4; Figure 3.15.). The final simulation (S1-S5) reveals the impact of altering only the description of plant respiration at night to include both the non-temperature dependent term and the temperature-dependent Q_{10} (Figure 3.13), with the standard Q_{10} employed to model day-time respiration. Modifying the formulation for nocturnal respiration alone has a great overall impact on annual rates of respiration and NPP, resulting in a maximum 10.6% decrease and 18.7% increase respectively.

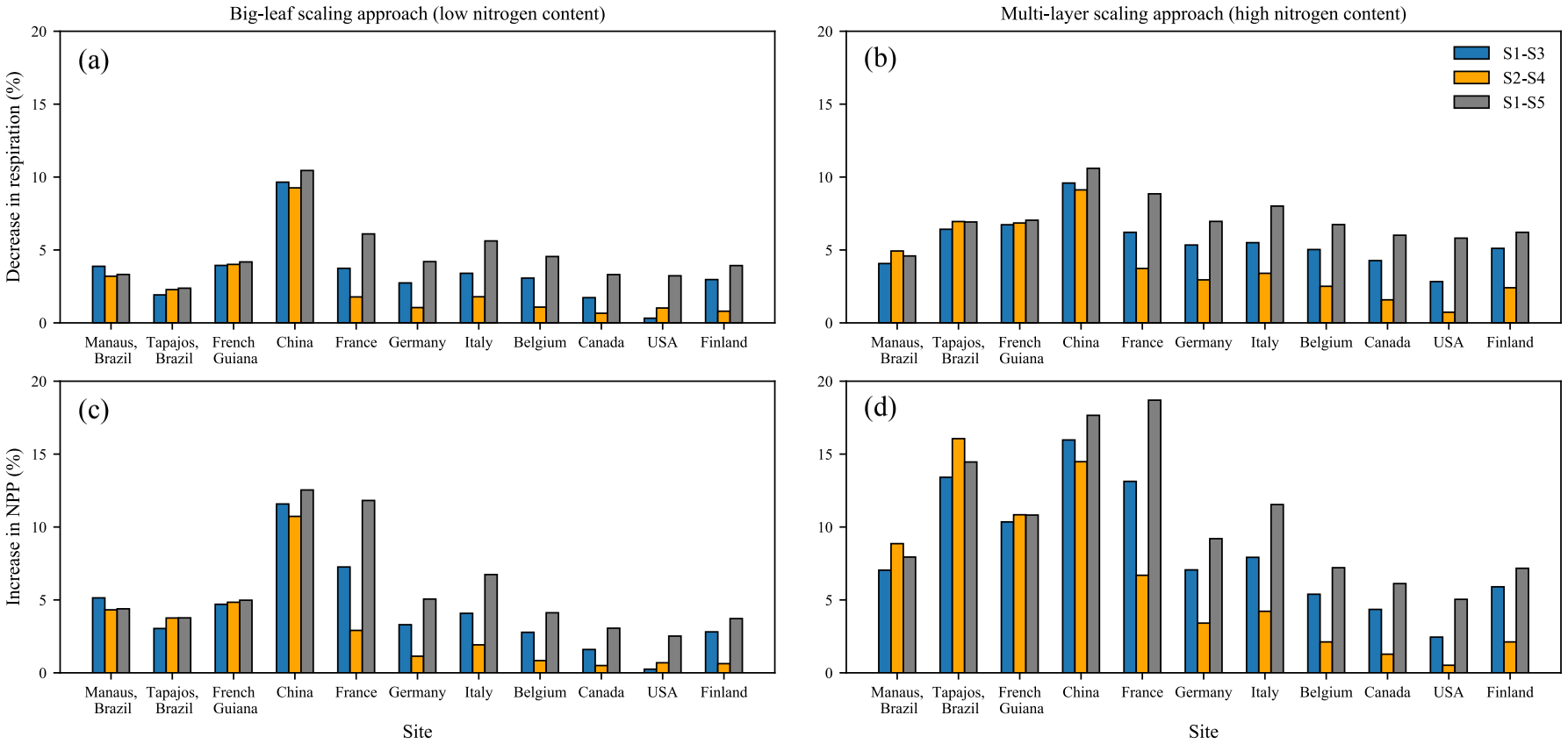


Figure 3.13. Effect of including the non-temperature dependency of nocturnal respiration with standard Q_{10} (S1-S3), the non-temperature dependency of nocturnal respiration with temperature-dependent Q_{10} (S2-S4), and the non-temperature dependency of nocturnal respiration with temperature-dependent Q_{10} at night-time only (S1-S5), as the percentage difference in the simulation of (a) annual respiration using the big leaf scaling approach, (b) annual respiration using the multi-layer scaling approach, (c) annual NPP using the big leaf scaling approach, and (d) annual NPP using the multi-layer scaling approach.

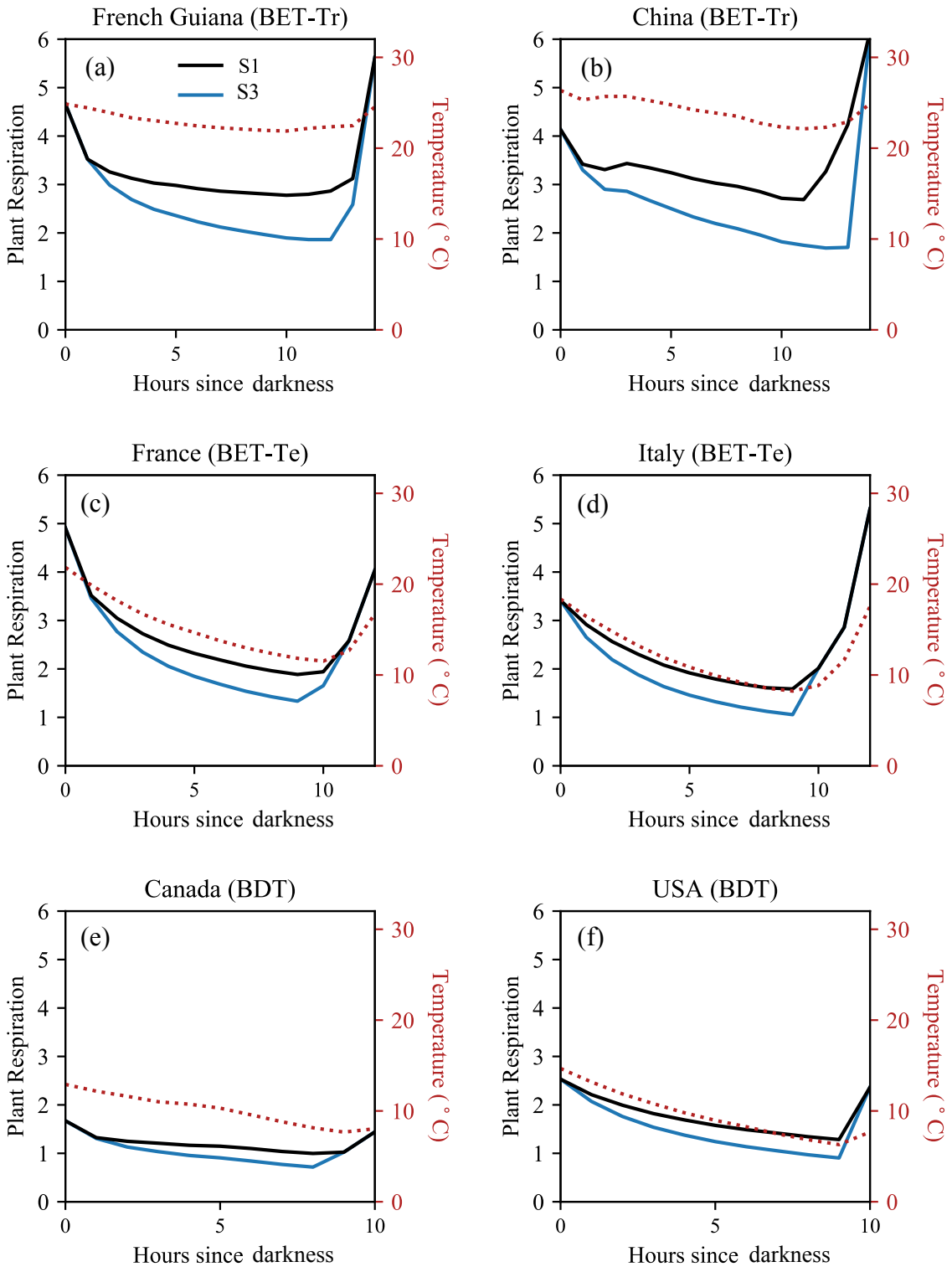


Figure 3.14. Nocturnal temperature change and modelled rate of plant respiration from sunset to sunrise using a standard Q_{10} (S1) and addition of the non-temperature dependent term (S3) for (a) French Guiana, (b) China, (c) France, (d) Italy, (e) Canada and (f) USA using the multi-layer scaling approach.

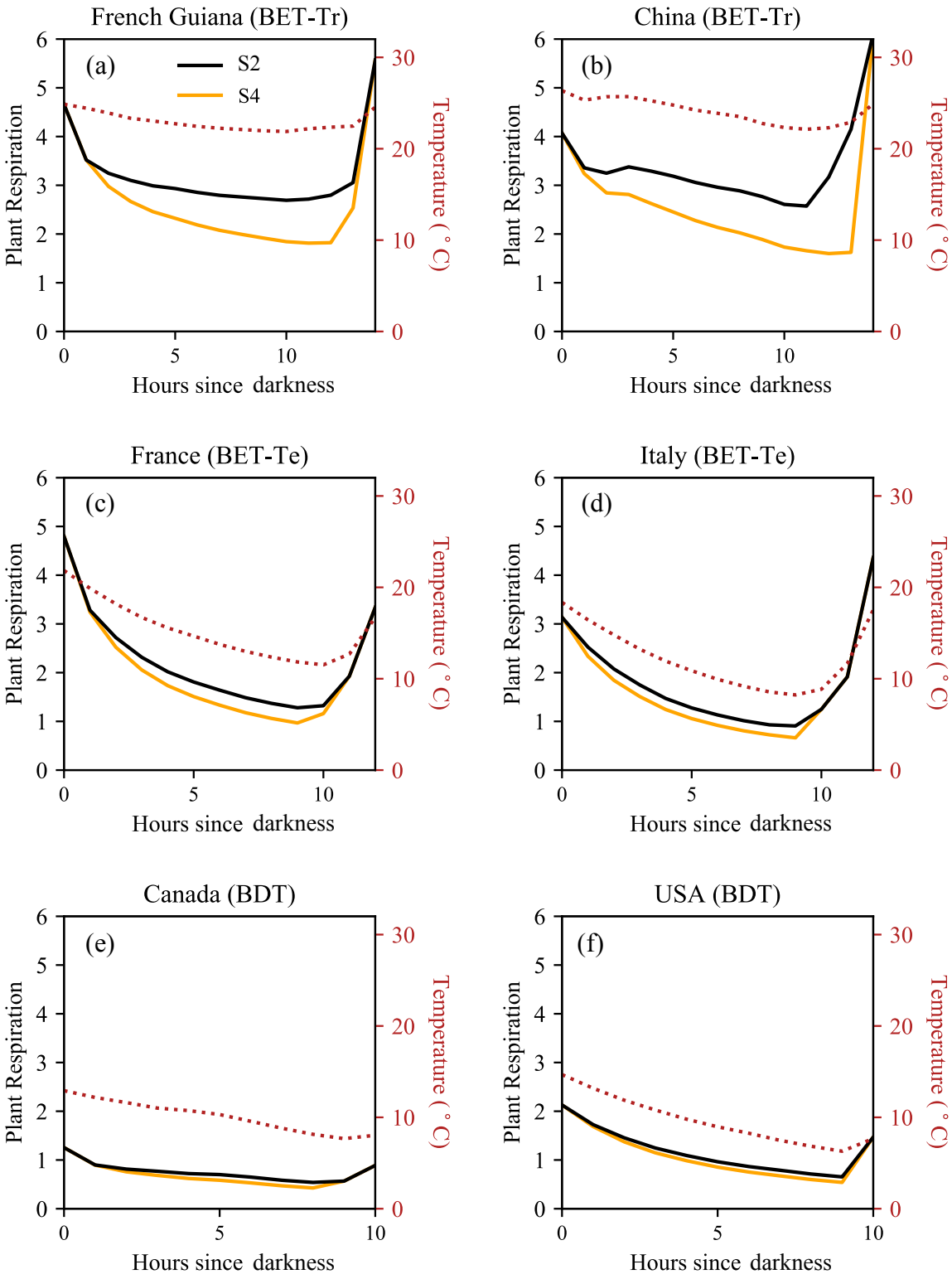


Figure 3.15. Nocturnal temperature change and modelled rate of plant respiration from sunset to sunrise using a temperature-dependent Q_{10} (S2) and addition of the non-temperature dependent term (S4) for (a) French Guiana, (b) China, (c) France, (d) Italy, (e) Canada and (f) USA using the multi-layer scaling approach.

4. Discussion

4.1. Variation in Nocturnal Respiration

4.1.1. Inherent and Apparent Q_{10}

The mean inherent Q_{10} (Q_{10inh}) value of 1.94 ± 0.09 (Figure 3.1.), calculated from the response of respiration to short-term artificial temperature manipulations applied to dark-adapted leaves in the daytime, aligns with current estimates and values in the wider literature. Lariguaderie and Korner (1995) found most species to exhibit Q_{10} values of between 2 and 2.5, producing an overall mean Q_{10} of 2.3. From analysis of the existing literature, Tjoelker *et al.* (2001) reported the mean Q_{10} of 65 species to be 2.5, with upper and lower 95% confidence intervals of 2.62 and 2.39 respectively. Further analysis of forest carbon flux data by Piao *et al*. (2010) suggests that the Q_{10} of forest respiration varies from 1.8 to 2.9 at the global scale. Therefore, the Q_{10inh} values found in this investigation fall within the range of Q_{10} values previously reported studies that also artificially manipulate the temperature of dark-adapted leaves in the daytime to determine the instantaneous temperature response of leaf respiration over the timescale of minutes (Ryan *et al*., 1997; Atkin *et al*., 2005a; Luyssaert *et al*., 2007). Due to this high consensus in the literature, a constant Q_{10} of 2 has gained wide acceptance in modelling the temperature response of leaf respiration.

It is commonly assumed in vegetation models that the process of respiration continues the same throughout the day and the night, responding only to short-term diurnal variations in temperature (Gifford, 2003). However, the mean apparent Q_{10} (Q_{10app}) of 4.15 ± 0.5 (Figure 3.1.), calculated from measurements of respiration under ambient temperature conditions at the start and end of the night, is significantly higher than the mean Q_{10inh} ($p<0.001$). The apparent Q_{10} values describe temporal variation in nocturnal leaf respiration in response to both natural variation in ambient temperature and the effect of temperature-independent controls. Values of Q_{10app} are consistently higher than corresponding values of Q_{10inh} across all species (Table 3.1.), indicating that mechanisms other than temperature co-regulate leaf respiration at night. The estimated temperature control of nocturnal leaf respiration is 0.46 (Figure 3.1.), suggesting temperature-independent factors may be accountable for approximately half of the observed variation in rates of leaf respiration at night, refuting the

common assumption that temperature is the main driver of respiration over the short-term (Reichstein *et al*., 2005). Despite evidence for the control of nocturnal respiration by temperature-independent mechanisms, their role has thus far remained unquantified and unaccounted for in models of leaf and plant respiration.

4.1.2. Variation in $R_{To}/R_{To\text{-}initial}$

Assuming that leaf respiration is entirely temperature-dependent, as suggested by the Q_{10} function, the rate of respiration as a fraction of the initial rate of respiration should not deviate from 1 throughout the night under constant temperature conditions. However, the basal rate of respiration (R_{To}) as a fraction of the initial respiration rate ($R_{To\text{-}initial}$) decreases with time from the onset of darkness, almost universal across the species in this study (Figure 3.2). Most vegetation models erroneously assume that respiration varies exponentially with temperature, whereas Figure 3.3. reveals the rate of nocturnal leaf respiration to also have a complex dependence on time in darkness. The time-dependency of respiration at night reflects the down-regulation of nocturnal respiratory metabolism due to endogenous mechanisms such as respiratory substrate availability, the demand for respiratory products, and the circadian clock. Therefore, the base rate of respiration cannot be considered constant for a 24-hour period as generally assumed in all modern field studies and models, and the use of a fixed exponential Q_{10} temperature function is inadequate to describe nocturnal variation in endogenous metabolism with natural variation in ambient temperature. Only variation in the respiratory rate of leaves is considered in the scope of this study, however there is evidence in the existing literature that demonstrates temperature-independent rhythms also occur in root and soil respiration. Leverenz *et al*. (1999) measured root plus soil respiration of *Fagus sylvatica* seedlings and plotted respiration rate against temperature and net photosynthesis over a 24-hour diel cycle. Post-dawn rates of respiration were significantly higher than pre-dusk rates of respiration at the same temperature and nocturnal respiration was markedly lower than day-time respiration under the same thermal conditions. Overall, respiration was found to increase from dawn and decrease in the evening, reaching the lowest rates of respiration at night, revealing a distinct diurnal trend in root plus soil respiration that occurs independent of temperature. The results of Leverenz *et al*. (1999) further show that R_{To} is not constant over a 24-hour period in root plus soil respiration, thereby corroborating the findings of this study and further refuting the use of a constant R_{To} in vegetation and earth system models. Ultimately, exclusive focus on the control of nocturnal respiration by

temperature is unwarranted and failure to account for the time-dependence and non-temperature dependency of nocturnal respiration is likely to result in inaccurate estimates of respiratory CO_2 release.

4.2. Respiratory Substrate Supply and Product Demand

4.2.1. Nocturnal Starch Degradation

Understanding the processes that influence temporal variation in respiration independent of temperature is crucial for the accurate modelling of CO_2 exchange between the land surface and the atmosphere. At tissue level, the rate of nocturnal leaf respiration may strongly depend on respiratory substrate availability (Whitehead *et al*., 2004). During darkness, leaf concentrations of non-structural carbohydrates typically decrease (Fondy and Geiger, 1982; Grimmer and Komor, 1999) due to the degradation of starch in a linear manner to provide a continuous supply of carbon throughout the night to sustain metabolism and growth (Gibon *et al*., 2004; Smith and Stitt, 2007; Graf and Smith, 2011). Strong correlations between the rate of respiration and concentration of carbohydrates in mature leaves have been reported in various species (Fondy and Geiger, 1982, Azcón-Bieto and Osmond, 1983; Farrar and Farrar, 1985; Stitt *et al*., 1990). Therefore, the marked decrease in the rate of nocturnal leaf respiration under constant temperature conditions partly reflects the decline in respiratory substrate availability throughout the night (Figure 3.2. and 3.3.). Despite ample evidence for a direct relationship between nocturnal respiration rate and carbohydrate status, many models do not represent substrates because their representation is perceived to be difficult (Thornley, 2011) and efforts to include non-structural carbohydrates are in their infancy (Jones *et al*., 2019).

Plant respiration has been widely observed to scale with rates of photosynthesis (O'Leary *et al*., 2017) for a variety of species across a wide range of environmental conditions (Reich *et al.,* 1998). The dependence of nocturnal respiration on photosynthetically produced substrate availability mediates the link between night-time metabolism and daytime metabolic productivity (Breeze and Elston, 1978; Azcón-Bieto and Osmond, 1983; Mullen and Koller, 1988; Noguchi *et al*., 1996; Noguchi and Terashima, 1997). Robust correlations between carbohydrates and respiration at night have been observed in experiments that subjected plants to varying photosynthetic conditions during the preceding light period (Azcón-Bieto *et*

al., 1983; Noguchi, 2005; Florez-Sarasa *et al*., 2012; Peraudeau *et al.,* 2015), indicating a relationship may exist between nocturnal respiration and photosynthesis during the preceding day. Following a day of favourable photosynthetic conditions, high concentrations of carbohydrates enhance respiratory capacity and facilitate higher rates of respiration at night (Lambers *et al*., 2008; Whitehead *et al*., 2004; Plaxton and Podesta, 2006). The size of the carbohydrate reserve also regulates the rate of sucrose export throughout the night, which itself is a major ATP demand (Bouma *et al*., 1995; O'Leary *et al*., 2017), causing supply and demand to be linked in the regulation of nocturnal respiration. Conversely, other studies have shown that day-time photosynthetic capacity may be related to the amount of respiration during the previous night. Turnball *et al*. (2002) found increased rates of nocturnal respiration due to elevated night-time temperature to result in increased photosynthesis on the following day. The coupling of respiration and photosynthesis is therefore complex and operates in both directions, involving multiple mechanisms, and must be considered in order to understand temporal variation in leaf and plant respiration.

4.2.2. Light Availability and Canopy Position

Due to the dependence of photosynthesis on irradiance, photosynthetic capacity is found to vary with canopy position due to changes in light availability (Hirose and Werger, 1987; Hollinger, 1989; Field, 1983; 1991; Evans, 1993; Anten *et al*., 1995; Hollinger, 1996). Consequently, carbohydrate concentration varies through a canopy as light extinction increases and carbon assimilation decreases, limiting the formation of respiratory substrates in the lower canopy (Atkin *et al*., 2000a). Upper canopy leaves receive the most direct sunlight and contain more soluble sugars and starch to support greater rates of respiration (Azcón-Bieto and Osmond, 1983). Therefore, respiratory capacity also varies with canopy position due to the link between photosynthetically produced substrate and light availability (Bolstad *et al*., 1999; Carswell *et al*., 2000; Meir *et al*., 2001; Griffin et al., 2002). Since the pioneering work of Boysen-Jensen (1932), shade-tolerant species have been recognised to generally exhibit lower rates of respiration than sun-adapted species. For the sun species, *Spinacia oleracea,* Noguchi *et al*. (1996) found the respiratory rate of leaves grown at 500μmol m^{-2} s^{-1} to be significantly higher than those of leaves grown under lower light intensities ($p<0.05$) due to an increase in the concentration of carbohydrates with higher daytime irradiance. Conversely, respiration rate of the shade-adapted species, *Alocasia macororrhiza,* was found to be independent of carbohydrate concentration (Noguchi *et al*.,

1996), indicating that the regulation of respiration in sun and shade species may differ. Noguchi and Terashima (1997) ascribed the low respiratory rate of the shade-adapted species, *Alocasia odora*, to its low demand for ATP and low ATP consumption rate by cellular processes such as phloem loading. Differences in the type of phloem loading and related energy cost may also influence respiratory rates. Symplastic loading, such as that in *Alocasia odora*, requires no energy cost whereas apoplastically loading plants require ATP for carbohydrate export (Noguchi *et al.,* 1996). The rate of respiration in sun species is thus likely to be determined by substrate supply, whereas the rate of respiration in shade species may be regulated more by the ATP demand of cellular processes such as phloem loading. Both the regulation and rate of leaf respiration is therefore likely to depend on light environment and vary with canopy position.

Sunlit leaves, positioned in the sunlight throughout most of the day, were selected for measurement in this study to capture the variation in nocturnal respiration that occurs independent of temperature, partly driven by changes in leaf carbohydrate status throughout the night. Data for only two shade-adapted species, *Alocasia macororrhiza* and *Alocasia odora,* were extracted from the existing literature and included in analysis (Noguchi and Terashima, 1997; Noguchi *et al*., 1996; 2001). Nocturnal respiration rate of the two shade-adapted species to decrease under constant temperature conditions, with $R_{To}/R_{To\text{-}initial}$ values of 0.88 and 0.78 for *Alocasia macororrhiza* and *Alocasia odora* respectively after eleven hours in darkness (Figure 3.2). However, the decline in $R_{To}/R_{To\text{-}initial}$ is significantly greater for the sun-adapted species extracted from the same studies. Figure 3.2. shows $R_{To}/R_{To\text{-}initial}$ of *Phaseolus vulgaris* to decrease to 0.48 after twelve hours in darkness, whereas $R_{To}/R_{To\text{-}initial}$ of *Spinacia oleracea* is 0.56 after eleven hours in darkness. The results from these studies indicate that the decline in the respiration rate of shaded species at night may be less significant than the decline observed for sunlit leaves, potentially due to differences in the regulation of respiration, substrate availability and energy demand of cellular processes such as phloem loading (Noguchi *et al*., 1996). Therefore, the novel model for the non-temperature dependency of nocturnal leaf respiration, which is predominantly based on the measurement of sunlit leaves, may be more representative of leaves in the upper canopy that are exposed to higher levels of radiation. Further research on nocturnal respiration in shaded leaves and understory species is needed to better determine the impact of light environment on respiration at night and ensure the model is representative of the entire canopy.

4.3. Circadian Clock Control

4.3.1. Rhythms in Leaf Respiration

The importance of endogenous rhythms in gas exchange presents a previously unrecognised challenge for interpreting and modelling land-atmosphere CO_2 exchange. The results of this study show that diel variation in leaf respiration cannot be interpreted according to environmental changes alone, but rather tropical and temperate plants possess endogenous rhythms that are currently poorly understood. Respiratory CO_2 release is the net effect of myriad processes, yet the circadian clock is the only established mechanism known to create self-sustained patterns with a 24-hour period under constant environmental conditions (McClung, 2006; Müller *et al.,* 2014). It is beyond the scope of this study to separate and quantify the individual roles of the circadian clock and other endogenous processes in the co-regulation of leaf respiratory metabolism at night. However, evidence for the control of nocturnal respiration by the circadian clock mechanism is apparent in other studies, although studies of this kind remain limited. Doughty *et al*. (2006) examined variation in the respiratory rate of leaves exposed to 20-48 hours of constant darkness and environmental conditions. The rate of respiration began to decline at 13:00LT and recover from 06:00LT, demonstrating the down-regulation of respiration at night which took the form of a sinusoidal wave over a 24-hour period without any further exposure to light. This pattern in respiratory CO_2 release does not reflect the linear degradation of starch and decrease in respiratory substrate availability that occurs in darkness (Graf *et al*., 2010), but rather reflects a rhythm characteristic of the circadian clock. Gessler *et al*. (2017) also detected sinusoidal rhythms in leaf-level respiration when transferred to constant darkness for a 30-hour period. The lack of a significant correlation between respiration rate and sugar and starch content indicates that substrate availability was not responsible for the observed rhythms in leaf respiratory CO_2 release, but rather implicates the circadian clock.

The circadian clock uses external cues to create a synchrony between the internal rhythmicity of the oscillator and the external rhythmicity of the environment in a process termed entrainment, enabling the plant to trigger metabolism responses at certain points during a diel cycle (Müller *et al*., 2014). Asynchronous circadian regulation may occur if the plant experiences different light and temperature regimes (Resco de Dios *et al*., 2016), resulting in a weak coupling of circadian rhythms between plant cells exposed to different environmental

cues which can also reset the clock and affect the rhythmic amplitude of circadian clock outputs (Rascher *et al*., 2001). Canopy position is therefore likely to affect the coordination and amplitude of rhythms in plant respiration due to different light and temperature regimes through the canopy. Shaded plants and understory species may not experience significant diurnal cycles of light compared to leaves in the upper canopy, resulting in clocks that are dissonant from the environment and not correctly tuned to day-night cycles. A pioneering study by Williams and Gorton (1998) was the first to test the relevance of circadian rhythms for modelling gas exchange in field settings by examining the effect of circadian rhythms on daily courses of CO_2 exchange for *Saururus cernuus* L. The authors found model goodness-of-fit to increase by only 1% when adding sinusoidal variation to a biochemical model of gas exchange, leading to the conclusion that circadian regulation of gas exchange in the field was insignificant. The negative results from this pioneering investigation may explain the subsequent lack of interest on this topic. However, it must be acknowledged that Williams and Gorton (1998) studied an understory species, grown under a closed canopy of *Alnus serrulate,* which typically experience low light levels punctuated with intermittent sunflecks. The results of this study corroborate the theory that regulation of leaf respiration by the circadian clock may be more prominent in upper canopy leaves and overstory plants due to the diminishment of environmental cues through the canopy (Resco de Dios *et al*., 2016). Therefore, the disparity in patterns of nocturnal respiration between the shade species (*Alocasia macororrhiza* and *Alocasia odora*) and sun species (*Phaseolus vulgaris* and *Spinacia oleracea*), previously discussed in Figure 3.2., may also be the result of differences in circadian clock entrainment and the amplitude of circadian rhythms.

4.3.2. Interactivity of the Circadian Clock and Carbon Metabolism

The effects of the circadian clock and respiratory substrate supply on nocturnal respiration meet in a complex nexus. Day-time assimilation of carbon to fuel respiratory metabolism at night results in a diurnal cycle of starch accumulation and depletion (Stitt and Zeeman, 2012; Zeeman *et al*., 2007). Recent reports have demonstrated the importance of the circadian clock in regulating carbohydrate assimilation and starch metabolism in order to optimise plant growth (Dodd *et al*., 2005; Graf *et al*., 2010; Graf and Smith, 2011; Stitt and Zeeman, 2012), with the results of some studies indicating starch synthesis and degradation to be under strict circadian control (Weise *et al*., 2006). The rate of starch degradation at night is believed to be controlled according to the dawn anticipated by the circadian clock, such that 95% of the

starch is used by dawn (Smith and Stitt, 2007; Gibon *et al*., 2004; 2009). Graf *et al*. (2010) found the rate of starch degradation to immediately decrease following a shortened light period with no symptoms of starvation throughout subsequent longer nights, demonstrating a plants remarkable ability to adjust the rate of starch degradation in response to changes in day length. When the circadian clock does not match the external light-dark cycle, growth rate is significantly reduced due to sucrose starvation at the end of the night, therefore the capacity to anticipate dawn is essential for the optimal utilisation of carbohydrate reserves for nocturnal respiration (Graf *et al*., 2010). The molecular nature of the timer that sets the rate of starch degradation remains to be elucidated, however a cluster of genes encoding enzymes implicated in starch metabolism have been found to be under circadian clock control (Harmer *et al*., 2000). Recent findings further indicate that the products of photosynthesis in turn feed back to the circadian clock to help set its timer and rhythm, implying that the circadian clock both controls and is controlled by carbon metabolism (Sanchez *et al*., 2011; Farre and Weise, 2012; Haydon *et al*., 2013).

The expression and amplitude of circadian rhythms in respiration may also be affected by the availability of carbohydrate, further complicating the interactive roles of the circadian clock and respiratory substrate supply. Hennessey *et al*. (1993) reported no rhythm in respiration to occur when leaves of *Phaseolus vulgaris* L. were transferred to constant darkness. Gessler *et al*. (2017) conducted a similar experiment using the same plant species entrained under a PAR of 500μmol m^{-2} s^{-1} and found significant circadian rhythms in leaf respiration, directly contradicting the results of Hennessey *et al*. (1993). The lack of rhythmicity in the experiment conducted by Hennessey *et al*. (1993) may be related to the fast depletion of respiratory substrate in darkness due to the entrainment of plants under low levels of radiation (200μmol m^{-2} s^{-1}), limiting the assimilation of carbohydrates to serve as respiratory substrate. When transferred to constant darkness, Gessler *et al*. (2017) observed a decrease in non-structural carbohydrate concentration. Although the circadian rhythm in respiration was sustained, decreasing substrate availability would likely dampen the amplitude of the rhythms over time, with substrate limitation beginning to control respiration. The depletion of carbohydrates and observed dampening of the circadian rhythm suggests the importance of circadian regulation as a driver of leaf respiration may be underestimated in both experiments and play a more significant role in natural environmental conditions where radiation can exceed 1500μmol m^{-2} s^{-1}. The roles of the circadian clock and respiratory substrate

availability appear intrinsically linked, highlighting the difficulty in separating the individual effect of each process on nocturnal respiration. The complex and synergistic relationship between these endogenous mechanisms also emphasises the importance of considering the effects of light availability, photosynthesis and canopy position in the study of leaf respiration.

4.3.3. Ecosystem Rhythms and Ecological Relevance

One of the major assumptions underlying many studies of land-atmosphere exchange is that diurnal patterns observed in ecosystem fluxes are driven almost exclusively by direct physiological responses to changes in the environment, such as cycles of light, temperature and humidity (Hollinger *et al*., 1994; Sellers *et al*., 1997; Chapin *et al.,* 2002; Hanson *et al*., 2004). However, this study has shown endogenous rhythms in metabolism to co-regulate diurnal patterns in plant gas exchange. The molecular mechanisms of circadian control are well described (Harmer, 2009) and the circadian clock is now recognised to be a central orchestrator of plant activity, with increasing evidence for circadian oscillations in leaf-level respiration (Doughty *et al*., 2006; Gessler *et al*., 2017). Despite this, ecological relevance of the circadian clock has been largely overlooked and its influence becomes more ambiguous at higher organisational scales.

Resco de Dios *et al*. (2012) used eddy covariance data from the AmeriFlux network to examine diurnal oscillations in Net Ecosystem Exchange (NEE) at seven sites, representative of contrasting climate regions and vegetation types. The authors observed significant rhythmic variation in day-time NEE to occur at six of the sites when analysing data under nearly constant environmental conditions. Variation in day-time NEE was between 20% and 90% of that observed under variable environmental conditions, averaging at 48% across all sites. Each environmental variable under constant conditions was found to typically explain less than 1% of NEE, contrasting with the current conventional understanding that daily NEE variations are driven almost exclusively by the environment. NEE is often dominated by soil CO_2 efflux (Janssens *et al*., 2001), yet Resco de Dios *et al*. (2012) found soil respiration to exhibit an invariant or different temporal trend, indicating the day-time rhythms in NEE were driven by plant gas exchange. However, the authors did not find rhythms in night-time NEE under constant conditions. As previously discussed, it is expected that a dilution of circadian effects will occur with increasing scale. First, if circadian regulation does not occur in soil

respiration it may mask rhythms in ecosystem scale fluxes. Second, leaves experience different light environments and environmental cues in a layered canopy, possibly resulting in uncoupled rhythms across leaves and plants which dilutes circadian rhythms at higher organisational levels. Furthermore, there is considerable uncertainty around the reliability of night-time eddy covariance measurements. Advective and low frequency flows of CO_2 are difficult to capture, particularly in periods of low air turbulence which are typical at night, often resulting in inaccurate estimates of ecosystem fluxes (Aubinet *et al*., 2012). A subsequent study by Resco de Dios *et al*. (2016), which examined both canopy and leaf-level fluxes under constant environmental conditions, found 20% to 79% of daily variation in the CO_2 exchange of *Phaseolus vulgaris* and *Gossypium hirsutum* canopies could be recreated fully independently of environmental change due to circadian entrainment. Circadian rhythms in canopy carbon assimilation were found to be comparable to that documented in temperature response curves, leading to diurnal flux variation of the same order of magnitude as that caused by changes in temperature. Circadian regulation was again diluted with increasing scale, yet a significant self-sustained 24-hour oscillation in carbon assimilation was still observed at canopy level. Resco de Dios *et al*. (2016) found a higher dilution of circadian regulation at canopy level in *Phaseolus vulgaris.* This could be explained by the higher LAI in *Phaseolus vulgaris* (7.5 m^2 m^{-2}) compared to *Gossypium hirsutum* (4.5 m^2 m^{-2}), resulting in a higher proportion of shaded leaves, further highlighting the relative importance of the structure of a layered canopy and the role of light availability in entraining the circadian clock and discerning rhythms at canopy and ecosystem scales.

Gessler *et al*. (2017) assessed whether circadian regulation of night-time respiration of *Phaseolus vulgaris* and *Gossypium hirsutum* scaled from leaf to canopy level. The authors found canopy respiration to exhibit significant temporal sinusoidal variation under constant environmental conditions when exposed to a 30-hour period of constant darkness. No significant relationship was found between respiration and temperature, relative humidity, or non-structural carbohydrate content, indicating environmental cues and substrate availability were not responsible for the variations. The patterns in respiration observed at canopy level reflected leaf-level oscillations and were comparable across both species, contrasting with previous studies that found night-time rhythms in ecosystem gas exchange to be insignificant (Resco de Dios *et al*., 2012). The results of Gessler *et al*. (2017) demonstrate the circadian clock to modulate biosphere-atmosphere interactions across different scales, providing a new understanding of ecological systems that directly connects molecular mechanisms with land-

surface processes in previously unrecognised ways. The control of leaf respiration by endogenous mechanisms such as the circadian clock must be accounted for in vegetation and earth system models to simulate ecosystem fluxes, with potentially large implications for studies of land-atmosphere exchange and current estimates of global carbon balance.

4.4. Implications for Modelling

4.4.1. Effect on Tropical and Temperate Forest Sites

Most biosphere models assume that leaf and plant respiration increase exponentially with temperature and simulate daytime and night-time respiration equivalently. Fatichi *et al.* (2019) suggest a possible justification for the use of this very simple method to model respiration is that respiration is less temporally dynamic than the process of photosynthesis, however this theory is rebutted by the significant decline in nocturnal respiration as a function of time in darkness exemplified in this study (Figure 3.2. and 3.3.). The data collected in this investigation directly contradicts the past two decades of literature on the exponential relationship between temperature and respiration that invariably predicts an increase in leaf respiration with increasing measurement temperature (Tjoelker *et al.,* 2001; Atkin and Tjoelker, 2003). This erroneous and incomplete theory of the control of plant respiration, upon which the exponential Q_{10} function to model plant respiratory CO_2 efflux is founded, forms the basis of virtually all modern studies on plant respiration. Although it has been acknowledged that models using a constant Q_{10} are biased (Tjoelker *et al*., 2001) and there is a growing appreciation of the inadequacies of the empirically derived temperature function (Davidson *et al*., 2006), it is dangerous to continue to ignore endogenous regulation which may have profound impacts on predicted ecosystem carbon exchange. Plant respiration is fuelled by and dependent upon a range of endogenous metabolism components, however the individual contribution of the processes responsible for the quantitative variation found in nocturnal respiratory rates remains unclear. Great difficulty lies in untangling the endogenous mechanisms that co-regulate respiration at night to determine their separate impacts, preventing the development of a fully mechanistic model. Therefore, this study proposes the use of an empirically derived non-temperature dependent term to represent the combined effect of these endogenous processes on the rate of nocturnal leaf respiration that otherwise remains unaccounted for (Eq. 10).

Plant respiratory CO_2 release has been identified as a major source of uncertainty in modelling the carbon cycle and is currently overestimated by vegetation and land surface models (Blyth *et al*., 2011; Huntingford *et al.,* 2017). Accounting for the non-temperature dependency of nocturnal respiration notably reduces annual rates of modelled respiration and increases simulated NPP across all forest sites in this study (Figure 3.13.), contrasting with other recent modelling advances. Huntingford *et al.* (2017) applied the new R_{d25} derived from the GlobResp dataset, a temperature sensitivity function and thermal acclimation response to JULES and found these advances to enhance plant respiration and lead to extremely low NPP. Contrarily, the non-temperature dependent term reduces respiration and increases NPP, with a particularly significant effect on tropical forest sites due to the impact of night length and nocturnal temperature decrease. The cumulative difference in nocturnal respiration due to the inclusion of non-temperature controls is likely to increase with length of night and slow the natural cooling of the environment (Figure 3.4). Tropical forests typically experience year-round warm temperatures and comparatively small ranges of diurnal and seasonal temperature and night length (Malhi *et al*., 1999). The cumulative difference in respiration between standard modelling (S1) and the use of the non-temperature dependent term (S3) was found to be most significant for tropical sites, such as French Guiana and China, due to greater night lengths (~12 hours) and minimal temperature change throughout the night (Figure 3.14). Tropical forests are responsible for approximately one third of global terrestrial primary productivity (Huntingford *et al.,* 2013), therefore the reduction in annual respiration and increase in NPP by up to ~10 and ~16% respectively presents important implications for modelling the carbon exchange of tropical forest biomes. Temperate forest study sites, such as those in France and Italy, experience shorter nights (~10 hours) and a greater decrease in nocturnal ambient temperatures (~10°C), indicating these sites are under greater temperature control, resulting in a reduced decrease in nocturnal respiration. Despite experiencing a low speed of cooling at night, the impact of the non-temperature dependent term is the least significant at sites such as the US and Canada that experience the shortest nights of less than ~8 hours (Figure 3.14. and 3.15), indicating that the effect of the novel term is more dependent on night length than cooling speed. Daytime respiration was not considered in the development of the novel modelling approach in this study. The new modelling of nocturnal respiration that includes both the non-temperature dependent term and the temperature-dependent Q_{10} (S1-S5) has a significant impact on rates of 24-hour plant respiration, resulting in up to a 10.6% reduction in respiration and 18.7%

increase in NPP when integrated at the annual scale (Figure 3.13). This highlights the influence of the parametrisation of respiration at night on the simulation of diurnal and annual fluxes which has previously been overlooked. A 10% reduction in annual rates of plant respiration due to the new modelling of nocturnal respiration in this study suggests that the current estimate of global plant respiratory carbon flux (~60 Gt C yr^{-1}; Canadell *et al*., 2007; IPCC, 2013) could be overestimated by up to ~6 Gt C yr^{-1}. The direction of the effect of the non-temperature dependent term on modelled respiration and NPP is consistent across all biomes and forest types in this study, suggesting that models have previously overestimated respiration and underestimated NPP, particularly in the tropics, which may have ramifications for estimates of global terrestrial carbon balance and storage. To further the site-specific modelling presented in this study, the global impact of the non-temperature dependent term across all geographic regions should be assessed by running global model simulations, enabling the effect of the novel term on estimates of global carbon balance to be evaluated.

4.4.2. Model Validation

It is often suspected that incorporation of empirical time-vary functions into current models to represent endogenous effects is likely to lead to only limited improvements in model fit and predictive capacity (Resco de Dios *et al*., 2012). However, evaluation of the formulation presented in this study (Figure 3.5 to 3.8) shows that addition of the novel non-temperature dependent term for nocturnal respiration significantly improves predictive capacity by reducing the simulation of respiration, resulting in more accurate estimations of leaf respiration throughout the night. A statistically significant difference was found between the effect of the temperature-independent term on tropical and temperate forests when incorporated into JULES, however the ambient datasets used for model evaluation contain measurements of only temperate species. Furthermore, the new model, which is founded upon the study of predominantly broadleaf species, may not accurately represent variation in nocturnal respiration of needleleaf species. Differences in nocturnal respiration between these PFTs may result in disparities between predicted and observed values of respiration that persist for the needleleaf species, *Picea abies* (Figure 3.7 and 3.8). Additional datasets taken under ambient conditions from tropical forest sites and further data sets from temperate broadleaf species are therefore required for further model evaluation. Despite the shortcomings and limited availability of the datasets used to evaluate the models, application

of the non-temperature dependent term is found to improve overall model performance and reduce model bias (Figure 3.9. and 3.10.).

Model evaluation shows application of a temperature-dependent Q_{10} to the description of leaf respiration causes only a minor reduction in respiratory rates at night, resulting in a model that still notably overestimates rates of respiration. The potential temperature-dependency of the Q_{10} function has received significant research attention (Wager, 1941; James, 1953; Ivanova *et al*., 1989; Gillooly *et al*., 2001; Tjoelker *et al*., 2001; Bruhn *et al.,* 2002; Covey-Crump *et al*. 2002; Atkin and Tjoelker, 2003), despite its relatively inconsequential effect on simulated rates of respiration observed in this study. The non-temperature dependent term for variation in nocturnal endogenous metabolism was found to generate a much larger reduction in predicted respiration than the temperature-dependent Q_{10}. After incorporating the new R_{d25} from GlobResp, Huntingford *et al*. (2017) found addition of the temperature sensitivity function to result in negligible changes in simulated respiration at the seven tropical forest sites and a minor reduction in respiration at the two temperate sites, substantiating the relatively inconsequential impact of the temperature-dependent Q_{10} found in this study (Figure 3.5. to 3.8). The acclimation of plant respiration to long-term changes in thermal environment and its impact on modelled CO_2 exchange has also received wide research attention and has been extensively studied (Billings *et al*., 1971; Larigauderie and Korner, 1995; Collier, 1996; Fitter *et al*., 1998; Tjoelker *et al*., 1999a; 1999b; Atkin *et al*., 2000b; 2000c; Covey-Crump *et al*., 2002; Slot *et al*., 2014; Vanderwel *et al*., 2015). Atkin *et al.* (2008) found accounting for the acclimatory response of plant respiration in a land surface model to have a negligible impact on predicted annual rates of global respiration, NPP and future atmospheric CO_2 concentrations. However, the authors did find acclimation to reduce predicted rates of respiration by up to 20% in some hot tropical regions, leading to the conclusion that the acclimation of respiration should always be included to model the response of the terrestrial carbon cycle to climate change. The impact of the non-temperature dependent term on rates of annual NPP in some regions obtained in this study (Figure 3.13) is of a similar order of magnitude to that of thermal acclimation in high-temperature biomes obtained by Atkin *et al*. (2008), with a greater overall effect on global respiration and NPP across all geographic locations in this study. Further addition of a thermal acclimation response to the study by Huntingford *et al.* (2017) minorly reduced respiration at the tropical sites and increased respiration at the temperate, cooler climate sites, London and Siberia. Inclusion of these functions by Huntingord *et al*. (2017) had a minimal overall impact on

simulated plant respiration across all sites in the study, especially when compared to the comparatively inordinate increase in respiration as a result of the new R_{d25} which does not account for temporal variation in endogenous respiratory metabolism. Wythers *et al*. (2005) also investigated the consequences of including both thermal acclimation and the temperature-variable Q_{10} function from Tjoelker *et al*. (2001) in an ecosystem model. The authors found the combined effect of both algorithms to reduce annual foliar respiration by 31-41% across the four sites in the study. A subsequent study by Wythers *et al*. (2013) which similarly incorporated both an acclimation response and a temperature-sensitive Q_{10} found the combined effect to increase NPP by an average of ~25% across the four sites. This increase in NPP due to the combined effect of thermal acclimation and a temperature-variable Q_{10} is of a similar order of magnitude to the impact of the non-temperature dependent term alone on NPP at tropical sites in this study. It also must be noted that Wythers *et al*. (2005; 2013) only represent temperate North American sites in these studies, therefore the results reflect the combined impact of thermal acclimation and a temperature-dependent Q_{10} at temperate forest sites only. Ultimately, regulation of nocturnal respiration by temperature-independent mechanisms may have a more consequential individual impact on simulations of terrestrial CO_2 exchange than thermal acclimation and the temperature-dependent Q_{10}, yet the non-temperature dependency of respiration has received a disproportionate amount of attention and efforts to measure, quantify and incorporate it in models remain scarce. The model evaluation presented emphasises the importance of validating the use of a non-temperature dependent term and demonstrates that inclusion of endogenous rhythms in nocturnal metabolism increases the biological realism of vegetation and land-surface models.

4.4.3. Modelling Considerations

Several factors in the modelling approach of this study must be considered in order to understand potential shortcomings of the model and enable the development of future models. First, the term describing the non-temperature dependency of nocturnal respiration is constructed using data from predominantly broadleaf trees and herbaceous species and a small number of grasses. The significant findings of this investigation provide a rationale for the further study of nocturnal rhythms in other plants, such as needleleaf species, to determine whether the model is representative of all PFTs. Second, the novel non-temperature dependent term is primarily founded upon the study of sunlit leaves, largely representative of leaves in the upper canopy exposed to a high light environment. As

previously discussed, there is sufficient evidence for a distinct difference in the respiration of sun and shade adapted plants (Noguchi and Terashima, 1997; Noguchi *et al*., 1996; 2001), signifying the need to measure and quantify temporal variation in nocturnal respiration of more shade-adapted leaves and understory species to ensure the model is representative of a layered canopy. Lastly, this study focuses exclusively on the non-temperature dependency of respiration at night. A principle feature of the circadian clock mechanism is that it drives 24-hour rhythms over a diel cycle, indicating there is also likely to be temporal variation in day-time dark respiration due to circadian clock control and other endogenous mechanisms that may exhibit diel oscillations. The improved Kok method, recently proposed by Buckley *et al.* (2017), could be employed to test for day-time rhythms in dark respiration in the light by measuring CO_2 assimilation under decreasing Photosynthetic Photon Flux Density (PPFD) at regular intervals over the diurnal cycle. Addition of these day-time measurements to the existing dataset of nocturnal respiration would enable the development of a 24-hour model of the non-temperature dependency of plant respiration over the entire diel cycle, offering a further improvement to the novel non-temperature dependent term for nocturnal respiration proposed in this study.

Datasets used to develop current models of leaf respiration assume the base rate of respiration is constant and do not consider the time at which measurements were taken during the diurnal cycle (e.g. GlobResp by Atkin *et al*., 2015; new model for plant respiration by Heskel *et al*., 2016), thereby failing to recognise the time-dependency of respiration, the importance of which has been demonstrated in this investigation. Consequently, temporal variation in endogenous metabolism may already be partly captured by existing models. The circadian clock has a diurnal temporal pattern, which co-varies with temporal cues of the environment, therefore any model that considers variation in environmental drivers is indirectly incorporating circadian clock regulation (Gessler *et al*., 2017). Furthermore, since temperature and endogenous metabolic status both co-vary with time, previous research establishing the effect of temperature on ecosystem respiration may be confounded by endogenous regulation and contribute to the observation that the temperature sensitivity of ecosystem respiration is not constant (Gessler *et al*., 2017). Empirical and mechanistic models of respiration that already incorporate diurnal changes in temperature are thus likely to indirectly absorb a large portion of the variation in daily carbon exchange attributed to endogenous rhythms in metabolism.

The time-dependency of respiration was not considered in the dataset employed by Tjoelker *et al*. (2001) to develop the temperature-dependent Q_{10} used in this study, therefore this term may also erroneously capture temporal changes in endogenous metabolism. For tropical forest sites, which experience only a minor decrease in temperature at night, there is little difference between the effect of the novel non-temperature dependent term when incorporating the standard (Figure 3.14.) or temperature-dependent Q_{10} (Figure 3.15.) This is also evident in Figure 3.13. which shows the effect of the non-temperature dependent term on annual rates of respiration and NPP to be of a similar magnitude when using a fixed Q_{10} (S1-S3) and temperature-dependent Q_{10} (S2-S4) at the tropical sites. Conversely, the effect of the novel term on rates of annual respiration and NPP at temperate sites, which experience a more significant drop in night-time temperatures (~10°C), is markedly reduced when using a temperature-dependent Q_{10}, a discrepancy that is consistent across all temperate and cold climate sites (Figure 3.13.) In these regions that experience greater night-time temperature change, the decrease in respiration that occurs at night appears to be partially accounted for by the temperature-dependent Q_{10} function, thereby reducing the overall effect of the non-temperature dependent term (Figures 3.14 and 3.15). This suggests the two terms overlap or interact and brings into question the validity of the temperature-dependent Q_{10} which has also been challenged by several studies reporting no temperature effect on Q_{10}. Bruhn *et al*. (2008) found high Q_{10} values for *Pringlea antiscorbutica* to coincide with high ambient measurement temperatures, contrasting to the concept of the temperature-dependent Q_{10} that decreases with rising temperature (Tjoelker *et al*., 2001; Atkin and Tjoelker, 2003). Atkin and Tjoelker (2003) explained this by reduced respiratory enzyme activity at low temperatures and respiratory substrate limitations, however the relatively high leaf carbohydrate concentrations for *Pringlea antiscorbutica* found by Bruhn *et al*. (2008) may partly negate this theory. Further cases in the published literature found no temperature effect on Q_{10}, such as for potato (Lungegardh, 1924) and *Quercus* and *Acer* species (Boldstad *et al*., 1999), and some studies show the opposite effect of increasing Q_{10} with increasing temperature (Stocker, 1935). The time-dependency of respiration must be considered in future research on the temperature-dependent Q_{10} function to resolve conflicts in the literature and validate the concept for modelling leaf and plant respiration.

4.5. Consequences for Land-Atmosphere Studies

It is important to consider the broader implications for studies of land-atmosphere exchange that rely upon the common assumption that the base rate of respiration is constant to quantify ecosystem carbon balance and its components. Eddy covariance micro-meterological techniques and ecology-based biometric methods are the two primary methodologies to quantify CO_2 exchange between terrestrial ecosystems and the atmosphere (Campioli *et al.,* 2016). Eddy covariance provides continuous observations at ecosystem scale and is the dominant methodology for the long-term monitoring of net ecosystem-atmosphere exchange, however the component processes of ecosystem GPP and respiration can only be estimated by post-processing data. Biometric methods for assessing forest carbon balance use a set of techniques such as plant growth assessment and chamber-based flux measurements to directly estimate the component processes that are subsequently upscaled, however they lack the high temporal frequency and continuity of eddy covariance. The different methods to quantify ecosystem carbon exchange are therefore subject to different sources of error and uncertainty and are often cross-checked against each other for consistency and accuracy.

Flux Partitioning Models (FPMs) are relied upon to separate eddy covariance NEE measurements into Gross Ecosystem Productivity (GEP) and Ecosystem Respiration (RE) and commonly follow two approaches: the extrapolation of night-time respiration measurements to the daytime, or the estimation of daytime respiration from light-response curves which is extrapolated to the night, both through the use of a temperature response function (Falge *et al.,* 2001). One of the key assumptions behind this extrapolation of night-time data to estimate daytime respiration and vice versa is that the base rate of respiration is constant. The annual Q_{10} method and the short-term exponential model developed by Reichstein *et al.* (2005) model RE as a function of temperature using the Q_{10} approach (Eq. 2) and an Arrhenius type equation from Lloyd and Taylor (1994) respectively. Both employ a base rate of respiration at a reference temperature and a temperature sensitivity function to extrapolate night-time respiration to the daytime. Other methods involve extrapolating respiration from light-response curves conditioned on daytime data which do not accurately represent the respiratory process at night and similarly use the temperature response of respiration for extrapolation, again assuming a constant base rate of respiration (Lasslop *et al*., 2010). Rates of GPP are subsequently calculated as the difference between measured NEE and modelled RE fluxes, therefore any error in estimates of RE is automatically

transferred to GPP and can influence understandings of terrestrial carbon flux (Luyssaert *et al*., 2009). This study has consistently shown that it is not appropriate to extrapolate night-time respiration to estimate daytime respiratory flux or vice versa, and respiration cannot be accurately modelled or estimated according to temperature control alone, thereby discrediting the FPMs discussed and casting doubt on current estimates of ecosystem fluxes derived from eddy covariance methods.

Flux partitioning methods can also be used to complete gaps in eddy covariance data time-series that occur under unfavourable meteorological conditions or instrument failure in a process termed gap-filling, allowing estimates of ecosystem CO_2 flux over long time periods (Falge *et al*., 2001; Stoy *et al*., 2006). Typically 20-60% of an annual eddy covariance dataset is missing (Moffat *et al*., 2007), therefore gap-filling using ill-founded FPMs driven solely by temperature can account for a large proportion of long-term eddy covariance datasets and time-series of ecosystem carbon exchange that are increasingly used for ecosystem model calibration and validation.

Flux partitioning of eddy covariance measurements are often checked for quality and consistency based on comparison with biometric measurements of NPP and respiration. Biometric and bottom-up scaling methods for estimating autotrophic respiration use chamber-based gas exchange measurements of leaf, stem and root respiration (Litton *et al*., 2007; Luyssaert *et al*., 2009; Malhi *et al.,* 2009). The significant impact of temporal variation in endogenous metabolic status is currently not recognised and therefore not captured by these biometric studies. Further error is induced when respiration measurements are upscaled and integrated at the annual level using empirical models that relate respiration to temperature and other environmental variables (Khomik *et al*., 2010). Eddy covariance and bottom-up biometric methods for estimating ecosystem fluxes of CO_2 and validating models of ecosystem exchange thus far fail to recognise the importance of non-temperature controls on rates of plant respiration, ultimately representing a fundamental issue in terrestrial biosphere modelling and land-atmosphere studies.

4.6. Plant Respiration and Climate Change

The unprecedented increase in atmospheric CO_2 concentration since the industrial era is likely to continue into the 21st century (Faitichi *et al.*, 2018). As a result of increasing CO_2

levels, climatic and atmospheric conditions are expected to change dramatically throughout the 21st century, with widespread shifts in temperature, precipitation and nutrient availability (Resco de Dios *et al*., 2009). Due to global climate change, the diurnal temperature regimes experienced by plants are changing; global average temperatures are predicted to rise, with the increase in temperature most pronounced at night (Easterling *et al*., 1997; Lambers *et al*., 2008; Kruse *et al*., 2011). Such changes are likely to have important implications for rates of plant respiration due to the temperature sensitivity of respiratory metabolism (Lambers *et al*., 2008). Ecosystem CO_2 exchange is also highly sensitive to the effects of night-time temperature on respiration (Houghton *et al*., 1998), with temperature mediated changes in respiration constituting an important component of the biosphere's response to climate change. Anderegg *et al.* (2015) found interannual variability of the global land carbon sink to have increased by 50-100% over the past fifty years, most strongly linked to tropical night-time warming through its effect on respiration. Night-time warming patterns are likely to differentially affect respiration more than photosynthesis, thereby increasing the proportion of carbon gained by photosynthesis that is subsequently expended by respiration, ultimately reducing carbon uptake (Peng *et al*., 2013; Xia *et al.,* 2014). As a result, Anderegg *et al*. (2015) predict future carbon gains in tropical ecosystems may be offset by greater respiratory losses due to night-time warming. Tropical forests account for 33% of annual primary productivity of the terrestrial biosphere (Beer *et al*., 2010), therefore the future carbon balance of tropical forests has major consequences for society and the rate of climate change. Furthermore, respiration driven losses in forest carbon due to warming constitutes a major scenario through which the terrestrial carbon sink could switch to a source in the 21st century (Cox *et al*., 2000; Sitch *et al.,* 2008; Friedlingstein *et al*., 2014). The findings of Anderegg *et al.* (2015) suggest the sensitivity of respiration to night-time temperatures is the primary mechanism driving variability of the terrestrial carbon sink. Therefore, a robust description of nocturnal respiration is required to accurately predict the response of terrestrial ecosystem carbon balance and storage to future climate change and warming and should be prioritised in the future development of earth system models.

Unprecedented changes in human and biophysical environments have caused the terrestrial biosphere to gain a new political prominence in the context of climate change and the terrestrial carbon cycle is now anchored in international accords such as the Paris Agreement, for which most signatories pledged to use the land carbon sink to meet their greenhouse gas mitigation targets (Grassi *et al*., 2017). Projections of the land carbon cycle and associated

datasets are now relied upon by broad stakeholder communities to mitigate and adapt to anthropogenic climate change, including scientists, policymakers, businesses, and non-governmental organisations (Le Quéré *et al*., 2018). Therefore, building the scientific understanding to meet the climate mitigation challenge requires a more robust quantification of the components of the contemporary carbon cycle and an improved capacity to anticipate its future evolution. There is also an urgent need for data on plant respiration in the agriculture industry, where more energy-efficient crops are required to improve global food security under climate change and an increasing global population (Scafaro *et al*., 2017). A more mechanistic understanding of the drivers of variability in rates of plant respiration is essential for identifying novel approaches to improve energy and carbon use efficiency in crop plants (O'Leary *et al.,* 2019). Ultimately, a better understanding of the terrestrial carbon cycle and an improved capacity to model its underlying processes is required to reliably predict future climate change and support the important development of climate policies. Therefore, the development of a non-temperature dependent term to model nocturnal plant respiration and account for the important effect of endogenous mechanisms in this study serves a much wider and significant purpose in the current political space.

4.7. Limitations

It is imperative to acknowledge the limitations of this investigation and discuss the influence they may exert on the findings and conclusions of this study, in addition to the modelling considerations previously discussed. To determine the temperature response of leaf respiration, artificial temperature manipulations were applied to leaves enclosed in a cuvette while the rest of the plant remained at ambient temperature. The temperature response of respiration measured during whole-shoot temperature manipulation is often markedly larger than those measured by independently manipulating temperature inside a leaf cuvette, resulting in different temperature response functions when leaf temperature is uncoupled from ambient plant temperature. Atkin *et al.* (2000b) found the temperature response of *Eucalyptus pauciflora* to produce a Q_{10} of 2.6 when plant and leaf temperature were the same, compared to a Q_{10} of 2.1 when only leaf temperature was altered. Similarly, the Q_{10} of *Populus deltoides* was found to be 2.1 when leaf temperature matched the rest of the stand, compared to 1.7 when leaf temperature was manipulated alone, resulting in a 21% difference in night-time CO_2 release over a 5-day period (Griffin *et al*., 2002). These results indicate that the temperature of the surrounding plant material has a notable influence on the temperature

response of leaf segments measured in the cuvette. To more accurately generate a temperature response curve, the entire plant should be subjected to changes in temperature using specialised chambers for whole plant respiration. As a result, the inherent Q_{10} values calculated in this study may underestimate the actual short-term temperature sensitivity of leaf respiration.

Further limitations arise from the LI-COR 6400XT equipment used for data collection in this investigation. Multiple CO_2 canisters were required to maintain a constant CO_2 concentration in the leaf chamber throughout the night. Changing the cannister during night-time measurements at constant temperature exposed the leaf to short-term fluctuations in CO_2 concentration over the timescale of a few minutes and minorly impacted the rate of respiration, identifiable in plots of the raw data. Hourly averages of respiration were calculated to resolve this issue and stabilise the overall trend. Differentiating between the effect of substrate availability and the circadian clock is also beyond the capacity of the equipment and experimental setup used in this study due to difficulties in maintaining a constant environment for a 24-hour period in field experimental conditions. Furthermore, data collection was only possible in growing season in the UK, therefore seasonal time constraints minimised opportunities for data collection.

5. Conclusions

5.1. Summary of Findings

The significant decline in the rate of respiration at night under constant temperature conditions observed in this study demonstrates the existence of nocturnal rhythms in endogenous metabolism, consistent across biomes, species and experimental conditions. The basal rate of respiration decreased by ~40% of the initial rate at the onset of darkness due to temperature independent controls such as substrate availability, product demand and the circadian clock which were found to be responsible for approximately half of the variation in rates of plant respiration at night. The down-regulation of respiration at night due to control by endogenous mechanisms refutes the common assumption that temperature is the only driver of respiration over the short-term and invalidates the use of a single exponential Q_{10} temperature function to model plant respiratory CO_2 efflux. The headline result of this study is that the base rate of respiration is not constant over a 24-hour period as generally assumed in all modern studies and models, further proving the use of a fixed exponential Q_{10} function is insufficient to fully describe nocturnal variation in endogenous metabolism with natural variation in ambient temperature. The development of a new function for nocturnal leaf respiration demonstrates how nocturnal variation in endogenous metabolism can be accounted for by coupling respiration to time of night. Evaluation of the new function revealed the standard description for respiration to consistently overpredict rates of nocturnal respiration throughout the night when compared to observed values. Inclusion of the non-temperature dependent term reduced the simulation of nocturnal respiration, improving overall model performance and reducing model bias in this study. Application of the term for the non-temperature dependency of nocturnal respiration to JULES reduced annual rates of modelled respiration by up to 10% and increased NPP by up to 16% across all tropical and temperate forest sites, suggesting that models have previously overestimated respiration and underestimated NPP, particularly in the tropics. The effect of the non-temperature dependent term on modelled respiration and NPP was found to be significantly greater than the effect of the widely studied temperature-dependent Q_{10} function and thermal acclimation response. Considering the significant impact of the non-temperature dependency of respiration, it has received a disproportionate amount of research attention and presents important implications for land-atmosphere studies, modelling terrestrial biosphere carbon exchange and storage, and global carbon balance. The findings of this study hope to stimulate further interest in this

pressing yet unexplored area of research to develop a deeper consideration of endogenous rhythms in plant respiratory metabolism and increase the biological realism of vegetation and earth system models.

5.2. Future Research

Progress achieved towards understanding the plant circadian clock mechanism and the regulation of plant respiration by substrate supply, product demand and respiratory capacity is remarkable, but much remains uncertain. It is critical that all future research on plant respiration considers the time-dependency of measurements and effort should be made to expand the existing dataset on the non-temperature dependency of respiration. The findings of this study present the opportunity to explore the expression of temperature-independent rhythms in respiration across PFTs and as a function of leaf canopy structure to develop a model that is representative of all PFTs and light environments. Furthermore, this study focuses exclusively on the non-temperature dependency of respiration at night. The investigation of day-time rhythms in dark respiration and addition of these measurements to the existing dataset of nocturnal respiration would enable the development of a 24-hour model of the non-temperature dependency of plant respiration over the entire diel cycle. This understanding could be coupled to models currently being developed to represent non-structural carbohydrate storage. The urgent need to predict the impacts of climate change is promoting the critical re-examination of models that are ultimately the only way to forecast future climate change, therefore the construction of vegetation and earth system models with robust parametrisations of the component processes remains a priority. Expanding the existing dataset on the temperature independent regulation of plant respiration will clarify fundamental controls on plant metabolism and support the development of a more accurate and comprehensive description of respiration in models which has been identified as a major source of uncertainty in modelling the global carbon cycle. Until the non-temperature dependency of plant respiratory metabolism is accounted for in modelling frameworks, the capacity of vegetation and earth system models to simulate vegetation dynamics and carbon balance remains limited.

Appendices

Appendix A – Definition of JULES parameters and symbols.

Symbol	Units	Description
a_{wl}	kg C m^{-2}	Allometric coefficient
D_{crit}	kg kg^{-1}	Critical humidity deficit
d_T		Rate of change of leaf turnover with temperature
f_0		Stomatal conductance parameter
f_{dr}		Leaf dark respiration coefficient
f_{T}		Q_{10} function for carboxylation of Rubisco
h	m	Canopy height
i_{v}	μmol CO$_2$ m^{-2} s^{-1}	Intercept for relationship between N_a and Vcmax$_{25}$
k		Light extinction coefficient
$\mathcal{L}$	kg C m^{-2}	Carbon content of leaf
L_{c}	m^2 m^{-2}	Canopy leaf area index
L_{max}	m^2 m^{-2}	Maximum LAI
L_{min}	m^2 m^{-2}	Minimum LAI
LMA	kg m^{-2}	Leaf mass per unit area
N_{a}	kg N m^{-2}	Leaf nitrogen per unit area
N_{l}	kg N m^{-2}	Leaf nitrogen content
n_{m}	kg N kg^{-1}	Top-leaf nitrogen concentration
N_{r}	kg N m^{-2}	Root nitrogen content
N_{S}	kg N m^{-2}	Stem nitrogen content
$\mathcal{R}$	kg C m^{-2}	Carbon content of roots
$\mathrm{R_d}$	mol CO$_2$ m^{-2} s^{-1}	Leaf dark respiration
$\mathrm{R_{dc}}$	mol CO$_2$ m^{-2} s^{-1}	Canopy dark respiration
r_{g}		Growth respiration coefficient
rootd	m	*e*-folding root depth
$\mathrm{R_p}$	kg C m^{-2} s^{-1}	Plant respiration
$\mathrm{R_{pg}}$	kg C m^{-2} s^{-1}	Plant growth respiration
$\mathrm{R_{pm}}$	kg C m^{-2} s^{-1}	Plant maintenance respiration
S	kg C m^{-2}	Carbon content of respiring stem
s_{v}	μmol CO$_2$ g N^{-1} s^{-1}	Slope between N_a and Vcmax$_{25}$

T_{c}	ºC	Leaf temperature
T_{low}	ºC	Lower temperature parameter for Vcmax
T_{off}	ºC	Threshold temperature for phenology
T_{opt}	ºC	Optimal temperature Vcmax
T_{upp}	ºC	Upper temperature parameter for Vcmax
V_{cmax}	mol CO_2 m^{-2} s^{-1}	Maximum rate of carboxylation of Rubisco at 25ºC
$V_{\mathrm{cmax2\,5}}$	mol CO_2 m^{-2} s^{-1}	Maximum rate of carboxylation of Rubisco at 25ºC
a	mol CO_2 [mol PAR photons]$^{-1}$	Quantum efficiency
β		Soil water stress factor
γ_0	[360 days]$^{-1}$	Minimum leaf turnover rate
γ_p	[360 days]$^{-1}$	Leaf growth rate
η_{sl}		Constant of proportionality relating live stemwood to canopy height and leaf area
μ_{rl}		Ratio of nitrogen concentrations in root and leaves
μ_{sl}		Ratio of nitrogen concentrations in stem and leaves
Π_{G}	kg C m^{-2} s^{-1}	Gross primary productivity
σ_{l}	kg C m^{-1} per unit LAI	Specific leaf density

Appendix B – Replicate level R^2 and MSE values for each function.

		Power		Exponential		Linear x & ln(y)		Linear ln(x) & ln(y)	
Species	**Replicate**	**R^2**	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**
Astronium graveolens	1	0.6126	0.0131	0.6206	**0.0127**	0.5715	0.0228	**0.6243**	0.0200
	2	0.0290	0.0208	**0.1458**	0.0183	0.1440	**0.0161**	0.0896	0.0171
	3	0.7163	0.0042	**0.7360**	**0.0037**	0.7200	0.0048	0.7136	0.0050
Castilla elastica	1	0.9372	**0.0007**	0.9069	0.0010	0.9132	0.0014	**0.9377**	0.0010
	2	0.8787	**0.0022**	0.7605	0.0043	0.7286	0.0081	**0.9092**	0.0027
	3	0.8678	**0.0013**	0.7464	0.0024	0.7328	0.0036	**0.8917**	0.0015
	4	**0.8334**	**0.0014**	0.8011	0.0016	0.7766	0.0025	0.8223	0.0020
Cecropia longipes	1	0.8760	0.0058	**0.8840**	**0.0054**	0.8172	0.0210	0.8576	0.0163
	2	**0.9537**	**0.0017**	0.9528	0.0018	0.9509	0.0040	0.8881	0.0090
	3	0.9080	**0.0033**	0.8784	0.0044	0.8267	0.0140	**0.9199**	0.0065
	4	**0.9067**	**0.0036**	0.8923	0.0041	0.8934	0.0087	0.7867	0.0173
	5	**0.7731**	**0.0152**	0.7317	0.0190	0.5268	0.1096	0.7292	0.0627
	6	0.0095	0.0327	**0.3045**	0.0230	0.2934	**0.0196**	0.2287	0.0214
Chrysophyllum cainito	1	0.8201	**0.0035**	0.7542	0.0048	0.7068	0.0097	**0.8287**	0.0057
	2	0.8776	**0.0019**	0.7779	0.0034	0.7360	0.0064	**0.8978**	0.0025
	3	0.6585	**0.0015**	0.6593	**0.0015**	**0.6701**	**0.0015**	0.5320	0.0022
	4	**0.8915**	**0.0025**	0.7815	0.0050	0.7589	0.0108	0.8894	0.0050
	5	0.9419	**0.0010**	**0.9432**	**0.0010**	0.9415	0.0017	0.8473	0.0043
	6	0.9336	0.0021	**0.9398**	**0.0019**	0.9325	0.0043	0.8817	0.0075
	7	0.3987	**0.0050**	0.3935	**0.0050**	0.3788	0.0062	**0.4054**	0.0059
	8	**0.6973**	**0.0061**	0.5912	0.0082	0.5121	0.0164	0.6972	0.0102
	9	0.6996	0.0071	**0.7110**	**0.0067**	0.6352	0.0142	0.6491	0.0136
Forsythia	1	0.9625	0.0003	**0.9629**	**0.0002**	0.9600	0.0003	0.9180	0.0007
	2	**0.7575**	**0.0005**	0.7530	**0.0005**	0.7472	0.0006	0.6405	0.0008
	3	**0.8204**	**0.0004**	0.5558	0.0008	0.5764	0.0008	0.3105	0.0013
	4	**0.9884**	**0.0002**	0.8597	0.0020	0.8719	0.0026	0.6179	0.0077
	5	0.9521	0.0009	**0.9550**	**0.0008**	0.9510	0.0014	0.9292	0.0020
	6	0.9332	0.0017	0.9319	**0.0015**	**0.9453**	0.0017	0.7801	0.0069
Hedera helix	1	0.9324	0.0025	0.9349	**0.0024**	**0.9387**	0.0042	0.8107	0.0130
	2	0.7199	0.0041	0.7558	**0.0031**	**0.7783**	0.0032	0.6826	0.0046
Heliconia	1	0.7847	0.0114	**0.8071**	**0.0100**	0.8003	0.0205	0.7684	0.0238
	2	0.6762	0.0090	**0.6810**	**0.0087**	0.6711	0.0140	0.6395	0.0154
	3	0.8788	0.0047	**0.8843**	**0.0044**	0.8108	0.0162	0.8486	0.0129
Inga villosissima	1	0.8982	0.0024	**0.9018**	**0.0023**	0.8766	0.0050	0.8732	0.0051
	2	0.8862	0.0012	**0.8879**	**0.0011**	0.8750	0.0017	0.8631	0.0018
	3	**0.7249**	**0.0024**	0.7113	0.0025	0.6999	0.0038	0.6820	0.0040
	4	**0.7140**	**0.0016**	0.7050	0.0016	0.6803	0.0022	0.6942	0.0021
	5	0.4940	**0.0068**	0.4824	0.0070	**0.4968**	0.0084	0.3893	0.0102
	6	0.4677	**0.0028**	0.4429	**0.0028**	0.4198	0.0033	**0.5017**	**0.0028**
	7	0.8897	**0.0015**	0.7635	0.0032	**0.7263**	0.0059	**0.9157**	0.0018
	8	**0.7647**	**0.0005**	0.7259	**0.0005**	**0.7308**	0.0006	0.7375	0.0006
Luehea seemannii	1	**0.9395**	**0.0021**	0.6595	0.0115	0.6917	0.0198	0.4450	0.0356
	2	**0.8435**	**0.0005**	0.8364	**0.0005**	0.8375	0.0006	0.8019	0.0007
	3	0.9091	**0.0014**	0.8548	0.0022	0.8286	0.0042	**0.9304**	0.0017
	4	0.6149	0.0038	0.6590	**0.0029**	**0.6722**	0.0029	0.5472	0.0040
	5	**0.7898**	**0.0015**	0.5424	0.0032	0.5065	0.0048	0.7714	0.0022
Miconia	1	**0.8466**	**0.0034**	0.6737	0.0073	0.6167	0.0162	0.8332	0.0071
	2	**0.7876**	**0.0049**	0.7466	0.0058	0.6976	0.0144	0.7333	0.0127

Musa	1	**0.6266**	**0.0064**	0.6218	0.0064	0.5662	0.0105	0.6216	0.0092
	2	**0.8286**	**0.0042**	0.6908	0.0077	0.6012	0.0207	0.8072	0.0100
	3	**0.3944**	**0.0057**	0.2439	0.0071	0.2094	0.0106	0.3720	0.0084
	4	0.8268	0.0062	0.8593	**0.0045**	**0.8556**	0.0070	0.7757	0.0108
	5	**0.5764**	**0.0027**	0.5702	**0.0027**	0.5561	0.0035	0.5523	0.0035
Oryza sativa	1	**0.9910**	**0.0003**	0.9336	0.0020	0.9219	0.0041	0.9943	**0.0003**
Quercus humboldtii	1	0.7480	0.0008	0.7628	**0.0007**	**0.7683**	**0.0007**	0.6240	0.0012
	2	**0.9547**	**0.0003**	0.8564	0.0011	0.8599	0.0015	0.9540	0.0005
	3	0.9531	0.0009	0.9560	**0.0008**	**0.9648**	0.0011	0.8636	0.0041
Tabebuia rosea	1	**0.9123**	**0.0006**	0.4433	0.0040	0.4323	0.0060	0.7119	0.0031
Triticum aestivum	1	**0.9368**	**0.0016**	0.3359	0.0171	0.3597	0.0284	0.6057	0.0175
	2	**0.8408**	**0.0054**	0.3939	0.0204	0.4003	0.0384	0.6399	0.0230
	3	0.9346	0.0028	0.8815	0.0051	0.9157	0.0080	**0.9735**	**0.0025**
	4	**0.9866**	**0.0007**	0.9703	0.0016	0.9840	0.0023	0.9793	0.0030
	5	0.9967	0.0002	0.9978	**0.0001**	**0.9989**	**0.0001**	0.9380	0.0079
	6	**0.9791**	**0.0011**	0.4075	0.0326	0.3390	0.0771	0.5673	0.0505
Unidentified	1	0.8556	0.0047	**0.8809**	**0.0036**	0.8790	0.0056	0.8166	0.0085

Appendix C – Species level R^2 and MSE values for each function.

	Power		Exponential		Linear x & ln(y)		Linear ln(x) & ln(y)	
Species	**R^2**	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**
Alocasia macrorrhiza	0.9728	0.0001	0.8987	0.0002	0.8963	0.0003	**0.9827**	**0.0000**
Alocasia odora	**0.5923**	**0.0022**	0.4514	0.0030	0.4516	0.0039	0.5328	0.0033
Astronium graveolens	0.5987	0.0086	**0.6312**	**0.0073**	0.6275	0.0089	0.5699	0.0103
Castilla elastica	0.9261	0.0008	0.8462	0.0016	0.8411	0.0025	**0.9572**	**0.0007**
Cecropia longipes	**0.7290**	**0.0076**	0.6352	0.0103	0.5194	0.0262	0.7187	0.0154
Chrysophyllum cainito	0.9348	**0.0010**	0.9011	0.0015	0.8926	0.0026	**0.9418**	0.0014
Eucalyptus camaldulensis	**0.9750**	**0.0010**	0.4425	0.0216	0.4562	0.0383	0.5879	0.0291
Flaveria linearis	**1.0000**	**0.0000**	0.9034	0.0006	0.9119	0.0007	0.9974	**0.0000**
Forsythia	**0.9945**	**0.0000**	0.9854	0.0001	0.9879	0.0001	0.8283	0.0018
Gossypium	**0.8096**	**0.0074**	0.3729	0.0243	0.2315	0.0548	0.5068	0.0352
Halimium halimifolium	0.8989	**0.0049**	0.8612	0.0067	0.8985	0.0120	**0.9239**	0.0090
Hedera helix	0.7481	0.0054	**0.7682**	**0.0047**	0.7389	0.0074	0.7262	0.0078
Heliconia	0.8817	0.0042	**0.8939**	**0.0036**	0.8872	0.0070	0.8714	0.0080
Hordeum vulgare	**0.9809**	**0.0008**	0.9464	0.0022	0.9576	0.0056	0.9263	0.0097
Inga villosissima	**0.9227**	**0.0006**	0.9041	0.0007	0.8931	0.0010	0.9089	0.0009
Luehea seemannii	**0.9080**	**0.0008**	0.9070	**0.0008**	0.8869	0.0013	0.8487	0.0018
Miconia	**0.9022**	**0.0020**	0.7905	0.0043	0.7385	0.0106	0.8688	0.0053
Musa	0.8098	**0.0026**	0.7706	0.0030	0.7296	0.0052	**0.8314**	0.0032
Phaseolus vulgaris	**0.9057**	**0.0032**	0.8996	0.0034	0.8994	0.0065	0.7523	0.0161
Quercus humboldtii	**0.9420**	**0.0006**	0.9413	**0.0006**	0.9365	0.0009	0.8322	0.0024
Spinacia oleracea	0.9066	**0.0026**	0.8762	0.0035	0.8669	0.0062	**0.9263**	0.0034
Triticum aestivum	**0.8174**	**0.0072**	0.5683	0.0172	0.5043	0.0472	0.7199	0.0266

Appendix D – R^2 and MSE values for each function fitted to all data and data grouped according to biome and experimental conditions.

	Power		Exponential		Linear x & ln(y)		Linear ln(x) & ln(y)	
	R^2	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**	**R^2**	**MSE**
Tropical	**0.5533**	**0.0096**	0.5260	0.0102	0.4646	0.0195	0.5164	0.0176
Temperate	**0.4823**	**0.0226**	0.4354	0.0247	0.3710	0.0649	0.4075	0.0611
Lab	**0.4967**	**0.0244**	0.3633	0.0318	0.3160	0.0780	0.3587	0.0311
Field	**0.5733**	**0.0091**	0.5567	0.0095	0.4948	0.0182	0.5323	0.0168
All	**0.4579**	**0.0169**	0.4096	0.0182	0.3374	0.0421	0.3733	0.0399

Appendix E – Nocturnal respiration data collected under constant temperature conditions for this study and extracted from the existing literature.

Reference	Species	Biome	Replicate	Time (hours since onset of darkness)	Temperature (ºC)	$R_{To}/R_{To\text{-}initia}$	Raw respiration (arbitrary units)
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	1	0	25	1.00	17.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	1	1.5	25	1.00	17.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	1	5	25	0.85	14.50
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	1	11	25	1.00	17.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	2	0	25	1.00	13.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	2	1.5	25	1.08	14.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	2	5	25	1.08	14.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	2	11	25	1.00	13.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	3	0	25	1.00	14.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	3	1.5	25	0.82	11.50
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	3	5	25	0.79	11.00
Noguchi et al. 1996	*Alocasia macrorrhiza*	Tropical	3	11	25	0.64	9.00
Noguchi & Terashima 1997	*Alocasia odora*	Tropical	1	0	20	1.00	25.00
Noguchi & Terashima 1997	*Alocasia odora*	Tropical	1	1.5	20	0.86	21.50
Noguchi & Terashima 1997	*Alocasia odora*	Tropical	1	3	20	0.80	20.00
Noguchi & Terashima 1997	*Alocasia odora*	Tropical	1	11	20	0.78	19.50
Noguchi et al. 2001	*Alocasia odora*	Tropical	2	0	20	1.00	35.00
Noguchi et al. 2001	*Alocasia odora*	Tropical	2	2	20	0.93	32.50
Noguchi et al. 2001	*Alocasia odora*	Tropical	2	5	20	0.93	32.50
Noguchi et al. 2001	*Alocasia odora*	Tropical	2	10	20	0.83	29.00
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	1	0	20	1.00	1.20
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	1	8	20	1.00	1.20
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	2	0	25	1.00	2.00
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	2	8	25	0.70	1.40
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	3	0	30	1.00	3.10
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	3	8	30	0.52	1.60
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	4	0	35	1.00	4.20
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	4	8	35	0.38	1.60
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	5	0	20	1.00	1.30
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	5	8	20	0.92	1.20
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	6	0	30	1.00	2.10
Bunce 2007	*Amaranthus hypochondriacus*	Tropical	6	8	30	0.71	1.50
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	1	0	17	1.00	55.00
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	1	1	17	1.02	56.00
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	1	5	17	1.10	60.50
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	1	14	17	0.96	53.00
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	2	0	17	1.00	27.50
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	2	1	17	1.00	27.50
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	2	5	17	1.05	29.00
O'Leary et al. 2017	*Arabidopsis thaliana*	Temperate	2	14	17	1.09	30.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	3	0	20	1.00	84.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	3	1	20	0.60	50.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	3	3	20	0.60	50.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	3	11	20	0.54	45.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	4	0	20	1.00	80.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	4	1	20	0.63	50.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	4	3	20	0.29	23.00
Trethewey & ap Rees 1994	*Arabidopsis thaliana*	Temperate	4	11	20	0.50	40.00
Watanabe et al. 2014	*Arabidopsis thaliana*	Temperate	5	0	23	1.00	49.50
Watanabe et al. 2014	*Arabidopsis thaliana*	Temperate	5	9	23	0.69	34.00
Watanabe et al. 2014	*Arabidopsis thaliana*	Temperate	6	0	23	1.00	51.50
Watanabe et al. 2014	*Arabidopsis thaliana*	Temperate	6	9	23	0.81	41.50
Slot (unpublished)	*Astronium graveolens*	Tropical	1	0	25	1.00	0.47
Slot (unpublished)	*Astronium graveolens*	Tropical	1	1	25	1.05	0.49
Slot (unpublished)	*Astronium graveolens*	Tropical	1	2	25	0.79	0.37
Slot (unpublished)	*Astronium graveolens*	Tropical	1	3	25	1.08	0.51
Slot (unpublished)	*Astronium graveolens*	Tropical	1	4	25	0.78	0.37
Slot (unpublished)	*Astronium graveolens*	Tropical	1	5	25	0.70	0.33
Slot (unpublished)	*Astronium graveolens*	Tropical	1	6	25	0.58	0.27
Slot (unpublished)	*Astronium graveolens*	Tropical	1	7	25	0.56	0.26
Slot (unpublished)	*Astronium graveolens*	Tropical	1	8	25	0.56	0.26
Slot (unpublished)	*Astronium graveolens*	Tropical	1	9	25	0.60	0.28
Slot (unpublished)	*Astronium graveolens*	Tropical	1	10	25	0.67	0.32
Slot (unpublished)	*Astronium graveolens*	Tropical	1	11	25	0.69	0.32
Slot (unpublished)	*Astronium graveolens*	Tropical	2	0	25	1.00	0.35
Slot (unpublished)	*Astronium graveolens*	Tropical	2	1	25	1.23	0.43
Slot (unpublished)	*Astronium graveolens*	Tropical	2	2	25	1.18	0.41
Slot (unpublished)	*Astronium graveolens*	Tropical	2	3	25	1.34	0.47
Slot (unpublished)	*Astronium graveolens*	Tropical	2	4	25	1.18	0.41
Slot (unpublished)	*Astronium graveolens*	Tropical	2	5	25	0.94	0.33
Slot (unpublished)	*Astronium graveolens*	Tropical	2	6	25	0.93	0.33
Slot (unpublished)	*Astronium graveolens*	Tropical	2	7	25	1.06	0.37
Slot (unpublished)	*Astronium graveolens*	Tropical	2	8	25	0.83	0.29
Slot (unpublished)	*Astronium graveolens*	Tropical	2	9	25	1.00	0.35
Slot (unpublished)	*Astronium graveolens*	Tropical	2	10	25	1.17	0.41
Slot (unpublished)	*Astronium graveolens*	Tropical	3	0	25	1.00	0.74
Slot (unpublished)	*Astronium graveolens*	Tropical	3	1	25	1.08	0.79
Slot (unpublished)	*Astronium graveolens*	Tropical	3	2	25	1.03	0.76
Slot (unpublished)	*Astronium graveolens*	Tropical	3	3	25	1.01	0.74
Slot (unpublished)	*Astronium graveolens*	Tropical	3	4	25	0.85	0.62

Slot (unpublished)	*Astronium graveolens*	Tropical	3	5	25	0.79	0.58
Slot (unpublished)	*Astronium graveolens*	Tropical	3	6	25	0.76	0.56
Slot (unpublished)	*Astronium graveolens*	Tropical	3	7	25	0.80	0.59
Slot (unpublished)	*Astronium graveolens*	Tropical	3	8	25	0.76	0.56
Slot (unpublished)	*Astronium graveolens*	Tropical	3	9	25	0.85	0.63
Slot (unpublished)	*Astronium graveolens*	Tropical	3	10	25	0.76	0.56
Slot (unpublished)	*Astronium graveolens*	Tropical	3	11	25	0.75	0.55
Fondy & Geiger 1982	*Beta vulgaris*	Temperate	1	0		1.00	5.00
Fondy & Geiger 1982	*Beta vulgaris*	Temperate	1	9.5		0.30	1.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	1	0	5	1.00	58.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	1	5	5	1.00	58.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	2	0	5	1.00	33.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	2	5	5	1.39	46.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	3	0	5	1.00	59.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	3	5	5	1.03	61.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	4	0	5	1.00	58.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	4	5	5	0.80	47.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	5	0	5	1.00	53.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	5	5	5	0.86	46.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	6	0	5	1.00	47.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	6	5	5	0.96	45.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	7	0	5	1.00	61.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	7	6	5	0.53	32.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	8	0	5	1.00	51.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	8	6	5	0.79	40.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	9	0	15	1.00	36.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	9	5	15	1.33	48.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	10	0	15	1.00	34.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	10	5	15	1.07	36.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	11	0	15	1.00	47.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	11	5	15	0.84	40.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	12	0	15	1.00	51.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	12	5	15	0.57	29.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	13	0	15	1.00	47.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	13	5	15	0.81	38.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	14	0	15	1.00	23.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	14	5	15	1.49	35.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	15	0	15	1.00	51.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	15	6	15	0.68	35.00
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	16	0	15	1.00	39.50
McCutchan & Monson 2001	*Bistorta bistortoides*	Temperate	16	6	15	0.70	27.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	1	0	5	1.00	71.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	1	6	5	0.67	47.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	2	0	5	1.00	80.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	2	6	5	0.62	49.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	3	0	5	1.00	55.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	3	6	5	1.13	62.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	4	0	5	1.00	62.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	4	6	5	0.87	54.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	5	0	15	1.00	58.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	5	6	15	0.83	48.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	6	0	15	1.00	64.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	6	6	15	0.75	48.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	7	0	15	1.00	56.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	7	6	15	0.86	48.50
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	8	0	15	1.00	47.00
McCutchan & Monson 2001	*Campanula rotundifolia*	Temperate	8	6	15	1.11	52.00
Slot (unpublished)	*Castilla elastica*	Tropical	1	0	25	1.00	0.34
Slot (unpublished)	*Castilla elastica*	Tropical	1	1	25	1.00	0.34
Slot (unpublished)	*Castilla elastica*	Tropical	1	2	25	0.84	0.29
Slot (unpublished)	*Castilla elastica*	Tropical	1	3	25	0.83	0.28
Slot (unpublished)	*Castilla elastica*	Tropical	1	4	25	0.83	0.28
Slot (unpublished)	*Castilla elastica*	Tropical	1	5	25	0.79	0.27
Slot (unpublished)	*Castilla elastica*	Tropical	1	6	25	0.78	0.26
Slot (unpublished)	*Castilla elastica*	Tropical	1	7	25	0.73	0.25
Slot (unpublished)	*Castilla elastica*	Tropical	1	8	25	0.72	0.24
Slot (unpublished)	*Castilla elastica*	Tropical	1	9	25	0.72	0.24
Slot (unpublished)	*Castilla elastica*	Tropical	1	10	25	0.67	0.23
Slot (unpublished)	*Castilla elastica*	Tropical	1	11	25	0.68	0.23
Slot (unpublished)	*Castilla elastica*	Tropical	2	0	25	1.00	0.35
Slot (unpublished)	*Castilla elastica*	Tropical	2	1	25	0.95	0.34
Slot (unpublished)	*Castilla elastica*	Tropical	2	2	25	0.78	0.27
Slot (unpublished)	*Castilla elastica*	Tropical	2	3	25	0.71	0.25
Slot (unpublished)	*Castilla elastica*	Tropical	2	4	25	0.68	0.24
Slot (unpublished)	*Castilla elastica*	Tropical	2	5	25	0.61	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	2	6	25	0.65	0.23
Slot (unpublished)	*Castilla elastica*	Tropical	2	7	25	0.59	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	2	8	25	0.63	0.22
Slot (unpublished)	*Castilla elastica*	Tropical	2	9	25	0.60	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	2	10	25	0.62	0.22
Slot (unpublished)	*Castilla elastica*	Tropical	2	11	25	0.60	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	3	0	25	1.00	0.26

Slot (unpublished)	*Castilla elastica*	Tropical	3	1	25	0.96	0.25
Slot (unpublished)	*Castilla elastica*	Tropical	3	2	25	0.85	0.22
Slot (unpublished)	*Castilla elastica*	Tropical	3	3	25	0.78	0.20
Slot (unpublished)	*Castilla elastica*	Tropical	3	4	25	0.73	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	3	5	25	0.79	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	3	6	25	0.72	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	3	7	25	0.76	0.20
Slot (unpublished)	*Castilla elastica*	Tropical	3	8	25	0.71	0.18
Slot (unpublished)	*Castilla elastica*	Tropical	3	9	25	0.73	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	3	10	25	0.69	0.18
Slot (unpublished)	*Castilla elastica*	Tropical	3	11	25	0.72	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	4	0	25	1.00	0.26
Slot (unpublished)	*Castilla elastica*	Tropical	4	1	25	0.98	0.26
Slot (unpublished)	*Castilla elastica*	Tropical	4	2	25	0.88	0.23
Slot (unpublished)	*Castilla elastica*	Tropical	4	3	25	0.93	0.24
Slot (unpublished)	*Castilla elastica*	Tropical	4	4	25	0.86	0.22
Slot (unpublished)	*Castilla elastica*	Tropical	4	5	25	0.80	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	4	6	25	0.79	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	4	7	25	0.72	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	4	8	25	0.82	0.21
Slot (unpublished)	*Castilla elastica*	Tropical	4	9	25	0.78	0.20
Slot (unpublished)	*Castilla elastica*	Tropical	4	10	25	0.72	0.19
Slot (unpublished)	*Castilla elastica*	Tropical	4	11	25	0.77	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	1	0	25	1.00	0.33
Slot (unpublished)	*Cecropia longipes*	Tropical	1	1	25	0.93	0.31
Slot (unpublished)	*Cecropia longipes*	Tropical	1	2	25	0.81	0.27
Slot (unpublished)	*Cecropia longipes*	Tropical	1	3	25	0.79	0.26
Slot (unpublished)	*Cecropia longipes*	Tropical	1	4	25	0.60	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	1	5	25	0.41	0.14
Slot (unpublished)	*Cecropia longipes*	Tropical	1	6	25	0.43	0.14
Slot (unpublished)	*Cecropia longipes*	Tropical	1	7	25	0.51	0.17
Slot (unpublished)	*Cecropia longipes*	Tropical	1	8	25	0.46	0.15
Slot (unpublished)	*Cecropia longipes*	Tropical	1	9	25	0.43	0.14
Slot (unpublished)	*Cecropia longipes*	Tropical	1	10	25	0.44	0.15
Slot (unpublished)	*Cecropia longipes*	Tropical	1	11	25	0.37	0.12
Slot (unpublished)	*Cecropia longipes*	Tropical	2	0	25	1.00	0.30
Slot (unpublished)	*Cecropia longipes*	Tropical	2	1	25	0.87	0.26
Slot (unpublished)	*Cecropia longipes*	Tropical	2	2	25	0.65	0.19
Slot (unpublished)	*Cecropia longipes*	Tropical	2	3	25	0.68	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	2	4	25	0.52	0.16
Slot (unpublished)	*Cecropia longipes*	Tropical	2	5	25	0.43	0.13
Slot (unpublished)	*Cecropia longipes*	Tropical	3	0	25	1.00	0.48
Slot (unpublished)	*Cecropia longipes*	Tropical	3	1	25	0.92	0.44
Slot (unpublished)	*Cecropia longipes*	Tropical	3	2	25	0.79	0.38
Slot (unpublished)	*Cecropia longipes*	Tropical	3	3	25	0.65	0.31
Slot (unpublished)	*Cecropia longipes*	Tropical	3	4	25	0.56	0.27
Slot (unpublished)	*Cecropia longipes*	Tropical	3	5	25	0.60	0.29
Slot (unpublished)	*Cecropia longipes*	Tropical	3	6	25	0.44	0.21
Slot (unpublished)	*Cecropia longipes*	Tropical	3	7	25	0.46	0.22
Slot (unpublished)	*Cecropia longipes*	Tropical	3	8	25	0.48	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	3	9	25	0.46	0.22
Slot (unpublished)	*Cecropia longipes*	Tropical	3	10	25	0.48	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	3	11	25	0.43	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	4	0	25	1.00	0.30
Slot (unpublished)	*Cecropia longipes*	Tropical	4	1	25	0.92	0.27
Slot (unpublished)	*Cecropia longipes*	Tropical	4	2	25	0.68	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	4	3	25	0.77	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	4	4	25	0.56	0.17
Slot (unpublished)	*Cecropia longipes*	Tropical	4	5	25	0.44	0.13
Slot (unpublished)	*Cecropia longipes*	Tropical	5	0	25	1.00	0.36
Slot (unpublished)	*Cecropia longipes*	Tropical	5	1	25	0.88	0.31
Slot (unpublished)	*Cecropia longipes*	Tropical	5	2	25	0.31	0.11
Slot (unpublished)	*Cecropia longipes*	Tropical	5	3	25	0.37	0.13
Slot (unpublished)	*Cecropia longipes*	Tropical	5	4	25	0.37	0.13
Slot (unpublished)	*Cecropia longipes*	Tropical	5	5	25	0.24	0.09
Slot (unpublished)	*Cecropia longipes*	Tropical	5	6	25	0.22	0.08
Slot (unpublished)	*Cecropia longipes*	Tropical	5	7	25	0.32	0.11
Slot (unpublished)	*Cecropia longipes*	Tropical	5	8	25	0.33	0.12
Slot (unpublished)	*Cecropia longipes*	Tropical	5	9	25	0.28	0.10
Slot (unpublished)	*Cecropia longipes*	Tropical	6	0	25	1.00	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	6	1	25	1.28	0.29
Slot (unpublished)	*Cecropia longipes*	Tropical	6	2	25	1.42	0.33
Slot (unpublished)	*Cecropia longipes*	Tropical	6	3	25	1.32	0.30
Slot (unpublished)	*Cecropia longipes*	Tropical	6	4	25	1.05	0.24
Slot (unpublished)	*Cecropia longipes*	Tropical	6	5	25	1.02	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	6	6	25	0.91	0.21
Slot (unpublished)	*Cecropia longipes*	Tropical	6	7	25	0.95	0.22
Slot (unpublished)	*Cecropia longipes*	Tropical	6	8	25	0.80	0.18
Slot (unpublished)	*Cecropia longipes*	Tropical	6	9	25	0.87	0.20
Slot (unpublished)	*Cecropia longipes*	Tropical	6	10	25	0.98	0.23
Slot (unpublished)	*Cecropia longipes*	Tropical	6	11	25	1.12	0.26
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	0	25	1.00	0.53

Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	1	25	0.89	0.47
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	2	25	0.92	0.49
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	3	25	0.69	0.36
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	4	25	0.67	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	5	25	0.66	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	6	25	0.66	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	7	25	0.60	0.32
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	8	25	0.55	0.29
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	9	25	0.66	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	1	10	25	0.63	0.34
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	0	25	1.00	0.51
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	1	25	0.93	0.47
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	2	25	0.85	0.43
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	3	25	0.74	0.38
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	4	25	0.69	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	5	25	0.65	0.33
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	6	25	0.67	0.34
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	7	25	0.66	0.34
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	8	25	0.62	0.32
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	9	25	0.62	0.32
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	2	10	25	0.69	0.35
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	0	25	1.00	0.64
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	1	25	1.08	0.70
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	2	25	0.95	0.61
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	3	25	1.03	0.67
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	4	25	0.95	0.61
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	5	25	0.98	0.63
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	6	25	0.94	0.60
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	7	25	0.95	0.61
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	8	25	0.85	0.55
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	9	25	0.91	0.58
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	3	10	25	0.87	0.56
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	0	25	1.00	0.33
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	1	25	0.89	0.29
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	2	25	0.68	0.22
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	3	25	0.69	0.23
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	4	25	0.60	0.20
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	5	25	0.59	0.19
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	6	25	0.58	0.19
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	7	25	0.55	0.18
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	8	25	0.51	0.17
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	9	25	0.62	0.20
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	4	10	25	0.48	0.16
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	0	25	1.00	0.42
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	1	25	0.98	0.41
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	2	25	0.87	0.36
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	3	25	0.88	0.36
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	4	25	0.74	0.31
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	5	25	0.79	0.33
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	6	25	0.66	0.27
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	7	25	0.66	0.27
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	5	8	25	0.61	0.25
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	0	25	1.00	0.42
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	1	25	0.97	0.40
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	2	25	0.78	0.33
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	3	25	0.85	0.36
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	4	25	0.79	0.33
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	5	25	0.65	0.27
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	6	25	0.64	0.27
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	7	25	0.54	0.22
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	8	25	0.52	0.22
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	9	25	0.55	0.23
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	10	25	0.48	0.20
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	6	11	25	0.50	0.21
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	0	25	1.00	0.28
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	1	25	1.03	0.29
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	2	25	1.05	0.29
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	3	25	0.89	0.25
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	4	25	0.94	0.26
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	5	25	0.80	0.22
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	6	25	0.90	0.25
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	7	25	0.78	0.22
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	8	25	1.00	0.28
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	9	25	0.83	0.23
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	7	10	25	0.85	0.24
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	0	25	1.00	0.40
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	1	25	1.01	0.41
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	2	25	0.80	0.32
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	3	25	0.70	0.28
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	4	25	0.77	0.31
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	5	25	0.60	0.24
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	6	25	0.56	0.23

Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	7	25	0.70	0.28
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	8	25	0.62	0.25
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	9	25	0.58	0.24
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	10	25	0.67	0.27
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	8	11	25	0.69	0.28
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	0	25	1.00	0.58
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	1	25	1.02	0.60
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	2	25	0.90	0.53
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	3	25	0.78	0.45
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	4	25	0.70	0.41
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	5	25	0.71	0.41
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	6	25	0.54	0.31
Slot (unpublished)	*Chrysophyllum cainito*	Tropical	9	7	25	0.78	0.45
Scafaro et al. 2017	*Eucalyptus camaldulensis*	Temperate	1	0	21.5	1.00	54.00
Scafaro et al. 2017	*Eucalyptus camaldulensis*	Temperate	1	0.5	21.5	0.56	30.50
Scafaro et al. 2017	*Eucalyptus camaldulensis*	Temperate	1	2.5	21.5	0.60	32.50
Scafaro et al. 2017	*Eucalyptus camaldulensis*	Temperate	1	6.5	21.5	0.50	27.00
Leonardos et al. 2006	*Flaveria linearis*	Tropical	1	0	25	1.00	25.00
Leonardos et al. 2006	*Flaveria linearis*	Tropical	1	1.5	25	0.90	22.50
Leonardos et al. 2006	*Flaveria linearis*	Tropical	1	7.5	25	0.80	20.00
Sitch (unpublished)	*Forsythia*	Temperate	1	0	17.6	1.00	0.80
Sitch (unpublished)	*Forsythia*	Temperate	1	1	17.6	0.99	0.79
Sitch (unpublished)	*Forsythia*	Temperate	1	2	17.6	0.97	0.77
Sitch (unpublished)	*Forsythia*	Temperate	1	3	17.6	0.91	0.72
Sitch (unpublished)	*Forsythia*	Temperate	1	4	17.6	0.88	0.70
Sitch (unpublished)	*Forsythia*	Temperate	1	5	17.6	0.86	0.68
Sitch (unpublished)	*Forsythia*	Temperate	1	6	17.6	0.83	0.66
Sitch (unpublished)	*Forsythia*	Temperate	1	7	17.6	0.82	0.65
Sitch (unpublished)	*Forsythia*	Temperate	1	8	17.6	0.79	0.63
Sitch (unpublished)	*Forsythia*	Temperate	1	9	17.6	0.78	0.62
Sitch (unpublished)	*Forsythia*	Temperate	1	10	17.6	0.78	0.63
Sitch (unpublished)	*Forsythia*	Temperate	2	0	18.4	1.00	0.71
Sitch (unpublished)	*Forsythia*	Temperate	2	1	18.4	0.98	0.70
Sitch (unpublished)	*Forsythia*	Temperate	2	2	18.4	0.95	0.68
Sitch (unpublished)	*Forsythia*	Temperate	2	3	18.4	0.93	0.66
Sitch (unpublished)	*Forsythia*	Temperate	2	4	18.4	0.93	0.66
Sitch (unpublished)	*Forsythia*	Temperate	2	5	18.4	0.94	0.67
Sitch (unpublished)	*Forsythia*	Temperate	2	6	18.4	0.95	0.67
Sitch (unpublished)	*Forsythia*	Temperate	2	7	18.4	0.93	0.66
Sitch (unpublished)	*Forsythia*	Temperate	2	8	18.4	0.93	0.66
Sitch (unpublished)	*Forsythia*	Temperate	2	9	18.4	0.88	0.62
Sitch (unpublished)	*Forsythia*	Temperate	2	10	18.4	0.83	0.59
Sitch (unpublished)	*Forsythia*	Temperate	3	0	16.4	1.00	0.54
Sitch (unpublished)	*Forsythia*	Temperate	3	1	16.4	0.98	0.53
Sitch (unpublished)	*Forsythia*	Temperate	3	2	16.4	1.01	0.54
Sitch (unpublished)	*Forsythia*	Temperate	3	3	16.4	1.03	0.55
Sitch (unpublished)	*Forsythia*	Temperate	3	4	16.4	1.05	0.56
Sitch (unpublished)	*Forsythia*	Temperate	3	5	16.4	1.01	0.54
Sitch (unpublished)	*Forsythia*	Temperate	3	6	16.4	0.98	0.53
Sitch (unpublished)	*Forsythia*	Temperate	3	7	16.4	0.97	0.52
Sitch (unpublished)	*Forsythia*	Temperate	3	8	16.4	0.95	0.51
Sitch (unpublished)	*Forsythia*	Temperate	3	9	16.4	0.91	0.49
Sitch (unpublished)	*Forsythia*	Temperate	3	10	16.4	0.90	0.49
Sitch (unpublished)	*Forsythia*	Temperate	4	0	17.9	1.00	0.57
Sitch (unpublished)	*Forsythia*	Temperate	4	1	17.9	1.00	0.57
Sitch (unpublished)	*Forsythia*	Temperate	4	2	17.9	0.98	0.56
Sitch (unpublished)	*Forsythia*	Temperate	4	3	17.9	1.00	0.57
Sitch (unpublished)	*Forsythia*	Temperate	4	4	17.9	0.97	0.55
Sitch (unpublished)	*Forsythia*	Temperate	4	5	17.9	0.94	0.54
Sitch (unpublished)	*Forsythia*	Temperate	4	6	17.9	0.86	0.49
Sitch (unpublished)	*Forsythia*	Temperate	4	7	17.9	0.84	0.48
Sitch (unpublished)	*Forsythia*	Temperate	4	8	17.9	0.77	0.44
Sitch (unpublished)	*Forsythia*	Temperate	4	9	17.9	0.72	0.41
Sitch (unpublished)	*Forsythia*	Temperate	4	10	17.9	0.65	0.37
Sitch (unpublished)	*Forsythia*	Temperate	5	0	18.9	1.00	0.54
Sitch (unpublished)	*Forsythia*	Temperate	5	1	18.9	1.00	0.54
Sitch (unpublished)	*Forsythia*	Temperate	5	2	18.9	0.91	0.49
Sitch (unpublished)	*Forsythia*	Temperate	5	3	18.9	0.82	0.44
Sitch (unpublished)	*Forsythia*	Temperate	5	4	18.9	0.78	0.42
Sitch (unpublished)	*Forsythia*	Temperate	5	5	18.9	0.75	0.41
Sitch (unpublished)	*Forsythia*	Temperate	5	6	18.9	0.70	0.38
Sitch (unpublished)	*Forsythia*	Temperate	5	7	18.9	0.66	0.35
Sitch (unpublished)	*Forsythia*	Temperate	5	8	18.9	0.65	0.35
Sitch (unpublished)	*Forsythia*	Temperate	5	9	18.9	0.65	0.35
Sitch (unpublished)	*Forsythia*	Temperate	5	10	18.9	0.62	0.33
Sitch (unpublished)	*Forsythia*	Temperate	6	0	18.4	1.00	0.60
Sitch (unpublished)	*Forsythia*	Temperate	6	1	18.4	1.03	0.62
Sitch (unpublished)	*Forsythia*	Temperate	6	2	18.4	1.02	0.61
Sitch (unpublished)	*Forsythia*	Temperate	6	3	18.4	0.98	0.58
Sitch (unpublished)	*Forsythia*	Temperate	6	4	18.4	0.90	0.54
Sitch (unpublished)	*Forsythia*	Temperate	6	5	18.4	0.82	0.49
Sitch (unpublished)	*Forsythia*	Temperate	6	6	18.4	0.76	0.45

Sitch (unpublished)	*Forsythia*	Temperate	6	7	18.4	0.70	0.42
Sitch (unpublished)	*Forsythia*	Temperate	6	8	18.4	0.68	0.41
Sitch (unpublished)	*Forsythia*	Temperate	6	9	18.4	0.66	0.40
Sitch (unpublished)	*Forsythia*	Temperate	6	10	18.4	0.65	0.39
Bunce 2007	*Glycine max*	Tropical	1	0	20	1.00	1.20
Bunce 2007	*Glycine max*	Tropical	1	8	20	1.08	1.30
Bunce 2007	*Glycine max*	Tropical	2	0	25	1.00	1.80
Bunce 2007	*Glycine max*	Tropical	2	8	25	1.17	2.10
Bunce 2007	*Glycine max*	Tropical	3	0	30	1.00	3.00
Bunce 2007	*Glycine max*	Tropical	3	8	30	0.77	2.30
Bunce 2007	*Glycine max*	Tropical	4	0	35	1.00	4.20
Bunce 2007	*Glycine max*	Tropical	4	8	35	0.55	2.30
Bunce 2007	*Glycine max*	Tropical	5	0	20	1.00	1.70
Bunce 2007	*Glycine max*	Tropical	5	8	20	0.94	1.60
Bunce 2007	*Glycine max*	Tropical	6	0	30	1.00	1.70
Bunce 2007	*Glycine max*	Tropical	6	8	30	1.00	1.70
Gessler et al. 2017	*Gossypium*	Temperate	1	0	19	1.00	38.50
Gessler et al. 2017	*Gossypium*	Temperate	1	6	19	0.52	20.00
Gessler et al. 2017	*Gossypium*	Temperate	1	12	19	0.73	28.00
Lehmann et al. 2016	*Halimium halimifolium*	Temperate	1	0	15	1.00	42.00
Lehmann et al. 2016	*Halimium halimifolium*	Temperate	1	1	15	0.79	33.00
Lehmann et al. 2016	*Halimium halimifolium*	Temperate	1	1.5	15	0.90	38.00
Lehmann et al. 2016	*Halimium halimifolium*	Temperate	1	2.5	15	0.62	26.00
Lehmann et al. 2016	*Halimium halimifolium*	Temperate	1	11.5	15	0.38	16.00
Bruhn (unpublished)	*Hedera helix*	Temperate	1	0	17.8	1.00	1.19
Bruhn (unpublished)	*Hedera helix*	Temperate	1	1	17.8	1.02	1.22
Bruhn (unpublished)	*Hedera helix*	Temperate	1	2	17.8	0.98	1.18
Bruhn (unpublished)	*Hedera helix*	Temperate	1	3	17.8	0.77	0.92
Bruhn (unpublished)	*Hedera helix*	Temperate	1	4	17.8	0.71	0.85
Bruhn (unpublished)	*Hedera helix*	Temperate	1	5	17.8	0.71	0.85
Bruhn (unpublished)	*Hedera helix*	Temperate	1	6	17.8	0.62	0.74
Bruhn (unpublished)	*Hedera helix*	Temperate	1	7	17.8	0.60	0.71
Bruhn (unpublished)	*Hedera helix*	Temperate	1	8	17.8	0.58	0.69
Bruhn (unpublished)	*Hedera helix*	Temperate	1	9	17.8	0.44	0.52
Bruhn (unpublished)	*Hedera helix*	Temperate	2	0	19.8	1.00	0.50
Bruhn (unpublished)	*Hedera helix*	Temperate	2	1	19.8	1.14	0.57
Bruhn (unpublished)	*Hedera helix*	Temperate	2	2	19.8	1.09	0.55
Bruhn (unpublished)	*Hedera helix*	Temperate	2	3	19.8	0.93	0.47
Bruhn (unpublished)	*Hedera helix*	Temperate	2	4	19.8	0.88	0.44
Bruhn (unpublished)	*Hedera helix*	Temperate	2	5	19.8	0.88	0.44
Bruhn (unpublished)	*Hedera helix*	Temperate	2	6	19.8	0.85	0.43
Bruhn (unpublished)	*Hedera helix*	Temperate	2	7	19.8	0.87	0.44
Bruhn (unpublished)	*Hedera helix*	Temperate	2	8	19.8	0.87	0.44
Bruhn (unpublished)	*Hedera helix*	Temperate	2	9	19.8	0.76	0.38
Bruhn (unpublished)	*Hedera helix*	Temperate	2	10	19.8	0.78	0.39
Newman (unpublished)	*Heliconia*	Tropical	1	0	24	1.00	0.28
Newman (unpublished)	*Heliconia*	Tropical	1	1	24	1.00	0.28
Newman (unpublished)	*Heliconia*	Tropical	1	2	24	1.07	0.30
Newman (unpublished)	*Heliconia*	Tropical	1	3	24	0.94	0.26
Newman (unpublished)	*Heliconia*	Tropical	1	4	24	0.59	0.17
Newman (unpublished)	*Heliconia*	Tropical	1	5	24	0.51	0.14
Newman (unpublished)	*Heliconia*	Tropical	1	6	24	0.56	0.16
Newman (unpublished)	*Heliconia*	Tropical	1	7	24	0.62	0.17
Newman (unpublished)	*Heliconia*	Tropical	1	8	24	0.64	0.18
Newman (unpublished)	*Heliconia*	Tropical	1	9	24	0.50	0.14
Newman (unpublished)	*Heliconia*	Tropical	1	10	24	0.50	0.14
Newman (unpublished)	*Heliconia*	Tropical	1	11	24	0.43	0.12
Newman (unpublished)	*Heliconia*	Tropical	1	12	24	0.42	0.12
Newman (unpublished)	*Heliconia*	Tropical	2	0	24	1.00	0.22
Newman (unpublished)	*Heliconia*	Tropical	2	1	24	1.14	0.26
Newman (unpublished)	*Heliconia*	Tropical	2	2	24	1.00	0.22
Newman (unpublished)	*Heliconia*	Tropical	2	3	24	0.74	0.17
Newman (unpublished)	*Heliconia*	Tropical	2	4	24	0.69	0.15
Newman (unpublished)	*Heliconia*	Tropical	2	5	24	0.86	0.19
Newman (unpublished)	*Heliconia*	Tropical	2	6	24	0.77	0.17
Newman (unpublished)	*Heliconia*	Tropical	2	7	24	0.80	0.18
Newman (unpublished)	*Heliconia*	Tropical	2	8	24	0.74	0.16
Newman (unpublished)	*Heliconia*	Tropical	2	9	24	0.61	0.14
Newman (unpublished)	*Heliconia*	Tropical	2	10	24	0.75	0.17
Newman (unpublished)	*Heliconia*	Tropical	2	11	24	0.69	0.15
Newman (unpublished)	*Heliconia*	Tropical	2	12	24	0.51	0.12
Newman (unpublished)	*Heliconia*	Tropical	3	0	24	1.00	0.18
Newman (unpublished)	*Heliconia*	Tropical	3	1	24	0.98	0.18
Newman (unpublished)	*Heliconia*	Tropical	3	2	24	0.86	0.16
Newman (unpublished)	*Heliconia*	Tropical	3	3	24	0.75	0.14
Newman (unpublished)	*Heliconia*	Tropical	3	4	24	0.65	0.12
Newman (unpublished)	*Heliconia*	Tropical	3	5	24	0.70	0.13
Newman (unpublished)	*Heliconia*	Tropical	3	6	24	0.60	0.11
Newman (unpublished)	*Heliconia*	Tropical	3	7	24	0.44	0.08
Newman (unpublished)	*Heliconia*	Tropical	3	8	24	0.45	0.08
Newman (unpublished)	*Heliconia*	Tropical	3	9	24	0.43	0.08
Newman (unpublished)	*Heliconia*	Tropical	3	10	24	0.50	0.09

Newman (unpublished)	*Heliconia*	Tropical	3	11	24	0.52	0.10
Newman (unpublished)	*Heliconia*	Tropical	3	12	24	0.46	0.09
Farrar & Farrar 1985	*Hordeum distichum*	Temperate	1	0	18	1.00	0.70
Farrar & Farrar 1985	*Hordeum distichum*	Temperate	1	7.5	18	0.87	0.61
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	0	20	1.00	62.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	0.5	20	0.77	47.50
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	1.5	20	0.69	43.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	2.5	20	0.69	43.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	3.5	20	0.60	37.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	4.5	20	0.53	33.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	5.5	20	0.49	30.50
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	6.5	20	0.47	29.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	7.5	20	0.40	25.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	8.5	20	0.37	23.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	9.5	20	0.30	18.50
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	10.5	20	0.32	20.00
Baysdorfer et al. 1987	*Hordeum vulgare*	Temperate	1	11.5	20	0.32	20.00
Newman (unpublished)	*Inga villosissima*	Tropical	1	0	22	1.00	0.71
Newman (unpublished)	*Inga villosissima*	Tropical	1	1	22	0.93	0.67
Newman (unpublished)	*Inga villosissima*	Tropical	1	2	22	0.95	0.68
Newman (unpublished)	*Inga villosissima*	Tropical	1	3	22	0.87	0.62
Newman (unpublished)	*Inga villosissima*	Tropical	1	4	22	0.82	0.59
Newman (unpublished)	*Inga villosissima*	Tropical	1	5	22	0.67	0.48
Newman (unpublished)	*Inga villosissima*	Tropical	1	6	22	0.63	0.45
Newman (unpublished)	*Inga villosissima*	Tropical	1	7	22	0.63	0.45
Newman (unpublished)	*Inga villosissima*	Tropical	1	8	22	0.66	0.47
Newman (unpublished)	*Inga villosissima*	Tropical	1	9	22	0.59	0.42
Newman (unpublished)	*Inga villosissima*	Tropical	1	10	22	0.57	0.41
Newman (unpublished)	*Inga villosissima*	Tropical	1	11	22	0.58	0.41
Newman (unpublished)	*Inga villosissima*	Tropical	1	12	22	0.60	0.43
Newman (unpublished)	*Inga villosissima*	Tropical	2	0	22	1.00	0.64
Newman (unpublished)	*Inga villosissima*	Tropical	2	1	22	1.02	0.66
Newman (unpublished)	*Inga villosissima*	Tropical	2	2	22	0.98	0.63
Newman (unpublished)	*Inga villosissima*	Tropical	2	3	22	0.92	0.59
Newman (unpublished)	*Inga villosissima*	Tropical	2	4	22	0.91	0.58
Newman (unpublished)	*Inga villosissima*	Tropical	2	5	22	0.84	0.54
Newman (unpublished)	*Inga villosissima*	Tropical	2	6	22	0.78	0.50
Newman (unpublished)	*Inga villosissima*	Tropical	2	7	22	0.76	0.49
Newman (unpublished)	*Inga villosissima*	Tropical	2	8	22	0.81	0.52
Newman (unpublished)	*Inga villosissima*	Tropical	2	9	22	0.78	0.50
Newman (unpublished)	*Inga villosissima*	Tropical	2	10	22	0.74	0.48
Newman (unpublished)	*Inga villosissima*	Tropical	2	11	22	0.76	0.49
Newman (unpublished)	*Inga villosissima*	Tropical	2	12	22	0.74	0.48
Newman (unpublished)	*Inga villosissima*	Tropical	3	0	22	1.00	0.67
Newman (unpublished)	*Inga villosissima*	Tropical	3	1	22	0.94	0.63
Newman (unpublished)	*Inga villosissima*	Tropical	3	2	22	0.92	0.62
Newman (unpublished)	*Inga villosissima*	Tropical	3	3	22	0.91	0.61
Newman (unpublished)	*Inga villosissima*	Tropical	3	4	22	0.83	0.56
Newman (unpublished)	*Inga villosissima*	Tropical	3	5	22	0.76	0.51
Newman (unpublished)	*Inga villosissima*	Tropical	3	6	22	0.86	0.58
Newman (unpublished)	*Inga villosissima*	Tropical	3	7	22	0.92	0.62
Newman (unpublished)	*Inga villosissima*	Tropical	3	8	22	0.79	0.53
Newman (unpublished)	*Inga villosissima*	Tropical	3	9	22	0.72	0.48
Newman (unpublished)	*Inga villosissima*	Tropical	3	10	22	0.74	0.50
Newman (unpublished)	*Inga villosissima*	Tropical	3	11	22	0.69	0.47
Newman (unpublished)	*Inga villosissima*	Tropical	3	12	22	0.77	0.52
Newman (unpublished)	*Inga villosissima*	Tropical	4	0	18	1.00	0.71
Newman (unpublished)	*Inga villosissima*	Tropical	4	1	18	0.99	0.71
Newman (unpublished)	*Inga villosissima*	Tropical	4	2	18	1.00	0.71
Newman (unpublished)	*Inga villosissima*	Tropical	4	3	18	0.97	0.69
Newman (unpublished)	*Inga villosissima*	Tropical	4	4	18	0.91	0.65
Newman (unpublished)	*Inga villosissima*	Tropical	4	5	18	0.92	0.65
Newman (unpublished)	*Inga villosissima*	Tropical	4	6	18	0.84	0.60
Newman (unpublished)	*Inga villosissima*	Tropical	4	7	18	0.84	0.60
Newman (unpublished)	*Inga villosissima*	Tropical	4	8	18	0.83	0.59
Newman (unpublished)	*Inga villosissima*	Tropical	4	9	18	0.86	0.61
Newman (unpublished)	*Inga villosissima*	Tropical	4	10	18	0.80	0.57
Newman (unpublished)	*Inga villosissima*	Tropical	4	11	18	0.78	0.56
Newman (unpublished)	*Inga villosissima*	Tropical	4	12	18	0.91	0.64
Newman (unpublished)	*Inga villosissima*	Tropical	5	0	18	1.00	0.80
Newman (unpublished)	*Inga villosissima*	Tropical	5	1	18	0.91	0.73
Newman (unpublished)	*Inga villosissima*	Tropical	5	2	18	1.15	0.92
Newman (unpublished)	*Inga villosissima*	Tropical	5	3	18	0.90	0.73
Newman (unpublished)	*Inga villosissima*	Tropical	5	4	18	0.88	0.71
Newman (unpublished)	*Inga villosissima*	Tropical	5	5	18	0.99	0.80
Newman (unpublished)	*Inga villosissima*	Tropical	5	6	18	1.02	0.82
Newman (unpublished)	*Inga villosissima*	Tropical	5	7	18	0.83	0.67
Newman (unpublished)	*Inga villosissima*	Tropical	5	8	18	0.86	0.69
Newman (unpublished)	*Inga villosissima*	Tropical	5	9	18	0.81	0.65
Newman (unpublished)	*Inga villosissima*	Tropical	5	10	18	0.68	0.55
Newman (unpublished)	*Inga villosissima*	Tropical	5	11	18	0.79	0.63
Newman (unpublished)	*Inga villosissima*	Tropical	5	12	18	0.84	0.68

Newman (unpublished)	*Inga villosissima*	Tropical	6	0	23	1.00	0.87
Newman (unpublished)	*Inga villosissima*	Tropical	6	1	23	1.02	0.89
Newman (unpublished)	*Inga villosissima*	Tropical	6	2	23	1.03	0.90
Newman (unpublished)	*Inga villosissima*	Tropical	6	3	23	1.06	0.92
Newman (unpublished)	*Inga villosissima*	Tropical	6	4	23	0.89	0.77
Newman (unpublished)	*Inga villosissima*	Tropical	6	5	23	0.87	0.75
Newman (unpublished)	*Inga villosissima*	Tropical	6	6	23	0.85	0.74
Newman (unpublished)	*Inga villosissima*	Tropical	6	7	23	0.85	0.74
Newman (unpublished)	*Inga villosissima*	Tropical	6	8	23	0.85	0.74
Newman (unpublished)	*Inga villosissima*	Tropical	6	9	23	0.89	0.77
Newman (unpublished)	*Inga villosissima*	Tropical	6	10	23	0.90	0.79
Newman (unpublished)	*Inga villosissima*	Tropical	6	11	23	0.91	0.79
Newman (unpublished)	*Inga villosissima*	Tropical	6	12	23	0.90	0.78
Newman (unpublished)	*Inga villosissima*	Tropical	7	0	23	1.00	1.35
Newman (unpublished)	*Inga villosissima*	Tropical	7	1	23	0.94	1.26
Newman (unpublished)	*Inga villosissima*	Tropical	7	2	23	0.84	1.13
Newman (unpublished)	*Inga villosissima*	Tropical	7	3	23	0.79	1.07
Newman (unpublished)	*Inga villosissima*	Tropical	7	4	23	0.72	0.98
Newman (unpublished)	*Inga villosissima*	Tropical	7	5	23	0.68	0.92
Newman (unpublished)	*Inga villosissima*	Tropical	7	6	23	0.65	0.88
Newman (unpublished)	*Inga villosissima*	Tropical	7	7	23	0.65	0.87
Newman (unpublished)	*Inga villosissima*	Tropical	7	8	23	0.64	0.87
Newman (unpublished)	*Inga villosissima*	Tropical	7	9	23	0.65	0.87
Newman (unpublished)	*Inga villosissima*	Tropical	7	10	23	0.66	0.89
Newman (unpublished)	*Inga villosissima*	Tropical	7	11	23	0.66	0.89
Newman (unpublished)	*Inga villosissima*	Tropical	7	12	23	0.66	0.89
Newman (unpublished)	*Inga villosissima*	Tropical	8	0	23	1.00	0.65
Newman (unpublished)	*Inga villosissima*	Tropical	8	1	23	0.97	0.62
Newman (unpublished)	*Inga villosissima*	Tropical	8	2	23	0.92	0.60
Newman (unpublished)	*Inga villosissima*	Tropical	8	3	23	0.89	0.58
Newman (unpublished)	*Inga villosissima*	Tropical	8	4	23	0.89	0.58
Newman (unpublished)	*Inga villosissima*	Tropical	8	5	23	0.92	0.59
Newman (unpublished)	*Inga villosissima*	Tropical	8	6	23	0.94	0.61
Newman (unpublished)	*Inga villosissima*	Tropical	8	7	23	0.93	0.60
Newman (unpublished)	*Inga villosissima*	Tropical	8	8	23	0.90	0.58
Newman (unpublished)	*Inga villosissima*	Tropical	8	9	23	0.87	0.56
Newman (unpublished)	*Inga villosissima*	Tropical	8	10	23	0.85	0.55
Newman (unpublished)	*Inga villosissima*	Tropical	8	11	23	0.85	0.55
Newman (unpublished)	*Inga villosissima*	Tropical	8	12	23	0.85	0.55
Slot (unpublished)	*Luehea seemannii*	Tropical	1	0	25	1.00	0.73
Slot (unpublished)	*Luehea seemannii*	Tropical	1	1	25	1.01	0.73
Slot (unpublished)	*Luehea seemannii*	Tropical	1	2	25	0.93	0.68
Slot (unpublished)	*Luehea seemannii*	Tropical	1	3	25	0.93	0.68
Slot (unpublished)	*Luehea seemannii*	Tropical	1	4	25	1.00	0.72
Slot (unpublished)	*Luehea seemannii*	Tropical	1	5	25	0.97	0.71
Slot (unpublished)	*Luehea seemannii*	Tropical	1	6	25	0.97	0.71
Slot (unpublished)	*Luehea seemannii*	Tropical	1	7	25	0.84	0.61
Slot (unpublished)	*Luehea seemannii*	Tropical	1	8	25	0.65	0.47
Slot (unpublished)	*Luehea seemannii*	Tropical	1	9	25	0.59	0.43
Slot (unpublished)	*Luehea seemannii*	Tropical	1	10	25	0.46	0.33
Slot (unpublished)	*Luehea seemannii*	Tropical	2	0	25	1.00	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	2	1	25	0.97	0.27
Slot (unpublished)	*Luehea seemannii*	Tropical	2	2	25	0.92	0.26
Slot (unpublished)	*Luehea seemannii*	Tropical	2	3	25	0.99	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	2	4	25	0.93	0.26
Slot (unpublished)	*Luehea seemannii*	Tropical	2	5	25	0.90	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	2	6	25	0.89	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	2	7	25	0.88	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	2	8	25	0.84	0.24
Slot (unpublished)	*Luehea seemannii*	Tropical	2	9	25	0.87	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	2	10	25	0.85	0.24
Slot (unpublished)	*Luehea seemannii*	Tropical	2	11	25	0.85	0.24
Slot (unpublished)	*Luehea seemannii*	Tropical	3	0	25	1.00	0.39
Slot (unpublished)	*Luehea seemannii*	Tropical	3	1	25	0.97	0.37
Slot (unpublished)	*Luehea seemannii*	Tropical	3	2	25	0.85	0.33
Slot (unpublished)	*Luehea seemannii*	Tropical	3	3	25	0.79	0.30
Slot (unpublished)	*Luehea seemannii*	Tropical	3	4	25	0.78	0.30
Slot (unpublished)	*Luehea seemannii*	Tropical	3	5	25	0.67	0.26
Slot (unpublished)	*Luehea seemannii*	Tropical	3	6	25	0.70	0.27
Slot (unpublished)	*Luehea seemannii*	Tropical	3	7	25	0.65	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	3	8	25	0.65	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	3	9	25	0.64	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	3	10	25	0.64	0.24
Slot (unpublished)	*Luehea seemannii*	Tropical	3	11	25	0.66	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	4	0	25	1.00	0.23
Slot (unpublished)	*Luehea seemannii*	Tropical	4	1	25	1.10	0.25
Slot (unpublished)	*Luehea seemannii*	Tropical	4	2	25	1.14	0.26
Slot (unpublished)	*Luehea seemannii*	Tropical	4	3	25	1.02	0.23
Slot (unpublished)	*Luehea seemannii*	Tropical	4	4	25	0.89	0.20
Slot (unpublished)	*Luehea seemannii*	Tropical	4	5	25	0.97	0.22
Slot (unpublished)	*Luehea seemannii*	Tropical	4	6	25	0.93	0.21
Slot (unpublished)	*Luehea seemannii*	Tropical	4	7	25	0.96	0.22

Slot (unpublished)	*Luehea seemannii*	Tropical	4	8	25	0.86	0.19
Slot (unpublished)	*Luehea seemannii*	Tropical	4	9	25	0.91	0.20
Slot (unpublished)	*Luehea seemannii*	Tropical	4	10	25	0.83	0.19
Slot (unpublished)	*Luehea seemannii*	Tropical	4	11	25	0.87	0.20
Slot (unpublished)	*Luehea seemannii*	Tropical	5	0	25	1.00	0.37
Slot (unpublished)	*Luehea seemannii*	Tropical	5	1	25	0.93	0.35
Slot (unpublished)	*Luehea seemannii*	Tropical	5	2	25	0.88	0.32
Slot (unpublished)	*Luehea seemannii*	Tropical	5	3	25	0.76	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	4	25	0.76	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	5	25	0.74	0.27
Slot (unpublished)	*Luehea seemannii*	Tropical	5	6	25	0.75	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	7	25	0.74	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	8	25	0.76	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	9	25	0.75	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	10	25	0.75	0.28
Slot (unpublished)	*Luehea seemannii*	Tropical	5	11	25	0.79	0.29
Newman (unpublished)	*Miconia*	Tropical	1	0	25	1.00	0.44
Newman (unpublished)	*Miconia*	Tropical	1	1	25	0.89	0.39
Newman (unpublished)	*Miconia*	Tropical	1	2	25	0.67	0.29
Newman (unpublished)	*Miconia*	Tropical	1	3	25	0.59	0.26
Newman (unpublished)	*Miconia*	Tropical	1	4	25	0.66	0.29
Newman (unpublished)	*Miconia*	Tropical	1	5	25	0.58	0.25
Newman (unpublished)	*Miconia*	Tropical	1	6	25	0.53	0.23
Newman (unpublished)	*Miconia*	Tropical	1	7	25	0.51	0.22
Newman (unpublished)	*Miconia*	Tropical	1	8	25	0.55	0.24
Newman (unpublished)	*Miconia*	Tropical	1	9	25	0.54	0.23
Newman (unpublished)	*Miconia*	Tropical	1	10	25	0.60	0.26
Newman (unpublished)	*Miconia*	Tropical	2	0	25	1.00	0.41
Newman (unpublished)	*Miconia*	Tropical	2	1	25	0.77	0.32
Newman (unpublished)	*Miconia*	Tropical	2	2	25	0.75	0.31
Newman (unpublished)	*Miconia*	Tropical	2	3	25	0.87	0.36
Newman (unpublished)	*Miconia*	Tropical	2	4	25	0.73	0.30
Newman (unpublished)	*Miconia*	Tropical	2	5	25	0.63	0.26
Newman (unpublished)	*Miconia*	Tropical	2	6	25	0.62	0.25
Newman (unpublished)	*Miconia*	Tropical	2	7	25	0.45	0.19
Newman (unpublished)	*Miconia*	Tropical	2	8	25	0.55	0.23
Newman (unpublished)	*Miconia*	Tropical	2	9	25	0.55	0.23
Newman (unpublished)	*Miconia*	Tropical	2	10	25	0.60	0.25
Newman (unpublished)	*Musa*	Tropical	1	0	26.5	1.00	0.88
Newman (unpublished)	*Musa*	Tropical	1	1	26.5	1.00	0.88
Newman (unpublished)	*Musa*	Tropical	1	2	26.5	1.07	0.94
Newman (unpublished)	*Musa*	Tropical	1	3	26.5	0.88	0.78
Newman (unpublished)	*Musa*	Tropical	1	4	26.5	0.85	0.75
Newman (unpublished)	*Musa*	Tropical	1	5	26.5	0.87	0.77
Newman (unpublished)	*Musa*	Tropical	1	6	26.5	0.80	0.70
Newman (unpublished)	*Musa*	Tropical	1	7	26.5	0.70	0.62
Newman (unpublished)	*Musa*	Tropical	1	8	26.5	0.65	0.57
Newman (unpublished)	*Musa*	Tropical	1	9	26.5	0.67	0.59
Newman (unpublished)	*Musa*	Tropical	1	10	26.5	0.69	0.61
Newman (unpublished)	*Musa*	Tropical	1	11	26.5	0.77	0.68
Newman (unpublished)	*Musa*	Tropical	1	12	26.5	0.84	0.74
Newman (unpublished)	*Musa*	Tropical	2	0	25	1.00	0.81
Newman (unpublished)	*Musa*	Tropical	2	1	25	0.85	0.69
Newman (unpublished)	*Musa*	Tropical	2	2	25	0.81	0.66
Newman (unpublished)	*Musa*	Tropical	2	3	25	0.65	0.52
Newman (unpublished)	*Musa*	Tropical	2	4	25	0.56	0.45
Newman (unpublished)	*Musa*	Tropical	2	5	25	0.58	0.48
Newman (unpublished)	*Musa*	Tropical	2	6	25	0.57	0.46
Newman (unpublished)	*Musa*	Tropical	2	7	25	0.48	0.39
Newman (unpublished)	*Musa*	Tropical	2	8	25	0.49	0.40
Newman (unpublished)	*Musa*	Tropical	2	9	25	0.45	0.37
Newman (unpublished)	*Musa*	Tropical	2	10	25	0.55	0.44
Newman (unpublished)	*Musa*	Tropical	2	11	25	0.59	0.48
Newman (unpublished)	*Musa*	Tropical	2	12	25	0.54	0.44
Newman (unpublished)	*Musa*	Tropical	3	0	25	1.00	0.47
Newman (unpublished)	*Musa*	Tropical	3	1	25	0.99	0.47
Newman (unpublished)	*Musa*	Tropical	3	2	25	0.94	0.44
Newman (unpublished)	*Musa*	Tropical	3	3	25	0.81	0.38
Newman (unpublished)	*Musa*	Tropical	3	4	25	0.73	0.35
Newman (unpublished)	*Musa*	Tropical	3	5	25	0.82	0.39
Newman (unpublished)	*Musa*	Tropical	3	6	25	0.78	0.37
Newman (unpublished)	*Musa*	Tropical	3	7	25	0.89	0.42
Newman (unpublished)	*Musa*	Tropical	3	8	25	0.74	0.35
Newman (unpublished)	*Musa*	Tropical	3	9	25	0.67	0.32
Newman (unpublished)	*Musa*	Tropical	3	10	25	0.77	0.36
Newman (unpublished)	*Musa*	Tropical	3	11	25	0.86	0.40
Newman (unpublished)	*Musa*	Tropical	3	12	25	0.90	0.42
Newman (unpublished)	*Musa*	Tropical	4	0	25	1.00	0.48
Newman (unpublished)	*Musa*	Tropical	4	1	25	1.17	0.56
Newman (unpublished)	*Musa*	Tropical	4	2	25	1.05	0.51
Newman (unpublished)	*Musa*	Tropical	4	3	25	0.89	0.43
Newman (unpublished)	*Musa*	Tropical	4	4	25	0.85	0.41

Newman (unpublished)	*Musa*	Tropical	4	5	25	0.82	0.40
Newman (unpublished)	*Musa*	Tropical	4	6	25	0.74	0.36
Newman (unpublished)	*Musa*	Tropical	4	7	25	0.72	0.35
Newman (unpublished)	*Musa*	Tropical	4	8	25	0.58	0.28
Newman (unpublished)	*Musa*	Tropical	4	9	25	0.70	0.34
Newman (unpublished)	*Musa*	Tropical	4	10	25	0.64	0.31
Newman (unpublished)	*Musa*	Tropical	4	11	25	0.68	0.33
Newman (unpublished)	*Musa*	Tropical	4	12	25	0.55	0.26
Newman (unpublished)	*Musa*	Tropical	5	0	26.4	1.00	0.80
Newman (unpublished)	*Musa*	Tropical	5	1	26.4	0.99	0.79
Newman (unpublished)	*Musa*	Tropical	5	2	26.4	1.00	0.79
Newman (unpublished)	*Musa*	Tropical	5	3	26.4	0.98	0.78
Newman (unpublished)	*Musa*	Tropical	5	4	26.4	0.93	0.74
Newman (unpublished)	*Musa*	Tropical	5	5	26.4	0.89	0.71
Newman (unpublished)	*Musa*	Tropical	5	6	26.4	0.82	0.65
Newman (unpublished)	*Musa*	Tropical	5	7	26.4	0.80	0.63
Newman (unpublished)	*Musa*	Tropical	5	8	26.4	0.86	0.68
Newman (unpublished)	*Musa*	Tropical	5	9	26.4	0.86	0.68
Newman (unpublished)	*Musa*	Tropical	5	10	26.4	0.97	0.77
Newman (unpublished)	*Musa*	Tropical	5	11	26.4	0.83	0.66
Newman (unpublished)	*Musa*	Tropical	5	12	26.4	0.77	0.61
Giuliani et al. 2019	*Oryza sativa*	Tropical	1	0	22	1.00	1.98
Giuliani et al. 2019	*Oryza sativa*	Tropical	1	1	22	0.76	1.51
Giuliani et al. 2019	*Oryza sativa*	Tropical	1	2	22	0.62	1.23
Giuliani et al. 2019	*Oryza sativa*	Tropical	1	3	22	0.57	1.13
Giuliani et al. 2019	*Oryza sativa*	Tropical	1	4	22	0.53	1.05
Gessler et al. 2017	*Phaseolus vulgaris*	Temperate	1	0	19	1.00	33.00
Gessler et al. 2017	*Phaseolus vulgaris*	Temperate	1	6	19	0.82	27.00
Gessler et al. 2017	*Phaseolus vulgaris*	Temperate	1	12	19	0.48	16.00
Noguchi et al. 2001	*Phaseolus vulgaris*	Temperate	2	0	20	1.00	97.50
Noguchi et al. 2001	*Phaseolus vulgaris*	Temperate	2	2	20	0.94	91.50
Noguchi et al. 2001	*Phaseolus vulgaris*	Temperate	2	5	20	0.68	66.50
Noguchi et al. 2001	*Phaseolus vulgaris*	Temperate	2	10	20	0.61	59.50
Azcon-Bieto et al. 1983	*Pisum sativum*	Temperate	1	0	21	1.00	0.67
Azcon-Bieto et al. 1983	*Pisum sativum*	Temperate	1	10	21	1.06	0.71
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	0	22	1.00	0.91
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	1	22	1.01	0.91
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	2	22	1.04	0.95
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	3	22	1.03	0.94
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	4	22	0.99	0.90
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	5	22	0.95	0.86
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	6	22	0.91	0.83
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	7	22	0.91	0.83
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	8	22	0.89	0.81
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	9	22	0.92	0.84
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	10	22	0.92	0.83
Newman (unpublished)	*Quercus humboldtii*	Tropical	1	11	22	0.88	0.80
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	0	22	1.00	0.75
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	1	22	0.88	0.66
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	2	22	0.90	0.68
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	3	22	0.82	0.62
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	4	22	0.82	0.62
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	5	22	0.76	0.58
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	6	22	0.74	0.56
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	7	22	0.75	0.56
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	8	22	0.76	0.57
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	9	22	0.74	0.56
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	10	22	0.70	0.53
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	11	22	0.70	0.53
Newman (unpublished)	*Quercus humboldtii*	Tropical	2	12	22	0.71	0.53
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	0	22	1.00	1.26
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	1	22	0.91	1.15
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	2	22	0.98	1.23
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	3	22	0.91	1.15
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	4	22	0.80	1.01
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	5	22	0.78	0.98
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	6	22	0.73	0.92
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	7	22	0.72	0.91
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	8	22	0.70	0.88
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	9	22	0.68	0.86
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	10	22	0.64	0.80
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	11	22	0.60	0.75
Newman (unpublished)	*Quercus humboldtii*	Tropical	3	12	22	0.59	0.74
Noguchi & Terashima 1995	*Spinacia oleracea*	Temperate	1	0	20	1.00	64.00
Noguchi & Terashima 1995	*Spinacia oleracea*	Temperate	1	1.5	20	0.92	59.00
Noguchi & Terashima 1995	*Spinacia oleracea*	Temperate	1	3	20	0.73	47.00
Noguchi & Terashima 1995	*Spinacia oleracea*	Temperate	1	11	20	0.55	35.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	2	0	25	1.00	54.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	2	1.5	25	0.94	51.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	2	5	25	0.64	35.00
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	2	11	25	0.61	33.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	3	0	25	1.00	43.00

Noguchi et al. 1996	*Spinacia oleracea*	Temperate	3	1.5	25	0.93	40.00
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	3	5	25	0.63	27.00
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	3	11	25	0.45	19.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	4	0	25	1.00	25.00
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	4	1.5	25	0.98	24.50
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	4	5	25	0.72	18.00
Noguchi et al. 1996	*Spinacia oleracea*	Temperate	4	11	25	0.64	16.00
Azcon-Bieto et al. 1983	*Spinacia oleracea*	Temperate	5	0	21	1.00	0.80
Azcon-Bieto et al. 1983	*Spinacia oleracea*	Temperate	5	10	21	0.64	0.51
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	0	23	1.00	0.84
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	1	23	0.78	0.66
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	2	23	0.75	0.63
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	3	23	0.72	0.60
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	4	23	0.75	0.62
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	5	23	0.74	0.62
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	6	23	0.65	0.55
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	7	23	0.68	0.57
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	8	23	0.68	0.57
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	9	23	0.69	0.57
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	10	23	0.69	0.57
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	11	23	0.72	0.60
Newman (unpublished)	*Tabebuia rosea*	Tropical	1	12	23	0.71	0.59
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	1	0	30	1.00	40.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	1	0.5	30	0.75	30.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	1	1	30	0.65	26.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	1	1.5	30	0.58	23.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	1	11	30	0.56	22.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	2	0	27	1.00	33.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	2	0.5	27	0.82	27.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	2	1	27	0.65	21.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	2	1.5	27	0.53	17.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	2	11	27	0.52	17.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	3	0	24	1.00	28.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	3	0.5	24	0.95	26.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	3	1	24	0.86	24.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	3	1.5	24	0.70	19.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	3	11	24	0.43	12.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	4	0	20	1.00	27.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	4	0.5	20	0.94	25.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	4	1	20	0.85	23.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	4	1.5	20	0.76	20.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	4	11	20	0.35	9.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	5	0	13.5	1.00	15.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	5	0.5	13.5	0.97	15.00
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	5	1	13.5	0.94	14.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	5	1.5	13.5	0.87	13.50
Azcon-Bieto & Osmon 1983	*Triticum aestivum*	Temperate	5	11	13.5	0.39	6.00
Scafaro et al. 2017	*Triticum aestivum*	Temperate	6	0	21.5	1.00	45.00
Scafaro et al. 2017	*Triticum aestivum*	Temperate	6	0.5	21.5	0.53	24.00
Scafaro et al. 2017	*Triticum aestivum*	Temperate	6	2.5	21.5	0.41	18.50
Scafaro et al. 2017	*Triticum aestivum*	Temperate	6	6.5	21.5	0.47	21.00
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	7	0	25	1.00	8.53
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	7	17	25	0.73	6.25
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	8	0	25	1.00	11.68
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	8	17	25	0.68	7.90
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	9	0	25	1.00	9.78
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	9	17	25	0.64	6.28
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	10	0	25	1.00	13.35
Averill & ap Rees 1994	*Triticum aestivum*	Temperate	10	17	25	0.65	8.64
Azcon-Bieto et al. 1983	*Triticum aestivum*	Temperate	11	0	21	1.00	0.73
Azcon-Bieto et al. 1983	*Triticum aestivum*	Temperate	11	10	21	0.75	0.55
Newman (unpublished)	Unidentified	Tropical	1	0	25	1.00	0.62
Newman (unpublished)	Unidentified	Tropical	1	1	25	1.05	0.65
Newman (unpublished)	Unidentified	Tropical	1	2	25	1.04	0.64
Newman (unpublished)	Unidentified	Tropical	1	3	25	0.91	0.57
Newman (unpublished)	Unidentified	Tropical	1	4	25	0.78	0.48
Newman (unpublished)	Unidentified	Tropical	1	5	25	0.65	0.40
Newman (unpublished)	Unidentified	Tropical	1	6	25	0.68	0.42
Newman (unpublished)	Unidentified	Tropical	1	7	25	0.65	0.40
Newman (unpublished)	Unidentified	Tropical	1	8	25	0.63	0.39
Newman (unpublished)	Unidentified	Tropical	1	9	25	0.63	0.39
Newman (unpublished)	Unidentified	Tropical	1	10	25	0.58	0.36

References

Aber, J. and Federer, C. (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems, *Oecologia*, 92: 463-474.

Allwood, J.M., Bosetti, V., Dubash, N.K., Gómez-Echeverri, L. and von Stechow, C. (2014) Glossary in Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Farahani, E., Kadner, S., Seyboth, K., Adler, A., Baum, I., Brunner, S., Eickemeier, P., Kriemann, B., Savolainen, J., Schlömer, S., von Stechow, C., Zwickel, T. and Minx, J.C. eds. *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Amthor, J. (1989) *Respiration and crop productivity*, Springer, New York.

Amthor, J. (1994) Plant respiratory responses to the environment and their effects on the carbon balance, in Wilkinson, R. ed. *Plant–environment interactions*, Marcel Dekker, New York: 501–554.

Anderegg, W., Ballantyne, A., Smith, W., Majkut, J., Rabin, S., Beaulieu, C., Birdsey, R., Dunne, J., Houghton, R., Myneni, R., Pan, Y., Sarmiento, J., Serota, N., Shevliakova, E., Tans, P. and Pacala, S. (2015) Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink, *Proceedings of the National Academy of Sciences*, 112(51): 15591-15596.

Anten, N., Schieving, F., Werger, M. (1995) Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species, *Oecologia,* 101: 504–513.

Arrhenius, S. (1889) Uber die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Sauren, *Zeitschrift fur Physik Chemie*, 4: 226–248.

Atkin, O. and Tjoelker M.G. (2003) Thermal acclimation and the dynamic response of plant respiration to temperature, *Trends in Plant Science*, 8(7): 343–351.

Atkin O., Millar A.H., Gardeström P. and Day D.A. (2000a) Photosynthesis, Carbohydrate Metabolism and Respiration in Leaves of Higher Plants, in Leegood R.C., Sharkey T.D. and von Caemmerer S. eds. *Photosynthesis*. *Advances in Photosynthesis and Respiration*, Springer, Dordrecht: 154-170.

Atkin, O., Edwards, E. and Loveys, B. (2000b) Response of root respiration to changes in temperature and its relevance to global warming, *New Phytologist*, 147(1): 141-154.

Atkin, O., Holly, C. and Ball, M. (2000c) Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration, *Plant, Cell and Environment*, 23(1): 15-26.

Atkin, O., Zhang, Q. and Wiskich, J. (2002) Effect of Temperature on Rates of Alternative and Cytochrome Pathway Respiration and Their Relationship with the Redox Poise of the Quinone Pool, *Plant Physiology*, 128(1): 212-222.

Atkin, O., Bruhn, D. and Tjoelker, M.G. (2005a) Response of Plant Respiration to Changes in Temperature: Mechanisms and Consequences of Variations in Q_{10} Values and Acclimation, in Lambers, H. and Ribas-Carbo, M. eds. *Plant Respiration. Advances in Photosynthesis and Respiration*, Springer, Dordrecht: 96-129.

Atkin, O., Bruhn, D., Hurry, V. and Tjoelker, M. (2005b) The hot and the cold: unravelling the variable response of plant respiration to temperature, *Functional Plant Biology*, 32(2): 87-105.

Atkin, O., Scheurwater, I. and Pons, T. (2007) Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures, *New Phytologist*, 174(2): 367-380.

Atkin, O., Atkinson, L., Fisher, R., Campbell, C., Zaragoza-Castells, J., Pitchford, J.W., Woodward, F.I. and Hurry, V. (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model, *Global Change Biology*, 14: 2709–2726.

Atkin, O., Millar, H. and Turnbull, M. (2010) Plant respiration in a changing world, *New Phytologist*, 187(2): 268-272.

Atkin, O., Meir, P. and Turnbull, M. (2014) Improving representation of leaf respiration in large-scale predictive climate-vegetation models, *New Phytologist*, 202(3): 743-748.

Atkin, O., Bloomfield, K., Reich, P., Tjoelker, M., Asner, G., Bonal, D., Bönisch, G., Bradford, M., Cernusak, L., Cosio, E., Creek, D., Crous, K., Domingues, T., Dukes, J., Egerton, J., Evans, J., Farquhar, G., Fyllas, N., Gauthier, P., Gloor, E., Gimeno, T., Griffin, K., Guerrieri, R., Heskel, M., Huntingford, C., Ishida, F., Kattge, J., Lambers, H., Liddell, M., Lloyd, J., Lusk, C., Martin, R., Maksimov, A., Maximov, T., Malhi, Y., Medlyn, B., Meir, P., Mercado, L., Mirotchnick, N., Ng, D., Niinemets, Ü., O'Sullivan, O., Phillips, O., Poorter, L., Poot, P., Prentice, I., Salinas, N., Rowland, L., Ryan, M., Sitch, S., Slot, M., Smith, N., Turnbull, M., VanderWel, M., Valladares, F., Veneklaas, E., Weerasinghe, L., Wirth, C., Wright, I., Wythers, K., Xiang, J., Xiang, S. and Zaragoza-Castells, J. (2015) Global variability in leaf respiration in relation to climate, plant functional types and leaf traits, *New Phytologist*, 206: 614–636.

Aubinet, M., Vesala, T. and Papale, D. (2012) *Eddy Covariance*: *A Practical Guide to Measurement and Data Analysis*, Dordrecht, Springer.

Averill, R. and ap Rees, T. (1995) The control of respiration in wheat (Triticum aestivum L.) leaves, *Planta*, 196(2): 344-349.

Azcón-Bieto, J. and Osmond, C. (1983) Relationship between Photosynthesis and Respiration: The Effect of Carbohydrate Status on the Rate of CO2 Production by

Respiration in Darkened and Illuminated Wheat Leaves, *Plant Physiology*, 71(3): 574-581.

Azcón-Bieto, J., Lambers, H. and Day, D. (1983) Effect of Photosynthesis and Carbohydrate Status on Respiratory Rates and the Involvement of the Alternative Pathway in Leaf Respiration, *Plant Physiology*, 72(3): 598-603.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X.,.Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K. T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S. (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapour and energy flux densities, *Bulletin of the American Meteorological Society*, 82: 2415–2433.

Ballantyne, A., Alden, C., Miller, J., Tans, P. and White, J. (2012) Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years, *Nature*, 488(7409): 70-72.

Barbour, M., Hunt, J., Kodama, N., Laubach, J., McSeveny, T., Rogers, G., Tcherkez, G. and Wingate, L. (2011) Rapid changes in δ13C of ecosystem-respired CO2 after sunset are consistent with transient 13C enrichment of leaf respired CO2, *New Phytologist*, 190(4): 990-1002.

Barnes, C. (1893) On the food of green plants, *Botanical Gazette,* 18: 403–411.

Baysdorfer, C., Sicher, R. and Kremer, D. (1987) Relationship between Fructose 2,6-Bisphosphate and Carbohydrate Metabolism in Darkened Barley Primary Leaves, *Plant Physiology*, 84(3): 766-769.

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M., Baldocchi, D., Bonan, G., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K., Roupsard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. and Papale, D. (2010) Terrestrial Gross Carbon Dioxide Uptake: Global Distribution and Covariation with Climate, *Science*, 329(5993): 834-838.

Belehradek, J. (1930) Temperature coefficients in biology, *Biological Reviews*, 5: 30-58.

Berry, J. and Raison, J. (1981) Responses of Macrophytes to Temperature in Lange, O., Nobel, P., Osmond, C., Ziegler, H. eds. *Physiological Plant Ecology I. Encyclopedia of Plant Physiology*, Springer, Berlin.

Best, M., Pryor, M., Clark, D., Rooney, G., Essery, R., Ménard, C., Edwards, J., Hendry, M., Porson, A., Gedney, N., Mercado, L., Sitch, S., Blyth, E., Boucher, O., Cox, P., Grimmond, C. and Harding, R. (2011) The Joint UK Land Environment Simulator (JULES), model description – Part 1: Energy and water fluxes, *Geoscientific Model Development*, 4(3): 677-699.

Billings, W., Godfrey, P., Chabot, B. and Bourque, D. (1971) Metabolic Acclimation to Temperature in Arctic and Alpine Ecotypes of *Oxyria digyna*, *Arctic and Alpine Research*, 3(4): 277-289.

Blyth, E., Clark, D., Ellis, R., Huntingford, C., Los, S., Pryor, M., Best, M. and Sitch, S. (2011) A comprehensive set of benchmark tests for a land surface model of simultaneous fluxes of water and carbon at both the global and seasonal scale, *Geoscientific Model Development*, 4(2): 255-269.

Bolstad, P., Mitchell, K., Vose, J. (1999) Foliar temperature – respiration response functions for broad-leaved tree species in the southern Appalachians, *Tree Physiology*, 19: 871–878.

Booth, B., Jones, C., Collins, M., Totterdell, I., Cox, P., Sitch, S., Huntingford, C., Betts, R., Harris, G. and Lloyd, J. (2012), High sensitivity of future global warming to land carbon cycle processes, *Environmental Research Letters*, 7(2).

Bouma, T., De Visser, R., Van Leeuwen, P., De Kock, M. and Lambers, H. (1995) The respiratory energy requirements involved in nocturnal carbohydrate export from starch-storing mature source leaves and their contribution to leaf dark respiration, *Journal of Experimental Botany*, 46(9): 1185-1194.

Boysen-Jensen, P. (1932) Die Stoffproduktion der Pflanzen, *Verlag von Gustav Fischer*, Jena.

Breeze, V. and Elston, J. (1978) Some effects of temperature and substrate content upon respiration and carbon balance of field beans (*Vicia faba* L.), *Annals of Botany*, 42: 863–876.

Bretzl, H. (1903) *Botanische Forschungen des Alexanderzuges*, Leipzig, B.G. Teubner, Germany.

Brienen, R., Phillips, O., Feldpausch, T., Gloor, E., Baker, T., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S., Vásquez Martinez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragão, L., Araujo-Murakami, A., Arets, E., Arroyo, L., Aymard, G., Bánki, O., Baraloto, C., Barroso, J., Bonal, D., Boot, R., Camargo, J., Castilho, C., Chama, V., Chao, K., Chave, J., Comiskey, J., Cornejo Valverde, F., da Costa, L., de Oliveira, E., Di Fiore, A., Erwin, T., Fauset, S., Forsthofer, M., Galbraith, D., Grahame, E., Groot, N., Hérault, B., Higuchi, N., Honorio Coronado, E., Keeling, H., Killeen, T., Laurance, W., Laurance, S., Licona, J., Magnussen, W., Marimon, B., Marimon-Junior, B., Mendoza, C., Neill, D., Nogueira, E., Núñez, P., Pallqui Camacho, N., Parada, A., Pardo-Molina, G., Peacock, J., Peña-Claros, M., Pickavance, G., Pitman, N., Poorter, L., Prieto, A., Quesada, C., Ramírez, F., Ramírez-Angulo, H., Restrepo, Z., Roopsind, A., Rudas, A., Salomão, R., Schwarz, M., Silva, N., Silva-Espejo, J., Silveira, M., Stropp, J., Talbot, J., ter Steege, H., Teran-Aguilar, J., Terborgh, J., Thomas-Caesar, R., Toledo, M., Torello-Raventos, M., Umetsu, R., van der Heijden, G., van der Hout, P., Guimarães Vieira, I., Vieira, S., Vilanova, E., Vos, V. and Zagt, R. (2015) Long-term decline of the Amazon carbon sink, *Nature*, 344(519).

Bruhn, D., Mikkelsen, T. and Atkin, O. (2002) Does the direct effect of atmospheric CO_2 concentration on leaf respiration vary with temperature? Responses in two species of Plantago that differ in relative growth rate, *Physiologia Plantarum*, 114(1): 57-64.

Bruhn, D., Edgerton, J., Loveys, B. and Ball, M. (2007) Evergreen leaf respiration acclimates to long-term nocturnal warming under field conditions, *Global Change Biology*, 13(6): 1216-1223.

Bruhn, D., Schortemeyer, M., Edwards, E., Egerton, J., Hocart, C., Evans, J. and Ball, M. (2008) The apparent temperature response of leaf respiration depends on the timescale of measurements: a study of two cold climate species, *Plant Biology*, 10(2): 185-193.

Buckley, T. and Adams, M. (2010) An analytical model of non-photorespiratory CO_2 release in the light and dark in leaves of C3 species based on stoichiometric flux balance, *Plant, Cell & Environment*, 34(1): 89-112.

Buckley, T., Vice, H. and Adams, M. (2017) The Kok effect in *Vicia faba* cannot be explained solely by changes in chloroplastic CO_2 concentration, *New Phytologist*, 216(4): 1064-1071.

Budde, R. and Randall, D. (1990) Pea leaf mitochondrial pyruvate dehydrogenase complex is inactivated in vivo in a light-dependent manner, *Proceedings of the National Academy of Sciences*, 87(2): 673-676.

Bunce, J. (2007) Direct and Acclimatory Responses of Dark Respiration and Translocation to Temperature, *Annals of Botany*, 100(1): 67-73.

Campbell, C., Atkinson, L., Zaragoza-Castells, J., Lundmark, M., Atkin, O. and Hurry, V. (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group, *New Phytologist*, 176(2): 375-389.

Campioli, M., Malhi, Y., Vicca, S., Luyssaert, S., Papale, D., Peñuelas, J., Reichstein, M., Migliavacca, M., Arain, M. and Janssens, I. (2016) Evaluating the convergence between eddy-covariance and biometric methods for assessing carbon budgets of forests, *Nature Communications*, 7(1).

Canadell, J., Le Quere, C., Raupach, M., Field, C., Buitenhuis, E., Ciais, P., Conway, T., Gillett, N., Houghton, R. and Marland, G. (2007) Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks, *Proceedings of the National Academy of Sciences*, 104(47): 18866-18870.

Carswell, F., Meir, P., Wandelli, E., Bonates, L., Kruijt, B., Barbosa, E., Nobre, A., Grace, J. and Jarvis, P. (2000) Photosynthetic capacity in a central Amazonian rain forest, *Tree Physiology*, 20(3): 179-186.

Chapin, F.S., Matson, P.A. and Mooney, H.A. (2002) *Principles of Terrestrial Ecosystem Ecology*, Springer-Verlag, New York, USA.

Chia-Looi, A. and Gumming, B. (1972) Circadian rhythms of dark respiration, flowering, net photosynthesis, chlorophyll content, and dry weight changes in *Chenopodium rubrum*, *Canadian Journal of Botany*, 50(11): 2219-2226.

Ciais, P., Sabine, C., Govindasamy, B., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R., Piao, S., and Thornton, P. (2013) Carbon and Other Biogeochemical Cycles, in Stocker, T., Qin, D., and Platner, G.-K. eds. *Climate Change 2013: The Physical Science Basis*, Cambridge University Press, Cambridge.

Clark, D., Mercado, L., Sitch, S., Jones, C., Gedney, N., Best, M., Pryor, M., Rooney, G., Essery, R., Blyth, E., Boucher, O., Harding, R. and Cox, P. (2011) The Joint UK Land Environment Simulator (JULES), Model description – Part 2: Carbon fluxes and vegetation, *Geoscientific Model Development Discussions*, 4(1): 641-688.

Collalti, A., Tjoelker, M., Hoch, G., Mäkelä, A., Guidolotti, G., Heskel, M., Petit, G., Ryan, M., Battipaglia, G., Matteucci, G. and Prentice, I. (2019), Plant respiration: Controlled by photosynthesis or biomass?, *Global Change Biology*: 1-15.

Collier, D. (1996) No difference in leaf respiration rates among temperate, subarctic, and arctic species grown under controlled conditions, *Canadian Journal of Botany*, 74(2): 317-320.

Covey-Crump, E., Attwood, R. and Atkin, O. (2002) Regulation of root respiration in two species of Plantago that differ in relative growth rate: the effect of short- and long-term changes in temperature, *Plant, Cell and Environment*, 25(11): 1501-1513.

Covey-Crump, E., Bykova, N., Affourtit, C., Hoefnagel, M., Gardestrom, P. and Atkin, O. (2007) Temperature-dependent changes in respiration rates and redox poise of the ubiquinone pool in protoplasts and isolated mitochondria of potato leaves, *Physiologia Plantarum*, 129: 175-184.

Covington, M., Maloof, J., Straume, M., Kay, S. and Harmer, S. (2008) Global transcriptome analysis reveals circadian regulation of key pathways in plant growth and development, *Genome Biology*, 9(8): R130.

Cox, P.M, Betts, R., Bunton, C., Essery, R., Rowntree, P. and Smith, J. (1999) The impact of new land surface physics on the GCM simulation of climate and climate sensitivity, *Climate Dynamics*, 15(3): 183-203.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. and Totterdell, I.J. (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature,* 408(6809): 184-187.

Cox, P.M. (2001) *Description of the TRIFFID Dynamic Global Vegetation Model, Hadley Centre Technical Note 24*, Hadley Centre, Met Office, UK.

Crous, K., Zaragoza-Castells, J., Ellsworth, D., Duursma, R., Low, M., Tissue, D. and Atkin, O. (2012) Light inhibition of leaf respiration in field-grown Eucalyptus saligna in

whole-tree chambers under elevated atmospheric CO_2 and summer drought, *Plant, Cell & Environment*, 35(5): 966-981.

Cuddington, K., Fortin, M., Gerber, L., Hastings, A., Liebhold, A., O'Connor, M. and Ray, C. (2013) Process-based models are required to manage ecological systems in a changing world, *Ecosphere*, 4(2): Article 20.

Darwin, F. (1898) Observations on stomata, Philosophical Transactions of the Royal Society of London, Series B, 190, 531–621.

Davidson, E. and Janssens, I. (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, 440(7081): 165-173.

Davidson, E., Janssens, I. and Luo, Y. (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}, *Global Change Biology*, 12(2): 154-164.

de Candolle, A.P. (1832) *Physiologie Vegetale*: *ou Exposition des forces et des fonctions vitals des detetaux*, Bechet jeune, Paris.

de Mairan, J. (1729) Observation botanique, *Histoire de l'Academie Royale*: 35-36.

Dehérain, P.P. and Moissan, H. (1874) Recherches sur l'absorption d'oxygene et l'emission d'acide carbonique par les plantes maintenues dans l'obscurite, *Annales des Sciences Naturelles Botanique*, 19: 321–357.

DeLucia, E., Drake, J., Thomas, R. and Gonzalez-Meler, M. (2007) Forest carbon use efficiency: is respiration a constant fraction of gross primary production?, *Global Change Biology*, 13(6): 1157-1167.

Dlugokencky, E. and Tans, P. (2019) Trends in atmospheric carbon dioxide, National Oceanic & Atmospheric Administration, *Earth System Research Laboratory (NOAA/ESRL),* available at: http:// www.esrl.noaa.gov/gmd/ccgg/trends/global.html, last access: 13 May 2019.

Dodd, A., Salathia, N., Hall, A., Kevei, E., Toth, R., Nagy, F., Hibberd, J., Millar, A. and Webb, A. (2005) Plant Circadian Clocks Increase Photosynthesis, Growth, Survival, and Competitive Advantage, *Science*, 309(5734): 630-633.

Doughty, C., Goulden, M., Miller, S. and da Rocha, H. (2006) Circadian rhythms constrain leaf and canopy gas exchange in an Amazonian forest, *Geophysical Research Letters*, 33(15).

Dunlap, J. (1999) Molecular Bases for Circadian Clocks, *Cell*, 96(2): 271-290.

Dunlap, J., Loros, J., and DeCoursey, P. (2004) *Chronobiology: Biological Timekeeping*, Sinauer Associates, Sunderland, MA.

Easterling, D., Horton, B., Jones, P., Peterson, T., Karl, T., Parker, D., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P. and Folland C. (1997) Maximum and Minimum Temperature Trends for the Globe, *Science*, 277(5324): 364-367.

Ellsworth, D. and Reich, P. (1996) Photosynthesis and leaf nitrogen in five Amazonian tree species during early secondary succession, *Ecology,* 77(2): 581–594.

Essery, R., Best, M., Betts, R., Cox, P.M. and Taylor, C. (2003) Explicit representation of subgrid heterogeneity in a GCM land surface scheme, Journal of Hydrometeorology, 4: 530-543.

Evans, J. (1993) Photosynthetic acclimation and nitrogen partitioning within a lucern canopy. II. Stability through time and comparison with a theoretical optimum, *Australian Journal of Plant Physiology*, 20: 69–82.

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N., Katul, G., Keronen, P., Kowalski, A., Lai, C., Law, B., Meyers, T., Moncrieff, J., Moors, E., Munger, J., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K. and Wofsy, S. (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange, *Agricultural and Forest Meteorology*, 107(1): 43-69.

Farquhar, G. and Busch, F. (2017) Changes in the chloroplastic CO_2 concentration explain much of the observed Kok effect: a model, *New Phytologist*, 214(2): 570-584.

Farquhar, G., von Caemmerer, S. and Berry, J. (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species, *Planta*, 149(1): 78-90.

Farrar, S.C. and Farrar, J.F. (1985) Carbon Fluxes in Leaf Blades of Barley, *New Phytologist*, 100(3): 271-283.

Farrar, J.F. and William, J. (1991) Control of the rate of respiration in roots: compartmentation, demand and the supply of substrate, in Emes, M. ed. *Compartmentation of plant metabolism in non-photosynthetic tissues*, Cambridge University Press, Cambridge: 167-188.

Farre, E.M. and Weise, S.E. (2012) The interactions between the circadian clock and primary metabolism, *Current Opinion in Plant Biology*, 15: 293–300.

Fatichi, S., Pappas, C., Zscheischler, J. and Leuzinger, S. (2019) Modelling carbon sources and sinks in terrestrial vegetation, *New Phytologist*, 221(2): 652-668.

Feugier, F. and Satake, A. (2013) Dynamical feedback between circadian clock and sucrose availability explains adaptive response of starch metabolism to various photoperiods, *Frontiers in Plant Science*, 3(305): 1-11.

Field, C. (1983) Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program, *Oecologia,* 56: 341–347.

Field, C. (1991) Ecological scaling of carbon gain to stress and resource availability, in Mooney, H., Winner, W. and Pell, E. eds. *Response of plants to multiple stresses*, Academic Press, New York, USA: 35–65.

Fitter, A., Graves, J., Self, G., Brown, T., Bogie, D. and Taylor, K. (1998) Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation, *Oecologia*, 114(1): 20-30.

Florez-Sarasa, I., Araújo, W., Wallström, S., Rasmusson, A., Fernie, A. and Ribas-Carbo, M. (2012) Light-responsive metabolite and transcript levels are maintained following a dark-adaptation period in leaves of Arabidopsis thaliana, *New Phytologist*, 195(1): 136-148.

Fluxdata (2019) *Fluxnet Site General Information*, available at: https://fluxnet.fluxdata.org/sites/site-list-and-pages/, last access: 20 January 2020.

Fondy B. and Geiger D. (1982) Diurnal pattern of translocation and carbohydrate metabolism in source leaves of *Beta vulgaris* L, *Plant Physiology*, 70: 671-676.

Forward, D. (1960) Effect of temperature on respiration in Ruhland, W. ed. *Encyclopedia of Plant Physiology*, Springer, Berlin: 234–258.

Friedlingstein, P., Meinshausen, M., Arora, V., Jones, C., Anav, A., Liddicoat, S. and Knutti, R. (2014) Uncertainties in CMIP5 Climate Projections due to Carbon Cycle Feedbacks, *Journal of Climate*, 27(2): 511-526.

Friedlingstein, P., Jones, M.W., O'Sullivan, M., Andrew, R.M., Hauck, J., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Bakker, D.C.E., Canadell, J.G., Ciais, P., Jackson, R.B., Anthoni, P., Barbero, L., Bastos, A., Bastrikov, V., Becker, M., Bopp, L., Buitenhuis, E., Chandra, N., Chevallier, F., Chini, L.P., Currie, K.I., Feely, R.A., Gehlen, M., Gilfillan, D., Gkritzalis, T., Goll, D.S., Gruber, N., Gutekunst, S., Harris, I., Haverd, V., Houghton, R.A., Hurtt, G., Ilyina, T., Jain, A.K., Joetzjer, E., Kaplan, J.O., Kato, E., Klein Goldewijk, K., Korsbakken, J.I., Landschutzer, P., Lauvset, S.K., Lefevre, N., Lenton, A., Lienert, S., Lombardozzi, D., Marland, G., McGuire, P.C., Melton, J.R., Metzl, N., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S.-I., Neill, C., Omar, A.M., Ono, T., Peregon, A., Pierrot, D., Poulter, B., Rehder, G., Resplandy, L., Robertson, E., Rodenbeck, C., Seferian, R., Schwinger, J., Smith, N., Tans, P.P., Tian, H., Tilbrook, B., Tubiello, F.N., van der Werf, G. R., Wiltshire, A. J. and Zaehle, S. (2019) Global Carbon Budget 2019, Earth System Science Data, 11(4): 1783-1838.

Gedney, N., Cox, P.M., and Huntingford, C. (2004) Climate feedback from wetland methane emissions, *Geophysical Research Letters*, 31(20).

Gessler, A., Roy, J., Kayler, Z., Ferrio, J., Alday, J., Bahn, M., del Castillo, J., Devidal, S., García-Muñoz, S., Landais, D., Martín-Gomez, P., Milcu, A., Piel, C., Pirhofer-Walzl, K., Galiano, L., Schaub, M., Haeni, M., Ravel, O., Salekin, S., Tissue, D., Tjoelker, M., Voltas, J., Hoch, G. and Resco de Dios, V. (2017) Night and day – Circadian regulation of night-time dark respiration and light-enhanced dark respiration in plant leaves and canopies, *Environmental and Experimental Botany*, 137: 14-25.

Gibon, Y., Bläsing, O., Palacios-Rojas, N., Pankovic, D., Hendriks, J., Fisahn, J., Höhne, M., Günther, M. and Stitt, M. (2004) Adjustment of diurnal starch turnover to short days:

depletion of sugar during the night leads to a temporary inhibition of carbohydrate utilization, accumulation of sugars and post-translational activation of ADP-glucose pyrophosphorylase in the following light period, *The Plant Journal*, 39(6): 847-862.

Gibon, Y., Pyl, E., Sulpice, R., Lunn, J., Hohne, M., Gunther, M. and Stitt, M. (2009) Adjustment of growth, starch turnover, protein content and central metabolism to a decrease of the carbon supply when *Arabidopsisis* is grown in very short photoperiods, *Plant, Cell & Environment*, 32(7): 859-874.

Gifford, R. (1994) The Global Carbon Cycle: a Viewpoint on the Missing Sink, *Functional Plant Biology*, 21(1).

Gifford, R. (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research, *Functional Plant Biology*, 30(2): 171.

Gillooly, J., Brown, J., West, B., Savage, V. and Charnov, E. (2001) Effects of Size and Temperature on Metabolic Rate, *Science*, 293(5538): 2248-2251.

Giuliani, R., Karki, S., Covshoff, S., Lin, H., Coe, R., Koteyeva, N., Quick, W., Von Caemmerer, S., Furbank, R., Hibberd, J., Edwards, G. and Cousins, A. (2019) Knockdown of glycine decarboxylase complex alters photorespiratory carbon isotope fractionation in Oryza sativa leaves, *Journal of Experimental Botany*, 70(10): 2773-2786.

Graf, A. and Smith, A. (2011) Starch and the clock: the dark side of plant productivity, *Trends in Plant Science*, 16(3): 169-175.

Graf, A., Schlereth, A., Stitt, M. and Smith, A.M. (2010) Circadian control of carbohydrate availability for growth in Arabidopsis plants at night, *Proceedings of the National Academy of Sciences*, 107(20): 9458-9463.

Grassi, G., House, J., Dentener, F., Federici, S., den Elzen, M. and Penman, J. (2017) The key role of forests in meeting climate targets requires science for credible mitigation, *Nature Climate Change*, 7(3): 220-226.

Greenham, K. and McClung, C. (2015) Integrating circadian dynamics with physiological processes in plants, *Nature Reviews Genetics*, 16(11): 598-610.

Griffin, K., Turnbull, M. and Murthy, R. (2002) Canopy position affects the temperature response of leaf respiration in *Populus deltoids*, *New Phytologist*, 154(3): 609-619.

Grimmer, C. and Komor, E. (1999) Assimilate export by leaves of *Ricinus communis* L. growing under normal and elevated carbon dioxide concentrations: the same rate during the day, a different rate at night, *Planta*, 209: 275-281.

Hanson, P., Amthor, J., Wullschleger, S., Wilson, K., Grant, R., Hartley, A., Hui, D., Hunt, Jr, E., Johnson, D., Kimball, J., King, A., Luo, Y., McNulty, S., Sun, G., Thornton, P., Wang, S., Williams, M., Baldocchi, D. and Cushman, R. (2004) Oak Forest Carbon

and Water Simulations: Model Intercomparisons and Evaluations against Independent Data, *Ecological Monographs*, 74(3): 443-489.

Harmer, S., Hogenesch, J., Straume, M., Chang, H., Han, B., Zhu, T., Wang, X., Kreps, J. and Kay, S. (2000) Orchestrated Transcription of Key Pathways in Arabidopsis by the Circadian Clock, *Science*, 290(5499): 2110-2113.

Harmer, S. (2009) The Circadian System in Higher Plants, *Annual Review of Plant Biology*, 60(1): 357-377.

Harper, A., Cox, P., Wiltshire, A., Jones, C., Mercado, L., Atkin, O., Reich, P. and Soudzilovskaia, N. (2016) Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4. 2) using plant trait information. *Geoscientific Model Development*, 9(7).

Harper, A., Powell, T., Cox, M., House, J., Huntingford, C., Lenton, T., Sitch, S., Burke, E., Chadburn, S., Collins, W., Comyn-Platt, E., Daioglou, V., Doelman, J., Hayman, G., Robertson, E., van Vuuren, D., Wiltshire, A., Webber, C., Bastos, A., Boysen, L., Ciais, P., Devaraju, N., Jain, A., Krause, A., Poulter, B. and Shu, S. (2018) Land-use emissions play a critical role in land-based mitigation for Paris climate targets, *Nature Communications*, 9(2938).

Haydon, M.J., Hearn, T.J., Bell, L.J., Hannah, M.A. and Webb, A.A. (2013) Metabolic regulation of circadian clocks, *Seminars in Cell and Developmental Biology*, 24: 414–421.

Hennessey, T., Freeden, A. and Field, C. (1993) Environmental effects on circadian rhythms in photosynthesis and stomatal opening, *Planta*, 189(3): 369-376.

Heskel, M., Atkin, O., Turnbull, M. and Griffin, K. (2013) Bringing the Kok effect to light: A review on the integration of daytime respiration and net ecosystem exchange, *Ecosphere*, 4(8): 98.

Heskel, M., O'Sullivan, O., Reich, P., Tjoelker, M., Weerasinghe, L., Penillard, A., Egerton, J., Creek, D., Bloomfield, K., Xiang, J., Sinca, F., Stangl, Z., Martinez-de la Torre, A., Griffin, K., Huntingford, C., Hurry, V., Meir, P., Turnbull, M. and Atkin, O. (2016) Convergence in the temperature response of leaf respiration across biomes and plant functional types, *Proceedings of the National Academy of Sciences*, 113(14): 3832-3837.

Hew, C.S., Thio, Y.C., Wong, S.Y., and Chin, T.Y. (1978) Rhythmic production of CO_2 by tropical orchid flowers, *Physiologia Plantarum,* 42(2): 226-230.

Hirose, T. and Werger, M. (1987) Maximizing daily photosynthesis with respect to the leaf nitrogen pattern in the canopy, *Oecologia*, 72: 520–526.

Hew, C., Ong, T. and Yap, W. (1994) Circadian Rhythm of Carbon Dioxide Production by Anthurium Flowers, *HortScience*, 29(9): 1025-1027.

Hollinger, D. (1989) Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest, *Functional Ecology*, 3: 53–62.

Hollinger, D. (1996) Optimality and nitrogen allocation in a tree canopy, *Tree Physiology*, 16: 627–634.

Hollinger, D., Kelliher, F., Byers, J., Hunt, J., McSeveny, T. and Weir, P. (1994) Carbon Dioxide Exchange between an Undisturbed Old-Growth Temperate Forest and the Atmosphere, *Ecology*, 75(1): 134-150.

Houghton, R.A. (2003) The Contemporary Carbon Cycle, in Turekian, K.K. and Holland, H.D. eds. *Treatise on Geochemistry*, Elsevier, Dordrecht: 473-513.

Houghton, R.A., Davidson, E.A., Woodwell, G.M. (1998) Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance, *Global Biogeochemical Cycles*, 12: 25–34.

Hubau, W., Lewis, S.L., Phillips, O.L, Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A.K., Ewango, C.E., Fauset, S., Mukinzi, J.M. and Sheil, D. (2020) Asynchronous carbon sink saturation in African and Amazonian tropical forests, *Nature*, 579(7797): 80-87.

Hunt, S. (2003) Measurements of photosynthesis and respiration in plants, *Physiologia Plantarum*, 117(3): 314-325.

Huntingford, C., Booth, B., Sitch, S., Gedney, N., Lowe, J., Liddicoat, S., Mercado, L., Best, M., Weedon, G., Fisher, R., Good, P., Zelazowski, P., Spessa, A. and Jones, C. (2010) IMOGEN: an intermediate complexity model to evaluate terrestrial impacts of a changing climate, *Geoscientific Model Development Discussions*, 3(3): 1161-1184.

Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L., Sitch, S., Fisher, R., Lomas, M., Walker, A., Jones, C., Booth, B., Malhi, Y., Hemming, D., Kay, G., Good, P., Lewis, S., Phillips, O., Atkin, O., Lloyd, J., Gloor, E., Zaragoza-Castells, J., Meir, P., Betts, R., Harris, P., Nobre, C., Marengo, J. and Cox, P. (2013) Simulated resilience of tropical rainforests to CO_2-induced climate change, *Nature Geoscience*, 6(4): 268-273.

Huntingford, C., Atkin, O., Martinez-de la Torre, A., Mercado, L., Heskel, M., Harper, A., Bloomfield, K., O'Sullivan, O., Reich, P., Wythers, K., Butler, E., Chen, M., Griffin, K., Meir, P., Tjoelker, M., Turnbull, M., Sitch, S., Wiltshire, A. and Malhi, Y. (2017) Implications of improved representations of plant respiration in a changing climate, *Nature Communications*, 8(1): 1602.

Hurry, V., Keerberg, O., Parnik, T., Öquist, G. and Gardeström, P. (1996) Effect of cold hardening on the components of respiratory decarboxylation in the light and in the dark in leaves of winter rye, *Plant Physiology*, 111: 713–719.

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

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Stocker, T.F., Qin, D., Plattner, G., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P. eds. Cambridge University Press, Cambridge.

Ivanova, T.L., Semikhatova, O.A., Judina, O.S. and Leina, G.D. (1989) The effect of temperature on the respiration of plants from different plant-geographic zones, in Semikhatova, O.A. ed. *Ecophysiological Investigations of Photosynthesis and Respiration in Plants*, Nauka Publishing, St Petersberg, Russia: 140–166.

James, W.O. (1953) *Plant Respiration*, Clarendon Press, Oxford.

Janssens, I., Lankreijer, H., Matteucci, G., Kowalski, A., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N., Vesala, T., Granier, A., Schulze, E., Lindroth, A., Dolman, A., Jarvis, P., Ceulemans, R. and Valentini, R. (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Global Change Biology*, 7(3): 269-278.

Jogireedy, V., Cox, P.M., Huntingford, C., Harding, R.J. and Mercado, L. (2006) An improved description of canopy light interception for use in a GCM land-surface scheme: calibration and testing against carbon fluxes at a coniferous forest, in *Hadley Centre Technical Note 63,* <http://www.metoffice.com/research/ hadleycentre/pubs/HCTN/index.html>.

Jones, C., McConnell, C., Coleman, K., Cox, P., Falloon, P., Jenkinson, D. and Powlson, D. (2005) Global climate change and soil carbon stocks; predictions from two contrasting models for the turnover of organic carbon in soil, *Global Change Biology*, 11(1): 154-166.

Jones, H. (1998) Stomatal control of photosynthesis and transpiration, *Journal of Experimental Botany*, 49: 387-398.

Jones, S., Rowland, L., Cox, P., Hemming, D., Wiltshire, A., Williams, K., Parazoo, N.C., Liu, J., da Costa, A.C.L., Meir, P., Mencuccini, M. and Harper, A. (2019) The Impact of a Simple Representation of Non-Structural Carbohydrates on the Simulated Response of Tropical Forests to Drought, Biogeosciences Discussions: 1-26.

Joos, F. and Spahni, R. (2008) Rates of change in natural and anthropogenic radiative forcing over the past 20,000 years, *Proceedings of the National Academy of Sciences*, 105(5): 1425-1430.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M., Reichstein, M., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C., Blonder, B., Bond, W., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-

Bares, J., Chambers, J., Chapin, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Durka, W., Elser, J., Enquist, B. J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernandez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R., Green, W., Gutierrez, A. G., Hickler, T., Higgins, S., Hodgson, J. G., Jalili, A., Jansen, S., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., Kuhn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., Llusia, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B., Messier, J., Moles, A., Muller, S., Nadrowski, K., Naeem, S., Niinemets, U., Nollert, S., Nuske, A., Ogaya, R., Joleksyn, J., Onipchenko, V. G., Onoda, Y., Ordonez, J., Overbeck, G., Ozinga, W., Patino, S., Paula, S., Pausas, J. G., Penuelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado, B., Sardans, J., Shiodera, S., Shipley, B., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., Wright, S. J., Zaehle, S., Zanne, A. E. and Wirth, C. (2011) *TRY: a global database of plant traits, Global Change Biology*, 17 (9): 2905-2935.

Keeling, C.D., Bacastow, R.B., Bainbridge, A.E., Ekdahl, C.A., Guenther, P.R., Waterman, L.S., and Chin, J.F.S. (1976) Atmospheric Carbon-Dioxide Variations at Mauna-Loa Observatory, Hawaii, *Tellus*, 28: 538–551.

Keenan, T., Migliavacca, M., Papale, D., Baldocchi, D., Reichstein, M., Torn, M. and Wutzler, T. (2019) Widespread inhibition of daytime ecosystem respiration, *Nature Ecology & Evolution*, 3(3): 407-415.

Khomik, M., Arain, M., Brodeur, J., Peichl, M., Restrepo-Coupé, N. and McLaren, J. (2010) Relative contributions of soil, foliar, and woody tissue respiration to total ecosystem respiration in four pine forests of different ages, *Journal of Geophysical Research*, 115(G3).

King, A., Gunderson, C., Post, W., Weston, D. and Wullschleger, S. (2006) Plant Respiration in a Warmer World, *Science,* 312: 536.

Klemedtsson, L., Ernfors, M., Björk, R.G., Weslien, P., Rütting, T., Crill, P. and Sikström, U. (2010) Reduction of greenhouse gas emissions by wood ash application to a *Picea abies (L.) Karst.* forest on a drained organic soil, *European Journal of Soil Science,* 61: 734–744.

Kok, B. (1948) A critical consideration of the quantum yield of Chlorella- photosynthesis, *Enzymologia,* 13: 1–56.

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

Kroner, Y. and Way, D. (2016) Carbon fluxes acclimate more strongly to elevated growth temperatures than to elevated CO_2 concentrations in a northern conifer, *Global Change Biology*, 22(8): 2913-2928.

Kruse, J. and Adams, M. (2008) Sensitivity of respiratory metabolism and efficiency to foliar nitrogen during growth and maintenance, *Global Change Biology*, 14(6): 1233-1251.

Kruse, J., Rennenberg, H. and Adams, M. (2011) Steps towards a mechanistic understanding of respiratory temperature responses, *New Phytologist*, 189(3): 659-677.

Laidler, K. (1972) Unconventional applications of the Arrhenius law, *Journal of Chemical Education*, 49(5).

Lambers, H., Chapin, F.S., Pons, T.L. (1998) *Plant physiological ecology*, Springer, New York, USA.

Lambers, H., Robinson, S.A. and Ribas-Carbo, M. (2005) Regulation of respiration in vivo, in Lambers, H., Robinson, S.A. and Ribas-Carbo, M. eds. *Plant Respiration. From Cell to Ecosystem*, Springer, Dordrecht: 1–15.

Lambers, H., Chapin, F.S. and Pons, T.L. (2008) *Plant Physiology Ecology,* Second Edition, Springer, viewed 16/05/19, <http://www.springer.com/gb/book/9780387783406>.

Larigauderie, A. and Korner, C. (1995) Acclimation of Leaf Dark Respiration to Temperature in Alpine and Lowland Plant Species, *Annals of Botany*, 76(3): 245-252.

Lasslop, G., Reichstein, M., Papale, D., Richardson, A., Arneth, A., Barr, A., Stoy, P. and Wohlfahrt, G. (2010) Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation, *Global Change Biology*, 16(1): 187-208.

Lavigne, M., Ryan, M., Anderson, D., Baldocchi, D., Crill, P., Fitzjarrald, D., Goulden, M., Gower, S., Massheder, J., McCaughey, J., Rayment, M. and Striegl, R. (1997) Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites, *Journal of Geophysical Research: Atmospheres*, 102(D24): 28977-28985.

Le Quéré, C., Andrew, R. M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A. C., Korsbakken, J. I., Peters, G. P., Canadell, J. G., Jackson, R. B., Boden, T. A., Tans, P. P., Andrews, O. D., Arora, V. K., Bakker, D. C. E., Barbero, L., Becker, M., Betts, R. A., Bopp, L., Chevallier, F., Chini, L. P., Ciais, P., Cosca, C. E., Cross, J., Currie, K., Gasser, T., Harris, I., Hauck, J., Haverd, V., Houghton, R. A., Hunt, C. W., Hurtt, G., Ilyina, T., Jain, A. K., Kato, E., Kautz, M., Keeling, R. F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metzl, N., Millero, F., Monteiro, P. M. S., Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., Nojiri, Y., Padin, X. A., Peregon, A., Pfeil, B., Pierrot, D., Poulter, B., Rehder, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Stocker, B. D., Tian, H., Tilbrook, B., Tubiello, F. N., van der Laan-Luijkx, I. T., van der Werf, G. R., van Heuven, S., Viovy, N., Vuichard, N., Walker, A. P., Watson, A. J., Wiltshire, A. J., Zaehle, S., and Zhu, D. (2018) Global Carbon Budget 2017, *Earth System Science Data*, 10: 405-448.

Lee, K. and Akita, S. (2000) Factors Causing the Variation in the Temperature Coefficient of Dark Respiration in Rice (*Oryza sativa L.*), *Plant Production Science*, 3(1): 38-42.

Lehmann, M., Wegener, F., Werner, R. and Werner, C. (2016) Diel variations in carbon isotopic composition and concentration of organic acids and their impact on plant dark respiration in different species, *Plant Biology*, 18(5): 776-784.

Leonardos, E., Micallef, B., Micallef, M. and Grodzinski, B. (2006) Diel patterns of leaf C export and of main shoot growth for Flaveria linearis with altered leaf sucrose–starch partitioning, *Journal of Experimental Botany*, 57(4): 801-814.

Leverenz, J., Bruhn, D. and Saxe, H. (1999) Responses of two provenances of *Fagus sylvatica* seedlings to a combination of four temperature and two CO_2 treatments during their first growing season: gas exchange of leaves and roots, *New Phytologist*, 144(3): 437-454.

LI-COR (2011) *Using the LI-6400/LI-6400XT Portable Photosynthesis System*, manual, LI-COR, Lincoln, Nebraska, USA, accessed on 24/04/17 <https://www.licor.com/documents/s8zyqu2vwndny903qutg>.

Litton, C., Raich, J., Ryan, M. (2007) Carbon allocation in forest ecosystems, *Global Change Biology*, 13: 2089–2109.

Lloyd, J. and Taylor, J. (1994) On the temperature dependence of soil respiration, Functional Ecology, 8: 315-323.

Lloyd, J., Grace, J., Miranda, A., Meir, P., Wong, G., Miranda, H., Wright, I., Gash, J. and McIntyre, J. (1995) A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties, *Plant, Cell and Environment*, 18(10): 1129-1145.

Logan, D. (2003) Mitochondrial Dynamics, New Phytologist, 160(3): 463-478.

Loreto, F., Velikova, V. and Di Marco, G. (2001) Respiration in the light measured by $^{12}CO_2$ emission in $^{13}CO_2$ atmosphere in maize leaves, *Functional Plant Biology*, 28(11): 1103.

Loveys, B., Atkinson, L., Sherlock, D., Roberts, R., Fitter, A. and Atkin, O. (2003) Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species, *Global Change Biology*, 9(6): 895-910.

Lundegardh, H. (1924) Der Temperaturfaktor bei Kohlensaure-assimilation und Atmung, *Biochemische Zeitschrift*, 154: 195– 234.

Luyssaert, S., Inglima, I., Jung, M., Richardson, A.D., Reichstein, M., Papale, D., Piao, S.L., Schulze, E.D., Wingate, L., Matteucci, G., Aragao, L.E.O.C., Aubinet, M., Beers, C., Bernhofer, C., Black, G.K., Bonal, D., Bonnefond, J.M., Chambers, J., Ciais, P., Cook, B., Davis, K.S., Dolman, A.J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P.J., Harding, R., Hollinger, D.Y., Hutyra, L.R., Kolari, P., Kruijt, B., Kutsch, W.L., Lagergren, F., Laurila, T., Law, B., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateu, J.,

Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E.J., Munger, J.W., Nikinmaa, E., Ollinger, S.V., Pita, G., Rebmann, C. and Roupsard, O. (2007) CO_2 balance of boreal, temperate, and tropical forests derived from a global database, *Global Change Biology*, 13(12): 2509-2537.

Luyssaert, S., Reichstein, M., Schulze, E., Janssens, I., Law, B., Papale, D., Dragoni, D., Goulden, M., Granier, A., Kutsch, W., Linder, S., Matteucci, G., Moors, E., Munger, J., Pilegaard, K., Saunders, M. and Falge, E. (2009) Toward a consistency cross-check of eddy covariance flux-based and biometric estimates of ecosystem carbon balance, *Global Biogeochemical Cycles*, 23(3).

Malhi Y., Baldocchi, D. and Jarvis, P. (1999) The carbon balance of tropical, temperate and boreal forests, *Plant, Cell and Environment*, 22(6): 715-740.

Malhi, Y., Aragao, L., Metcalfe, D., Paiva, R., Qesada, C., Almeida, S., Anderson, L., Brando, P., Chambers, J., da Costa, A., Hutyra, L., Oliveira, P., Patino, S., Pyle, E., Robertson, A. and Teixeira, L. (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests, *Global Change Biology*, 15(5): 1255-1274.

Masarie, K.A. and Tans, P.P. (1995) Extension and Integration of Atmospheric Carbon Dioxide Data into a Globally Consistent Measurement Record, Journal of Geophysical Research, 100: 11593–11610.

McClung, C. (2006) Plant Circadian Rhythms, *The Plant Cell*, 18(4): 792-803.

McCutchan, C. and Monson, R. (2002) Night-time respiration rate and leaf carbohydrate concentrations are not coupled in two alpine perennial species, *New Phytologist*, 149(3): 419-430.

Meir, P., Grace, J., and Miranda, A. (2001) Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature, *Functional Ecology*, 15: 378–387.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A. and Jarvis, P. (2002) Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area, *Plant, Cell and Environment*, 25(3): 343-357.

Melillo, J., McGuire, A., Kicklighter, D., Moore, B., Vorosmarty, C. and Schloss, A. (1993) Global climate change and terrestrial net primary production, *Nature*, 363, 234-240.

Mercado, L., Huntingford, C., Gash, J., Cox, P. and Jogireedy, V. (2007) Improving the representation of radiation interception and photosynthesis for climate model applications, *Tellus B*, 59(3).

Mercado, L., Bellouin, N., Sitch, S., Boucher, O., Huntingford, C., Wild, M. and Cox, P. (2009a) Impact of changes in diffuse radiation on the global land carbon sink, *Nature*, 458(7241): 1014-1017.

Mercado, L., Lloyd, J., Dolman, A., Sitch, S. and Patiño, S. (2009b) Modelling basin-wide variations in Amazon forest productivity – Part 1: Model calibration, evaluation and upscaling functions for canopy photosynthesis, *Biogeosciences*, 6(7): 1247-1272.

Mesplé, F., Troussellier, M., Casellas, C. and Legendre, P. (1996) Evaluation of simple statistical criteria to qualify a simulation, *Ecological Modelling*, 88(1-3): 9-18.

Michael, T., Mockler, T., Breton, G., McEntee, C., Byer, A., Trout, J., Hazen, S., Shen, R., Priest, H., Sullivan, C., Givan, S., Yanovsky, M., Hong, F., Kay, S. and Chory, J. (2008) Network Discovery Pipeline Elucidates Conserved Time-of-Day–Specific cis-Regulatory Modules, *PLoS Genetics*, 4(2): e14.

Moffat, A., Papale, D., Reichstein, M., Hollinger, D., Richardson, A., Barr, A., Beckstein, C., Braswell, B., Churkina, G., Desai, A., Falge, E., Gove, J., Heimann, M., Hui, D., Jarvis, A., Kattge, J., Noormets, A. and Stauch, V. (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agricultural and Forest Meteorology*, 147(3-4): 209-232.

Monsi, M. and Saeki, T (1953) Ueber den Lichtfaktor in den Planzenge-sellschaften und seine Bedeutung fuer die Stoffproduktion, *Japanese Journal of Botany*, 14: 22–52.

Mullen, J.A. and Koller, H.R. (1988) Trends in carbohydrate depletion, respiratory carbon loss, and assimilate export from soybean leaves at night, *Plant Physiology*, 86: 517–521.

Müller, L., von Korff, M. and Davis, S. (2014) Connections between circadian clocks and carbon metabolism reveal species-specific effects on growth control, *Journal of Experimental Botany*, 65(11): 2915-2923.

Müller, L., von Korff, M. and Davis, S. (2014) Connections between circadian clocks and carbon metabolism reveal species-specific effects on growth control, *Journal of Experimental Botany*, 65(11): 2915-2923.

Nabuurs, G., Lindner, M., Verkerk, P., Gunia, K., Deda, P., Michalak, R. and Grassi, G. (2013) First signs of carbon sink saturation in European forest biomass, *Nature Climate Change*, 3(9): 792-796.

Noguchi, K. (2005) Effects of light intensity and carbohydrate status on leaf and root respiration, in Lambers, H. and Ribas-Carbo, M. eds. *Plant respiration. From Cell to Ecosytem*, Springer, Dordrecht: 63–83.

Noguchi, K., Sonoike, K. and Terashima, I. (1996) Acclimation of Respiratory Properties of Leaves of *Spinacia oleracea* L., a Sun Species, and of *Alocasia macrorrhiza* (L.) G. Don., a Shade Species, to Changes in Growth Irradiance, *Plant and Cell Physiology*, 37(3): 377-384.

Noguchi, K. and Terashima, I. (1997) Different regulation of leaf respiration between *Spinacia oleracea*, a sun species, and *Alocasia odora*, a shade species, *Physiologia Plantarum*, 101(1): 1-7.

Noguchi, K., Go, C., Miyazawa, S., Terashima, I., Ueda, S. and Yoshinari, T. (2001) Costs of protein turnover and carbohydrate export in leaves of sun and shade species, *Functional Plant Biology*, 28(1).

O'Leary, B., Lee, C., Atkin, O., Cheng, R., Brown, T. and Millar, A. (2017) Variation in Leaf Respiration Rates at Night Correlates with Carbohydrate and Amino Acid Supply, *Plant Physiology*, 174(4): 2261-2273.

O'Leary, B., Asao, S., Millar, A. and Atkin, O. (2019) Core principles which explain variation in respiration across biological scales, *New Phytologist*, 222(2): 670-686.

Ow, L., Whitehead, D., Walcroft, A. and Turnbull, M. (2010) Seasonal variation in foliar carbon exchange in Pinus radiata and Populus deltoides: respiration acclimates fully to changes in temperature but photosynthesis does not, *Global Change Biology*, 16(1): 288-302.

Pallas, J., Samish, Y. and Willmer, C. (1974) Endogenous Rhythmic Activity of Photosynthesis, Transpiration, Dark Respiration, and Carbon Dioxide Compensation Point of Peanut Leaves, *Plant Physiology*, 53(6): 907-911.

Peng, S., Piao, S., Ciais, P., Myneni, R., Chen, A., Chevallier, F., Dolman, A., Janssens, I., Peñuelas, J., Zhang, G., Vicca, S., Wan, S., Wang, S. and Zeng, H. (2013) Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation, *Nature*, 501(7465): 88-92.

Peraudeau, S., Lafarge, T., Roques, S., Quiñones, C., Clement-Vidal, A., Ouwerkerk, P., Van Rie, J., Fabre, D., Jagadish, K. and Dingkuhn, M. (2015) Effect of carbohydrates and night temperature on night respiration in rice, *Journal of Experimental Botany*, 66(13): 3931-3944.

Piao, S., Luyssaert, S., Ciais, P., Janssens, I., Chen, A., Cao, C., Fang, J., Friedlingstein, P., Luo, Y. and Wang, S. (2010) Forest annual carbon cost: a global-scale analysis of autotrophic respiration, *Ecology*, 91(3): 652-661.

Piñeiro, G., Perelman, S., Guerschman, J. and Paruelo, J. (2008) How to evaluate models: Observed vs. predicted or predicted vs. observed?, *Ecological Modelling*, 216(3-4): 316-322.

Plaxton, W. and Podestá, F. (2006) The Functional Organization and Control of Plant Respiration, *Critical Reviews in Plant Sciences*, 25(2): 159-198.

Porte, A. and Loustau, D. (1998) Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year old *Pinus pinaster*, *Tree physiology,* 18: 223–232.

Porte, A., Bosc, A., Champion, I. and Loustau, D. (2000) Estimating the foliage area of maritime pine (*Pinus pinaster* Ait.) branches and crowns with application to modelling the foliage area distribution in the crown, *Annals of Forest Science*, 57: 73–86.

Prentice, I.C., , Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quere, C., Scholes, R.J. and Wallace, D.W.R. (2001) Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change, in Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., va der Linden, P.J., Dai, X., Maskell, K., and Johnson, C.A. eds. *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge: 183–237.

Price, J.T. and Warren, R. (2016) *Review of the Potential of "Blue Carbon" Activities to Reduce Emissions*, available at: http://avoid-net-uk.cc.ic.ac.uk/wpcontent/uploads/delightful- downloads/2016/03/Literature-review-of-the-potential-of- bluecarbon-activities-to-reduce-emissions-AVOID2-WPE2.pdf.

Rand, D., Shulgin, B., Salazar, D. and Millar, A. (2004) Design principles underlying circadian clocks, *Journal of the Royal Society Interface*, 1: 119–130.

Rascher, U., Hutt, M., Siebke, K., Osmond, B., Beck, F., Luttge, U. (2001) Spatiotemporal variation of metabolism in a plant circadian rhythm: the biological clock as an assembly of coupled individual oscillators, *Proceedings of the National Academy of Sciences of the United States of America,* 98.

Reich, P., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C. and Bowman, W.D. (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups, *Oecologia*, 114(4): 471-482.

Reichstein, M., Tenhunen, J., Roupsard, O., Ourcival, J., Rambal, S., Dore, S. and Valentini, R. (2002) Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics, *Functional Ecology*, 16(1): 27-39.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D. and Valentini, R. (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm, *Global Change Biology*, 11(9): 1424-1439.

Rensing, L., and Ruoff, P. (2002) Temperature effect on entrainment, phase shifting, and amplitude of circadian clocks and its molecular bases, *Chronobiology International*, 19(5): 807–864.

Rensing, S.A., Lang, D., Zimmer, A.D., Terry, A., Salamov, A., Shapiro, H., Nishiyama, T., Perroud, P., Lindquist, E., Kamisugi, Y., Tanahashi, T., Sakakibara, K., Fujita, T., Oishi, K., Shin-I, T., Kuroki, Y., Toyoda, A., Suzuki, Y., Hashimoto, S., Yamaguchi, K., Sugano, S., Kohara, Y., Fujiyama, A., Anterola, A., Aoki, S., Ashton, N., Barbazuk, W., Barker, E., Bennetzen, J., Blankenship, R., Cho, S., Dutcher, S., Estelle, M., Fawcett, J., Gundlach, H., Hanada, K., Heyl, A., Hicks, K., Hughes, J.,

Lohr, M., Mayer, K., Melkozernov, A., Murata, T., Nelson, D., Pils, B., Prigge, M., Reiss, B., Renner, T., Rombauts, S., Rushton, P., Sanderfoot, A., Schween, G., Shiu, S., Stueber, K., Theodoulou, F., Tu, H., Van de Peer, Y., Verrier, P., Waters, E., Wood, A., Yang, L., Cove, D., Cuming A., Hasebe, M., Lucas, S., Mishler, B., Reski, R., Grigoriev, I., Quatrano, R. and Boore, J. (2008) The Physcomitrella genome reveals evolutionary insights into the conquest of land by plants, *Science*, 319: 64–69.

Resco de Dios, V., Hartwell, J. and Hall, A. (2009) Ecological implications of plants' ability to tell the time, *Ecology Letters*, 12(6): 583-592.

Resco de Dios, V., Goulden, M., Ogle, K., Richardson, A., Hollinger, D., Davidson, E., Alday, J., Barron-Gafford, G., Carrara, A., Kowalski, A., Oechel, W., Reverter, B., Scott, R., Varner, R., Díaz-Sierra, R. and Moreno, J. (2012) Endogenous circadian regulation of carbon dioxide exchange in terrestrial ecosystems, *Global Change Biology*, 18(6): 1956-1970.

Resco de Dios, V., Gessler, A., Ferrio, J.P., Alday, J., Bahn, M., del Castillo, J., Devidal, S., Garcia-Munoz, S., Kayler, Z., Landais, D., Martin-Gomez, P., Milcu, A., Piel, C., Pirhofer-Walzl, K., Ravel, O., Salekin, S., Tissue, D., Tjoelker, M., Voltas, J. and Roy, J. (2016) Circadian rhythms have significant effects on leaf-to-canopy scale gas exchange under field conditions, *GigaScience,* 5(1): 43.

Ryan, M. (1991) Effects of Climate Change on Plant Respiration, *Ecological Applications*, 1(2): 157-167.

Ryan, M., Lavigne, M. and Gower, S. (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate, *Journal of Geophysical Research: Atmospheres*, 102(D24): 28871-28883.

Sanchez, A., Shin, J. and Davis, S. (2011) Abiotic stress and the plant circadian clock, *Plant Signaling and Behavior*, 6(2): 223-231.

Scafaro, A., Negrini, A., O'Leary, B., Rashid, F., Hayes, L., Fan, Y., Zhang, Y., Chochois, V., Badger, M., Millar, A. and Atkin, O. (2017) The combination of gas-phase fluorophore technology and automation to enable high-throughput analysis of plant respiration, *Plant Methods*, 13(1).

Schimel, D., VEMAP Participants and Braswell, B. (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance, *Ecological Monographs*, 67(2): 251-271.

Schimel, D., Enting, I.G., Heimann, M., Wigley, T.M.L., Raynaud, D., Alves, D. and Siegenthaler, U. (2005) CO_2 and the Carbon Cycle, in Wigley, T.M.L. and Schimel, D. eds. *The Carbon Cycle*, Cambridge University Press, Cambridge: 7-37.

Schimel, D., Stephens, B. and Fisher, J. (2014) Effect of increasing CO_2 on the terrestrial carbon cycle, *Proceedings of the National Academy of Sciences*, 112(2): 436-441.

Seibt, U., Wingate, L. and Berry, J. (2007) Nocturnal stomatal conductance effects on the $\delta^{18}O$ signatures of foliage gas exchange observed in two forest ecosystems, *Tree Physiology*, 27(4): 585-595.

Sellers, P. (1985) Canopy reflectance, photosynthesis and transpiration, *International Journal of Remote Sensing*, 6(8): 1335-1372.

Sellers, P., Berry, J., Collatz, G., Field, C. and Hall, F. (1992) Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme, *Remote Sensing of Environment*, 42(3): 187-216.

Sellers, P., Dickinson, R., Randall, D., Betts, A., Hall, F., Berry, J., Collatz, G., Denning, A., Mooney, H., Nobre, C., Sato, N., Field, C. and Henderson-Sellers, A. (1997) Modeling the Exchanges of Energy, Water, and Carbon Between Continents and the Atmosphere, *Science*, 275(5299): 502-509.

Shapiro, J., Griffin, K., Lewis, J. and Tissue, D. (2004) Response of Xanthium strumarium leaf respiration in the light to elevated CO_2 concentration, nitrogen availability and temperature, *New Phytologist*, 162(2): 377-386.

Sitch, S., Smith, B., Prentice, I., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J., Levis, S., Lucht, W., Sykes, M., Thonicke, K. and Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9(2): 161-185.

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R. A., Ciais, P., Cox, P. M., Friedlingstein, P., Jones, C. D., Prentice, I. C. and Woodward, F. I. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs), *Global Change Biology*, 14: 2015–2039.

Slot, M., Rey-Sánchez, C., Gerber, S., Lichstein, J., Winter, K. and Kitajima, K. (2014) Thermal acclimation of leaf respiration of tropical trees and lianas: response to experimental canopy warming, and consequences for tropical forest carbon balance, *Global Change Biology*, 20(9): 2915-2926.

Smith, A. and Stitt, M. (2007) Coordination of carbon supply and plant growth, *Plant, Cell & Environment*, 30(9): 1126-1149.

Smith, E. and Rose, K. (1995) Model goodness-of-fit analysis using regression and related techniques, *Ecological Modelling*, 77(1): 49-64.

Smith, N. and Dukes, J. (2013) Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO_2, *Global Change Biology*, 19: 45–63.

Sokolov, A., Kicklighter, D., Melillo, J., Felzer, B., Schlosser, C. and Cronin, T. (2008) Consequences of Considering Carbon–Nitrogen Interactions on the Feedbacks between Climate and the Terrestrial Carbon Cycle, *Journal of Climate*, 21(15): 3776-3796.

Stitt, M., & Zeeman, C. (2012) Starch turnover: Pathways, regulation and role in growth, *Current Opinion in Plant Biology*, 15: 282–292.

Stitt, M., von Schaewen, A. and Willmitzer, L. (1991) "Sink" regulation of photosynthetic metabolism in transgenic tobacco plants expressing yeast invertase in their cell wall involves a decrease of the Calvin-cycle enzymes and an increase of glycolytic enzymes, *Planta*, 183(1): 40-50.

Stocker, O. (1935) Assimilation und Atmung westjavanischer Tropenbaume, *Planta*, 24, 402–445.

Stoy, P., Katul, G., Siqueira, M., Juang, J., Novick, K., Uebelherr, J. and Oren, R. (2006) An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration, *Agricultural and Forest Meteorology*, 141(1): 2-18.

Tarvainen, L., Wallin, G., Räntfors, M. and Uddling, J. (2013) Weak vertical canopy gradients of photosynthetic capacities and stomatal responses in a fertile Norway spruce stand, *Oecologia*, 173(4): 1179-1189.

Tarvainen, L., Räntfors, M. and Wallin, G. (2015) Seasonal and within-canopy variation in shoot-scale resource-use efficiency trade-offs in a Norway spruce stand, *Plant, Cell & Environment*, 38(11): 2487-2496.

Tcherkez, G., Cornic, G., Bligny, R., Gout, E. and Ghasghaie, J. (2005) In Vivo Respiratory Metabolism of Illuminated Leaves, *Plant Physiology*, 138(3): 1596-1606.

Tcherkez, G., Bligny, R., Gout, E., Mahe, A., Hodges, M. and Cornic, G. (2008) Respiratory metabolism of illuminated leaves depends on CO_2 and O_2 conditions, *Proceedings of the National Academy of Sciences*, 105(2): 797-802.

Tcherkez, G., Mahe, A., Gauthier, P., Mauve, C., Gout, E., Bligny, R., Cornic, G. and Hodges, M. (2009) In Folio Respiratory Fluxomics Revealed by 13C Isotopic Labeling and H/D Isotope Effects Highlight the Noncyclic Nature of the Tricarboxylic Acid "Cycle" in Illuminated Leaves, *Plant Physiology*, 151(2): 620-630.

Tcherkez, G., Mahé, A., Géurard, F., Boex-Fontvieille, E., Gout, E., Lamothe, M., Barbour, M. and Bligny, R. (2012) Short-term effects of CO_2 and O_2 on citrate metabolism in illuminated leaves, *Plant, Cell & Environment*, 35(12): 2208-2220.

Tcherkez, G., Gauthier, P., Buckley, T., Busch, F., Barbour, M., Bruhn, D., Heskel, M., Gong, X., Crous, K., Griffin, K., Way, D., Turnbull, M., Adams, M., Atkin, O., Farquhar, G. and Cornic, G. (2017a) Leaf day respiration: low CO_2 flux but high significance for metabolism and carbon balance, *New Phytologist*, 216(4): 986-1001.

Tcherkez, G., Gauthier, P., Buckley, T., Busch, F., Barbour, M., Bruhn, D., Heskel, M., Gong, X., Crous, K., Griffin, K., Way, D., Turnbull, M., Adams, M., Atkin, O., Bender, M., Farquhar, G. and Cornic, G. (2017b) Tracking the origins of the Kok effect, 70 years after its discovery, *New Phytologist*, 214(2): 506-510.

Thornley, J. (1970) Respiration, growth and maintenance in plants, *Nature,* 227: 304-305.

Thornley, J. (2011) Plant growth and respiration re-visited: maintenance respiration defined – it is an emergent property of, not a separate process within, the system – and why the respiration : photosynthesis ratio is conservative, *Annals of Botany*, 108(7): 1365-1380.

Thornton, P., Lamarque, J., Rosenbloom, N. and Mahowald, N. (2007) Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability, *Global Biogeochemical Cycles*, 21(4).

Tjoelker, M., Oleksyn, J. and Reich, P. (1999a) Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate, *Global Change Biology*, 5(6): 679-691.

Tjoelker, M., Reich, P. and Oleksyn, J. (1999b) Changes in leaf nitrogen and carbohydrates underlie temperature and CO_2 acclimation of dark respiration in five boreal tree species *Plant, Cell and Environment*, 22(7): 767-778.

Tjoelker, M., Oleksyn, J. and Reich, P. (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10}, *Global Change Biology*, 7(2): 223-230.

Trethewey, R. and ap Rees, T. (1994) The role of the hexose transporter in the chloroplasts of Arabidopsis thaliana L., *Planta*, 195(2): 168-174.

Tsai, T., Choi, Y.S., Ma, W., Pomerening, J.R., Tang, C., Ferrell, J.E. (2008) Robust, tuneable biological oscillations from interlinked positive and negative feedback loops, *Science*, 321: 126–129.

Turnbull, M., Murthy, R., and Griffin, K. (2002) The relative impacts of daytime and night-time warming on photosynthetic capacity in *Populus deltoides*, Plant, Cell and Environment, 25: 1729–1737.

Turnbull, M., Whitehead, D., Tissue, D., Schuster, W., Brown, K. and Griffin, K. (2003) Scaling foliar respiration in two contrasting forest canopies. *Functional Ecology*, 17(1): 101-114.

Valentini, R., Matteucci, G., Dolman, A., Schulze, E., Rebmann, C., Moors, E., Granier, A., Gross, P., Jensen, N., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guðmundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S. and Jarvis, P. (2000) Respiration as the main determinant of carbon balance in European forests, *Nature*, 404(6780): 861-865.

van't Hoff, J.H. (1898) Lectures on Theoretical and Physical Chemistry, *Part 1. Chemical Dynamics*, Edward Arnold, London.

Vanderwel, M., Slot, M., Lichstein, J., Reich, P., Kattge, J., Atkin, O., Bloomfield, K., Tjoelker, M. and Kitajima, K. (2015) Global convergence in leaf respiration from estimates of thermal acclimation across time and space, *New Phytologist*, 207(4): 1026-1037.

Vanlerberghe, G. (2013) Alternative Oxidase: A Mitochondrial Respiratory Pathway to Maintain Metabolic and Signaling Homeostasis during Abiotic and Biotic Stress in Plants, *International Journal of Molecular Sciences*, 14(4): 6805-6847.

Wager, H. (1941) On the respiration and carbon assimilation rates of some arctic plants as related to temperature, *New Phytologist*, 40: 1-19.

Watanabe, C., Sato, S., Yanagisawa, S., Uesono, Y., Terashima, I. and Noguchi, K. (2014) Effects of Elevated CO_2 on Levels of Primary Metabolites and Transcripts of Genes Encoding Respiratory Enzymes and Their Diurnal Patterns in Arabidopsis thaliana: Possible Relationships with Respiratory Rates, *Plant and Cell Physiology*, 55(2): 341-357.

Weise, S.E., Schrader, S., Kleinbeck, K. and Sharkey, T. (2006) Carbon Balance and Circadian Regulation of Hydrolytic and Phosphorolytic Breakdown of Transitory Starch, *Plant Physiology*, 141(3): 879-886.

Whitehead, D., Griffin, K., Turnbull, M., Tissue, D., Engel, V., Brown, K., Schuster, W. and Walcroft, A. (2004) Response of total night-time respiration to differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy: implications for modelling canopy CO_2 exchange, *Global Change Biology*, 10(6): 925-938.

Williams, W. and Gorton, H. (1998) Circadian rhythms have insignificant effects on plant gas exchange under field conditions, *Physiologia Plantarum*, 103(2): 247-256.

Wingate, L., Ogée, J., Burlett, R. and Bosc, A. (2010) Strong seasonal disequilibrium measured between the oxygen isotope signals of leaf and soil CO_2 exchange, *Global Change Biology,* 16: 3048-3064.

Wingate, L., Ogée, J., Burlett, R., Bosc, A., Devaux, M., Grace, J., Loustau, D. and Gessler, A. (2010) Photosynthetic carbon isotope discrimination and its relationship to the carbon isotope signals of stem, soil and ecosystem respiration, *New Phytologist*, 188(2): 576-589.

Wright, I., Reich, P., Atkin, O., Lusk, C., Tjoelker, M. and Westoby, M. (2005) Irradiance, temperature and rainfall influence leaf dark respiration in woody plants: evidence from comparisons across 20 sites, *New Phytologist*, 169(2): 309-319.

Wythers, K., Reich, P., Tjoelker, M. and Bolstad, P. (2005) Foliar respiration acclimation to temperature and temperature variable Q_{10} alter ecosystem carbon balance, *Global Change Biology*, 11(3): 435-449.

Wythers, K., Reich, P. and Bradford, J. (2013) Incorporating temperature-sensitive Q_{10} and foliar respiration acclimation algorithms modifies modeled ecosystem responses to global change, *Journal of Geophysical Research: Biogeosciences*, 118: 77–90.

Xia, J., Chen, J., Piao, S., Ciais, P., Luo, Y. and Wan, S. (2014) Terrestrial carbon cycle affected by non-uniform climate warming, *Nature Geoscience*, 7(3): 173-180.

Xu, C. and Griffin, K. (2006) Seasonal variation in the temperature response of leaf respiration in Quercus rubra: foliage respiration and leaf properties, *Functional Ecology*, 20(5): 778-789.

Xu, M., De Biase, T., Qi, Y., Goldstein, A. and Liu, Z. (2001) Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California, *Tree Physiology*, 21(5): 309-318.

Zeeman, C., Smith, S.M., and Smith, A.M. (2007) The diurnal metabolism of leaf starch, *Biochemical Journal*, 401,13–28.

Zha, T., Kellomaki, S. and Wang, K-Y. (2003) Seasonal variation in respiration of 1-year-old shoots of Scots pine exposed to elevated carbon dioxide and temperature for 4 years, A*nnals of Botany*, 92: 89-96.