Climate Change Sensitivity of Photosynthesis and Respiration in Tropical Trees

Myriam Mujawamariya

2021

This thesis is submitted at the University of Rwanda, School of Science, Department of Biology for the award of PhD degree in Biological Sciences and at the University of Gothenburg, Faculty of Science, Department of Biological and Environmental Sciences for the award of PhD degree in Natural Sciences, specializing in Environmental Sciences. The thesis will be publicly defended on the 16th June 2021 at 13:00 h, in an aula at the University of Rwanda, Kigali, and on a secure webinar link published one day ahead of the event.

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The author performing gas exchange measurements on trees at a Rwanda-TREE site

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Declaration

I, Myriam Mujawamariya declare that this thesis entitled Climate Change Sensitivity of Photosynthesis and Respiration in Tropical Trees is the result of my own work, except where specifically acknowledged.

Myriam Mujawamariya

Signature:

Date: 24/02/2021

Main supervisor: Prof. Johan Uddling

Signature:

Date: 24/02/2021

To my father Jean Baptiste NGARUKIYE

To my mother Marianne MUKARUTABANA

To my sons Aimé Prince TURIKUMWE MUGISHA and Yanis NSHUTI MANZI

To my brothers and sisters

I dedicate this thesis

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And

To the Lord, God Almighty, without His grace I would have never found the right path. What shall I render to Jehovah, for He has done so very much for me! I will always bow down and honor You, You are Faithful God.

Abstract

Tropical climate is getting warmer, with more pronounced dry periods in large areas. The productivity and climate feedbacks of future tropical forests depend on the ability of trees to acclimate their physiological processes, such as photosynthesis and leaf respiration, to these new conditions. However, knowledge on this in tropical tree species is currently limited due to data scarcity.

In this thesis, I have studied warming and seasonal drought responses of photosynthesis and leaf dark respiration (R_d) in early-successional (ES) and late-successional (LS) species originating from Afromontane and transitional rainforest vegetation zones. My research used an elevation gradient approach with different designs in different studies: existing mature trees of four species growing at five locations at different elevation (Paper I); multispecies plantations established at three sites at different elevation and vegetation zones in an elevation experiment named Rwanda TRopical Elevation Experiment (Rwanda-TREE), using either plants freely rooted in the soil (Paper II and III) or plants growing in pots with the same soil at all sites (Paper IV).

The results demonstrated that in existing mature trees leaf stomatal conductance (g_s), transpiration (E) and light saturated net photosynthesis (A_n) decreased at warmer, lower-elevation sites during dry season, while patterns were absent (for g_s and A_n) or opposite (for E) in the wet season. In Rwanda-TREE, I found that A_n under non-drought conditions decreased in trees grown at the warmest, low-elevation site, in LS but not in ES species, while A_n was strongly and equally reduced in ES and LS species during the dry season at the two warmer sites, but not at the high-elevation site. Rates of leaf R_d measured at 20 °C were strongly reduced in trees grown at the warmer sites, leading to constancy or even declines in R_d at prevailing nighttime temperatures. Drought also reduced R_d. The pot study showed that the optimum temperature of A_n and its underlying biochemical processes did not significantly increase in warm-grown trees, indicating limited thermal acclimation capacity of photosynthesis.

The findings of this thesis have several important implications for the projection of future tropical biosphere–atmosphere interactions. Firstly, the pronounced seasonality in altitudinal patterns suggest that tropical tree water use and CO_2 uptake will be substantially reduced if dry seasons become more pronounced in a warmer climate. Secondly, the strong thermal acclimation of leaf R_d observed here should be accounted for to avoid model overestimation of the impact of global warming on leaf respiration in tropical forests. Thirdly, the contrasting responses of photosynthesis to warming in ES and LS species may imply potential functional shifts in tree community composition of tropical forests in a warmer climate. Fourthly, my results also indicate that acclimation capacity of the thermal optimum of photosynthesis may be considerably weaker in tropical montane tree species compared to temperate and boreal species. With these findings, my thesis contributes to reducing the knowledge gaps regarding tropical tree responses to climate change, which is key for improving projections of future climate change responses and feedbacks of tropical forests.

Keywords: Carbon dioxide, Climate change, Drought, Elevation gradient, Photosynthesis, Respiration, Tropical montane forest, Tropical trees, Warming.

List of Papers

Paper I. **Mujawamariya, M.**, Manishimwe, A., Ntirugulirwa, B., Zibera, E., Ganszky, D., Ntawuhiganayo, B.E., Nyirambangutse, B., Nsabimana, D., Wallin, G., and Uddling, J. (2018). Climate sensitivity of tropical trees along an elevation gradient in Rwanda. *Forests*, 9, 647: 1-19; doi:10.3390/f9100647.

Paper II. **Mujawamariya, M**., Wittemann, M., Dusenge, M.E., Manishimwe, A., Ntirugulirwa, B., Zibera, E., Nsabimana, D., Wallin, G., Uddling, J. Contrasting warming responses of photosynthesis in early- and late-successional tropical trees. Manuscript.

Paper III. **Mujawamariya, M.,** Wittemann, M., Manishimwe, A., Ntirugulirwa, B., Zibera, E., Nsabimana, D., Wallin, G., Uddling, J. and Dusenge, M.E. (2021). Complete or over-compensatory thermal acclimation of leaf dark respiration in African tropical trees. *New Phytologist* 229: 2548-2561. doi: 10.1111/nph.17038.

Paper IV. Dusenge, M. E., Wittemann, M., **Mujawamariya, M.,** Ntawuhiganayo, E. B., Zibera, E., Ntirugulirwa, B., Nsabimana, D., Way, D. A., Uddling, J., Wallin, G. Limited thermal acclimation of photosynthesis in tropical montane rainforests tree species. Manuscript submitted to *Global Change Biology*.

The papers and their respective supplementary material are appended in the end of the thesis and are reproduced with permission from the respective journals.

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List of Symbols and Abbreviations

A_{n}	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})
A_{n25}	Net photosynthesis at 25 °C (μmol CO_2 m^{-2} s^{-1})
A_{n25N}	A_{n25} normalized to total leaf N (μmol $[g\ N]^{-1}$ s^{-1})
A_{n25P}	A_{n25} normalized to total leaf P (μmol $[g\ P]^{-1}$ s^{-1})
C	Carbon
C_{a}	Ambient air CO_2 concentration
C_{i}	Intercellular CO_2 concentration (μmol mol^{-1})
CO_2	Carbon dioxide
DBH	Diameter at breast height (cm)
E	Leaf transpiration (mmol H_2O m^{-2} s^{-1})
ES	Early-successional
g_{heat}	Leaf boundary layer conductance for heat (mol m^{-2} s^{-1})
g_{s}	Stomatal conductance for water vapour (mmol H_2O m^{-2} s^{-1})
g_1	Empirical slope parameter of the combined stomatal-photosynthesis model
J_{max}	Maximum rate of photosynthetic electron transport (μmol m^{-2} s^{-1})
LMA	Leaf mass per unit area (g m^{-2})
LS	Late-successional
N_a	Leaf nitrogen per unit area (g N m^{-2})
N_m	Leaf nitrogen per unit dry mass (mg N g^{-1})
P_a	Leaf phosphorus content per unit area (g P m^{-2})
P_m	Leaf phosphorus per unit dry mass (mg P g^{-1})

PPFD	Photosynthetic photon flux density (μmol photons m^{-2} s^{-1})
Q_{10}	Change in reaction rate in response to 10 °C increase in temperature
Rwanda-TREE	Rwanda TRopical Elevation Experiment
R_d	Leaf dark respiration rate (μmol CO_2 m^{-2} s^{-1})
R_{growth}	Leaf R_d at mean nighttime growth temperature (μmol CO_2 m^{-2} s^{-1})
R_{d20}	Leaf R_d at 20 °C
R_{d20N}	R_{d20} normalized to total leaf N (μmol [g N]$^{-1}$ s^{-1})
T	Temperature (°C)
T_{air}	Air temperature (°C)
T_{leaf}	Leaf temperature (°C)
T_{opt}	Optimum temperature (°C)
T_{optA}	Optimum temperature of net photosynthesis (°C)
T_{optV}	Thermal optimum of maximum Rubisco carboxylation capacity (°C)
T_{optJ}	Thermal optimum of photosynthetic electron transport capacity (°C)
V_{cmax}	Maximum velocity of Rubisco carboxylation (μmol m^{-2} s^{-1})
V_{max25}	Maximum velocity of Rubisco carboxylation at 25 °C (μmol m^{-2} s^{-1})
VPD or D	Vapor pressure deficit of air (kPa)
WUE	Leaf photosynthetic water use efficiency (mmol CO_2 [mol H_2O]$^{-1}$)

1. General Introduction

Global mean temperature has increased by approximately 1.2 °C from the 1850-1900 period to 2020 (Rohde & Hausfather, 2020) and is predicted to continue to rise by 2-4°C this century (Huntingford *et al.,* 2012). In addition, more frequent and severe drought events are predicted over the 21st century in tropical regions (Malhi *et al.*, 2008; Chadwick *et al.*, 2015). Trees are considered as a key driver for the global carbon cycle through their exchange of huge amounts of carbon dioxide (CO_2) with the atmosphere (Bonan, 2008; Arneth *et al.*, 2010). Through photosynthesis, terrestrial vegetation absorbs much carbon (C), approximately 123 Gt of C from the atmosphere every year (Beer *et al.*, 2010) and almost half of this assimilated C (60 Gt of C) is released back to the atmosphere through autotrophic respiration (Beer *et al.,* 2010; Ciais *et al.,* 2013) (Figure 1). Given the on-going global warming and that vegetation CO_2 fluxes are much larger compared to CO_2 emissions by anthropogenic activities (Le Quéré *et al.,* 2016), changes in terrestrial vegetation CO_2 fluxes could result in either mitigation or acceleration of climate change (Smith & Dukes, 2013).

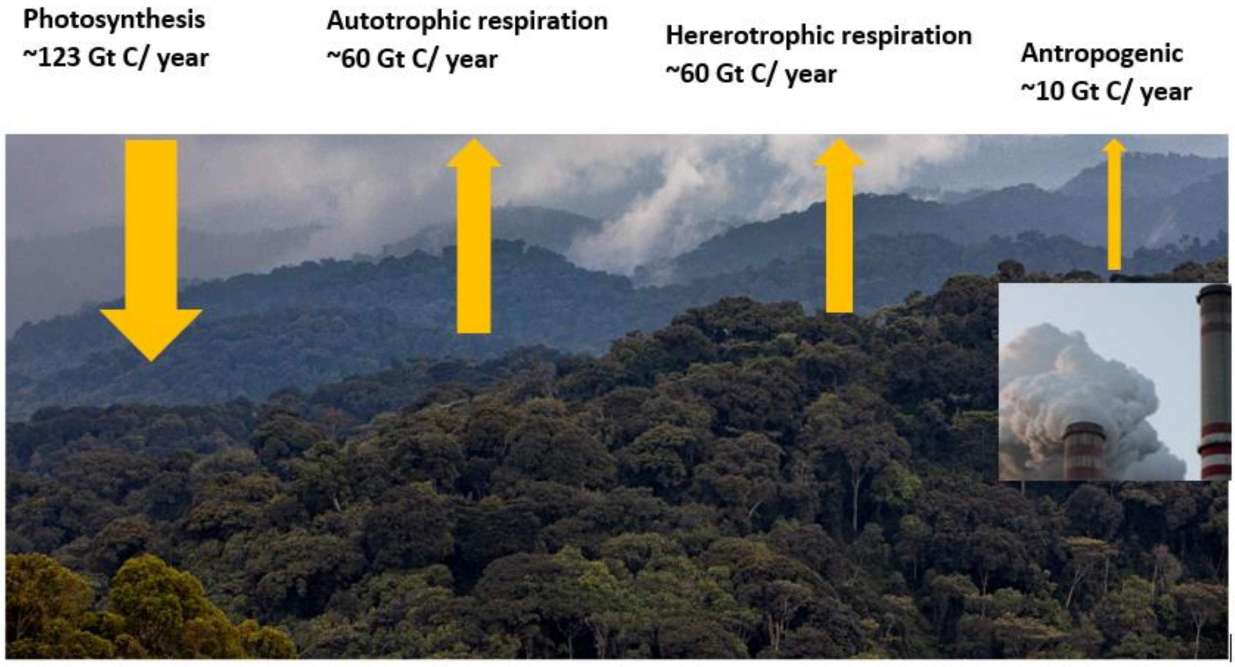


Figure 1: *Simplified illustration of global vegetation carbon fluxes in comparison to heterotrophic and anthropogenic emissions (Nyungwe photo by Johan Wingborg, University of Gothenburg).*

Although tropical forests cover only 15% of the planet's land surface (Pan *et al.*, 2013), they account for more than one-third of terrestrial biosphere net primary production (Beer *et al.*, 2010; Malhi *et al.*, 2010). They also represent a major C sink. Globally, intact tropical forests accumulate more C than their boreal and temperate counterparts. It was estimated to be 1.2 Gt C yr^{-1} for tropical forests and 0.5 and 0.7 Gt C yr^{-1} for boreal and temperate forests, respectively, for the 1990-2007 period (Pan *et al.*, 2011). This highlights the great role of tropical forests as a major C sink, counteracting the ongoing rise in atmospheric CO_2 and global warming (Bonan, 2008). However, given the on-going global mean temperature rise, the terrestrial carbon sink could switch to a carbon source during the 21st century (Hubau *et al.*, 2020; Sullivan *et al.*, 2020), leading to a positive C cycle–climate feedback which in turn would accelerates global surface warming (Beer *et al.*, 2010; Anderegg *et al.*, 2015).

Photosynthetic performance forms the basis of ecosystem production. Warming is expected to benefit tree photosynthesis and growth in cool areas, but not in warm areas. There is experimental evidence that moderate warming stimulates photosynthesis and tree growth in temperate and boreal tree species but often has negative effects in tropical species (Way & Oren, 2010; Liang *et al.,* 2013; Reich *et al.,* 2018). This is likely because tropical species are currently operating closer to their thermal optimum of net photosynthesis (A_n) compared to temperate and boreal species (Huang *et al.,* 2019). However, there is considerably less data on how tropical species respond to warming compared to temperate and boreal species, hindering our ability to predict how tropical forests will respond to a future, warmer climate (Reed *et al.,* 2012). There is thus a need for more studies on temperature sensitivity of tropical trees.

Climate change and variability has been the potential driver of recent changes in tropical forests. Declining biomass accumulation of mature tropical trees has been reported for the Amazon rainforest during recent decades, causing a long term decline in C sink strength of these forests in a changing climate (Brienen *et al.*, 2015). In addition, community composition shifts have been observed, indicating that some tropical tree species are not able to successfully compete under warming (Feeley *et al.*, 2013). Strong warming sensitivity of tropical trees has been demonstrated by recent studies along tropical elevation gradients, reporting significant shifts towards lower relative abundances of higher-elevation (i.e. cooler-adapted) tree species during the last three decades (Fadrique *et al.*, 2018). African tropical forests contribute significantly to global forest C storage and sequestration (Sullivan *et al.*, 2020). They currently take up approximately 0.7 x 10^{-9} Gt of C per hectare per year, but this C sink strength is predicted to decrease by 14 % due to climate change by 2030 (Hubau *et al.*, 2020). The decline in C gain and sink strength may occur if respiration (autotrophic and/or heterotrophic) increases or if A_n decreases, or if both scenarios occur simultaneously in hotter and drier conditions. It is therefore important to improve our understanding of the effects of temperature rise on the functioning of tropical trees, for better prediction of both their future C sink strength and changes in tree competitiveness and community composition in a warmer world.

2. Literature Review & Aims

2.1. Photosynthesis responses to rising temperature and seasonal drought

Thermal acclimation of photosynthesis

The thermal niche of a species is determined by both adaptation and acclimation of physiological, morphological, and biochemical traits (Berry & Bjorkman, 1980). It is well known that photosynthesis is highly temperature dependent (Kattge & Knorr, 2007; Lin *et al.*, 2012), like all enzyme mediated metabolic processes (Arcus *et al.*, 2016). In the short term, A_n increases with increasing leaf temperature until it reaches a maximum value at an optimum temperature (T_{opt}), above which rates then decline (Sage & Kubien, 2007; Slot & Winter, 2017b) (Figure 2). The decline in photosynthesis occurring beyond the T_{opt} is attributed to negative effects on photosynthetic biochemistry, increasing respiration, and stomatal closure as result of increased leaf-to-air vapor pressure deficit (VPD) accompanying rise in temperature (Sage & Kubien, 2007; Lin *et al.*, 2012; Slot & Winter, 2017b). However, the extent to which these processes acclimate to warming and thus contribute to increase T_{opt} towards warmer temperature is poorly known in tropical species.

In tropical forest trees, the T_{opt} of photosynthesis has been shown to be close to the ambient air temperatures (Slot & Winter, 2017b; Tan *et al.,* 2017; Huang *et al.,* 2019). Tropical trees have experienced relatively stable temperature for both seasonal and long-term scale (Trewin, 2014) and are therefore hypothesized to have less ability to acclimate to warming (Janzen, 1967). Consequently, on-going global warming threatens to decrease A_n and the C sink capacity of tropical forests (Slot & Winter, 2017b). However, plants may thermally acclimate, resulting in improved performance at the new, warmer conditions, relative to the performance of non-acclimated plants (Berry & Bjorkman, 1980).

The adjustments of photosynthesis to warming are driven by acclimation of biochemical, stomatal (Crous *et al.,* 2018; Dusenge *et al.,* 2020) and respiratory processes (Sage & Kubien, 2007; Lin *et al.,* 2012). Photosynthesis may acclimate biochemically to elevated temperatures by increasing the T_{opt} of the maximum rates of photosynthetic carboxylation (V_{cmax}) and electron transport (J_{max}) (Smith & Dukes, 2017; Kumarathunge *et al.,* 2019). Optimum photosynthesis can increase also if leaf dark respiration (R_d) is downregulated or if stomatal limitation of A_n decreases under warmer growth conditions.

Studies on photosynthetic responses to warming in tropical tree species have reported different results. Net photosynthesis measured at 25 °C was not affected by warming in a couple of studies (Crous *et al.,* 2018; Fauset *et al*., 2019). Rates of A_n measured at growth temperature were shown to be constant across growth treatment (Scafaro *et al.,* 2017; Fauset *et al.,* 2019), to increase with warming (Li *et al.,* 2020) but to decline with warming (Cheesman & Winter, 2013; Drake *et al.,* 2015; Slot & Winter, 2018). In addition, some studies reported a significant increase in T_{opt} of A_n in plants grown at warmer temperatures (Read, 1990; Cunningham & Read, 2003; Slot *et al.,* 2017a), while this was not observed in others (Crous *et al.*, 2018; Carter *et al.*, 2020). Altogether, these results indicate that there is a large, and poorly understood, varibility in how photosynthesis responds to warming among tropical tree species.

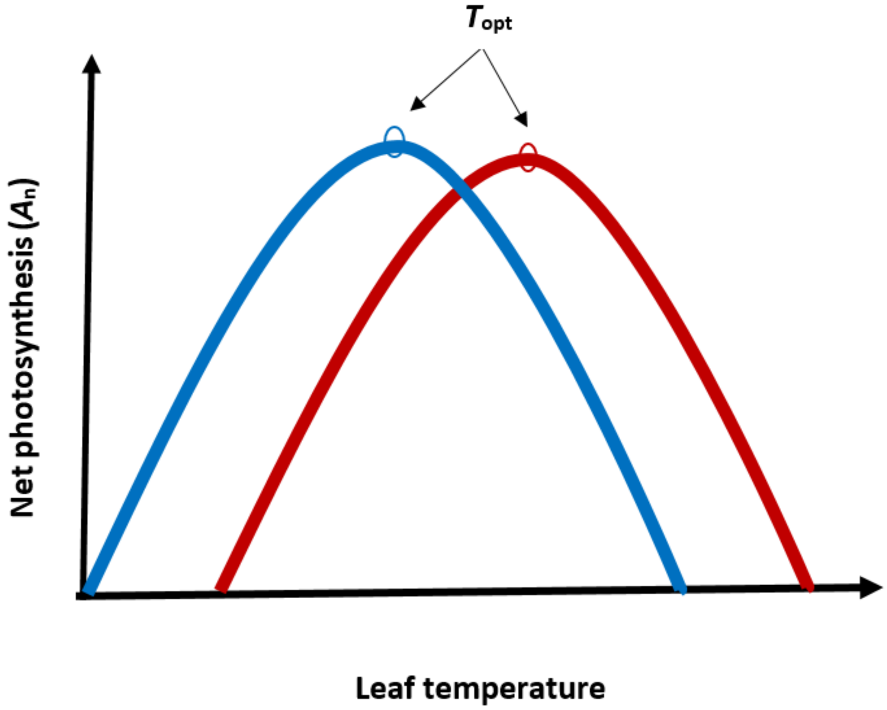


Figure 2*. Illustration of temperature response of net photosynthesis, A_n. In the short term, photosynthesis rate increases with temperature to an optimum (T_{opt}) and afterwards decreases at higher temperatures. Blue color represent plant grown at cool temperature and red color represent plant grown at warm temperature, with blue and red circles representing optimum temperatures for cool- and warm-grown plants, respectively. (Modified from Yamori et al., 2014 Photosynthesis Research).*

The biochemical mechanisms controlling A_n are well described and represented in the C_3 photosynthesis model of Farquhar *et al.* (1980). It stipulates that photosynthesis is either limited by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation or by the regeneration of the Rubisco substrate, ribulose-1,5-bisphosphate, which in turn are governed by V_{cmax} and J_{max}, respectively. Previous studies have indicated that light-saturated A_n is usually V_{cmax} limited, particularly in trees (Hikosaka *et al.*, 2006; De Kauwe *et al.,* 2016). Rates of V_{cmax} respond to short-term increases in temperature by increasing exponentially up to a thermal optimum and thereafter decrease (Medlyn *et al.*, 2002; Kattge & Knorr, 2007). The responses of V_{cmax} measured at a common temperature, usually 25 °C (V_{cmax25}), to elevated growth temperature vary among studies. Most global meta-analyses indicate lack of patterns in how V_{cmax25} responds to increased growth temperature (Kattge *et al.,* 2009; Way & Oren, 2010; Kumarathunge *et al.,* 2019). However, based on optimality theory of photosynthetic capacity, V_{cmax25} should be lower in plants grown at elevated temperature (Wang *et al.*, 2020). Individual studies including tropical species reported no significant change in V_{cmax25} with warming in controlled chamber experiments with trees (Scafaro *et al.,* 2017; Crous *et al.,* 2018; Fauset *et al*., 2019) and in an understorey field experiment (Carter *et al.,* 2020). Whether V_{cmax25} increases, decreases or is constant with warming in tropical tree species grown in more sun-exposed field settings remains highly uncertain.

Stomatal conductance (g_s) responds to increasing air temperatures both in short and long terms (Way *et al.,* 2015). In the short term, high temperatures and the associated increase in VPD usually decrease g_s and impose stronger limitation of A_n (Doughty and Goulden, 2008; Tan *et al.,* 2017). However, there is no clear pattern regarding the long-term g_s responses to warming. In warming experiments with tropical species, g_s measured at growth conditions was decreased with warming in some studies (Drake *et al.,* 2015; Wu *et al.,* 2018; Fauset *et al.,* 2019; Carter *et al.,* 2020), but not in others (Kruse *et al.,* 2017; Crous *et al.,* 2018; Li *et al.,* 2020). How g_s will respond to warming under ecologically realistic conditions is very uncertain.

Leaf R_d acclimates to elevated temperatures such that respiration at a given temperature is decreased in plants grown in warmer climate, thus decreasing leaf carbon losses (Atkin & Tjoelker, 2003; Slot & Kitayima, 2015). This topic is treated in section 2.2 below.

Acclimation of A_n may have major consequences for tree functioning and the global carbon cycle in a warmer climate. As evident from the text above, it is not clear which processes drive the responses of A_n to elevated temperature in tropical tree species growing in the field. Without a better understanding of the environmental responses of A_n, predicting future tropical carbon fluxes will remain uncertain (Smith & Dukes, 2013; Mercado *et al.*, 2018).

The effect of drought on net photosynthesis

Most tropical forests are reported to experience seasonal dry periods (Corlett, 2016), with photosynthetic metabolism exhibiting associated seasonality (Guan *et al.,* 2015; Restrepo-Coupe *et al.,* 2013). During drier periods, lower soil water availability strongly limits CO_2 and water vapour fluxes between tropical ecosystems and the atmosphere (Santhos *et al.,* 2018). It has been shown that drought and heat stresses interact such that drought increases the heat effect and vice-versa (Zhao *et al.,* 2013). Drought exacerbates heat stress through the limited capacity for transpirational leaf cooling under lower soil moisture availability. Also, heat stress increases drought stress by speeding up evapotranspiration and soil water depletion under increased atmospheric VPD. Drought has been shown to reduce leaf-level A_n in several tropical studies (Santhos *et al.,* 2018; Miranda *et al.,* 2005; Doutghy *et al.,* 2015; Stahl *et al.,* 2013). With intensified dry seasons projected over large tropical areas, it is important to understand the interacting effects of heat and drought on tree physiology and canopy fluxes of CO_2 and water vapour in forests with different temperature and rainfall regimes.

2.2. Leaf respiration responses to rising temperature and seasonal drought

The effect of temperature on leaf dark respiration

In tropical forests, leaf R_d constitute a high proportion of the total plant respiration (Metcalfe *et al.*, 2010; Huntingford *et al.*, 2013). Leaf R_d is important for the plant as it produces ATP, reducing equivalents and carbon skeletons needed for plant growth and cellular maintenance (O'Leary *et al.*, 2019). Leaf R_d responds to temperature and in the short-term (minutes to hour) it increases exponentially with increasing temperature up to about 50 °C or more (Atkin & Tjoelker, 2003; O'Sullivan *et al.*, 2013). However, R_d usually acclimates when plants are grown at warmer temperatures. Respiratory thermal acclimation is defined as the adjustment of respiration rates to changes in temperature over time (Atkin & Tjoelker, 2003). Acclimation of R_d to elevated temperature is usually characterized by lower R_d rates in warm-grown plants compared to cool-grown counterparts when rates are measured at a common leaf temperature (Atkin & Tjoelker, 2003) (Figure 3). Acclimation can be considered complete (homeostasis) when warm- and cool-grown plants exhibit similar R_d at their respective growth temperatures (Atkin *et al.,* 2005) (Figure 3). However, thermal acclimation of R_d is usually partial rather than complete, such that R_d measured at respective growth temperature is still higher in warm-grown trees compared to cool-grown counterparts (Slot & Kitajima, 2015). Complete homeostasis (Cheesman & Winter, 2013; Slot & Kitajima, 2015) as well as complete lack of thermal acclimation of R_d (Crous *et al.*, 2017; Kurepin *et al.*, 2018) may occur but seem quite rare.

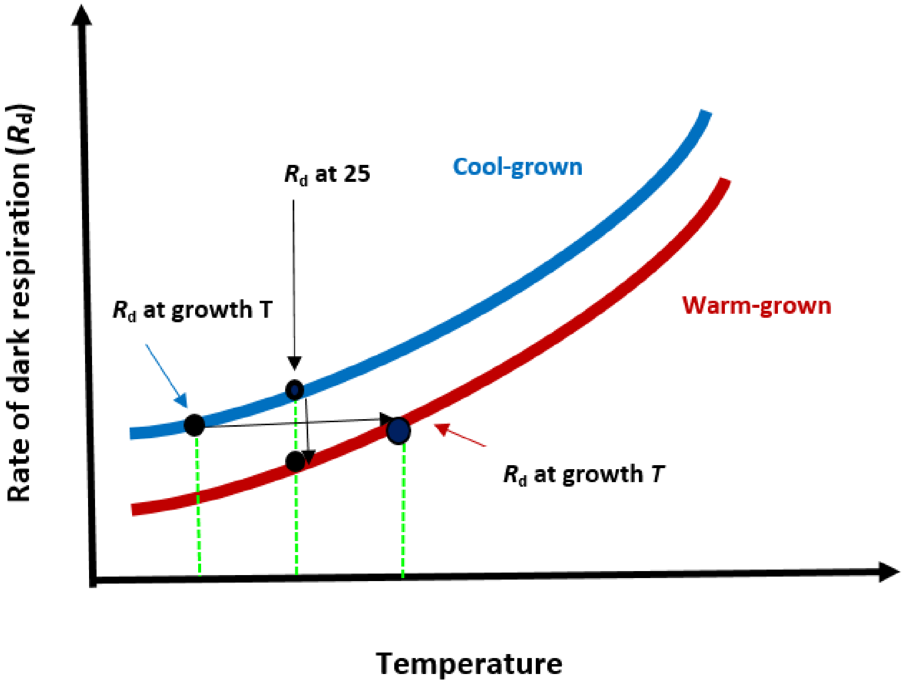


Figure 3. *Schematic illustration of thermal acclimation of leaf dark respiration, R_d. Blue curve indicates temperature response of R_d in cool- grown plant and red curve shows temperature response of R_d in warm-grown plants. Black vertical arrow points out the downward shift in leaf R_d in warm-grown plant compared to their cool-grown counterparts when measured at a common temperature (here at 25 °C). Black horizontal arrow shows equal rates of R_d in cool- and warm-grown plants measured at their respective growth temperature (full acclimation).*

Thermal acclimation of R_d has been studied in some tropical tree species, either grown in controlled-environment chambers (Cheesman & Winter, 2013; Scafaro *et al.*, 2017; Slot & Winter, 2018) or with warming applied to individual branches for short periods (Slot *et al.*, 2014). In most of these studies, partial acclimation occurred, but the magnitude to which thermal acclimation of R_d reduces respiratory CO_2 release in warm-grown tropical tree species under realistic field settings is still highly uncertain. Is it partial, lacking or perhaps complete (i.e. leading to homoeostasis)?

The effect of drought on leaf R_d

Drought commonly reduces photosynthesis through decreased g_s and photosynthetic capacity (Slot *et al.,* 2008; Ayub *et al.,* 2011). In many cases, drought also decreases R_d, most likely because of declined substrate availability for respiration (Galmés *et al.,* 2007; Atkin & Macherel, 2009). When photosynthesis is decreased during drought, the energy cost of sucrose production for phloem loading also declines (Lawlor & Fock, 1977). Thus, declines in leaf R_d in response to drought may be linked to declines in both sugar substrates availability and the energy required for their transport (Atkin & Macherel, 2009). However, in some studies, R_d was instead increased under dry conditions (Miranda *et al.,* 2005; Slot *et al.,* 2008; Metcalfe *et al.,* 2010). This response may serve to provide energy for cellular maintenance (Atkin & Macherel, 2009), particularly for hydraulic repair needed in drought conditions (Brodersen & McElrone, 2013). In other studies, leaf R_d was unaltered in response to drought (Atkin & Macherel, 2009; Gimeno *et al.,* 2010). To my knowledge, no study to date has investigated the impacts of drought on R_d in African tropical tree species.

2.3. Carbon metabolism and plant successional groups

Tropical forests are highly diverse (Prance, 1977, 2000; Govaerts, 2001). Given high plant diversity in these biomes, and the spatial variation in light availability caused by canopy gap dynamics (Wright *et al.*, 2010), plant species exhibit different life history strategies from light-demanding early-successional (ES) to shade-tolerant late-successional (LS) species along a so-called ‘fast-slow’ growth continuum (Wright *et al.,* 2003). The two groups differ in such way that

ES species have traits associated with rapid resource acquisition and growth, while LS have more conservative resource use and grow more slowly (Wright *et al.,* 2010). Being fast-growing, ES species typically have higher photosynthesis than slower-growing LS species, as observed in tropical studies (Dusenge *et al.,* 2015; Ziegler *et al.,* 2020). Moreover, ES species also seem to have generally higher acclimation capacity and, thus, lower sensitivity to warming compared to LS species (Cheesman & Winter, 2013; Slot & Winter, 2018; Carter *et al.,* 2020). The potentially lower ability of LS species to acclimate to elevated temperatures may be exacerbated by high leaf temperature. In studies with seedlings of tropical tree species in Rwanda, LS species with low transpiration and large leaf size exhibited considerably higher leaf temperatures compared to ES species (Vårhammar *et al.*, 2015; Ntawuhiganayo *et al*., 2020). Therefore, observations of similar thermal optima of photosynthesis across tropical tree species regardless their position on the slow-fast continuum (Vårhammar *et al*., 2015, Slot & Winter, 2017b) may in reality mean stronger heat stress in LS species with warmer leaves under field conditions. We need solid knowledge on whether different successional strategy groups differ in their ability to physiologically acclimate to warming to predict possible changes in tree community composition in a changing climate, which in turn is important for both carbon storage and biodiversity (Johnson *et al.*, 2016; Zhang *et al.*, 2016).

2.4. Key knowledge gaps

Photosynthesis and autotrophic respiration are two major physiological processes regulating the exchange of carbon between terrestrial biosphere and atmosphere (Figure 1). A recent study on temperature sensitivity of tropical forests across a pantropical network of permanent plots showed declines in carbon gain driven by high daytime rather than by high nighttime temperatures (Sullivan *et al.*, 2020). This was suggested to be due to decreases in photosynthesis while respiration may readily acclimate to warming. However, our knowledge regarding the acclimation potential of photosynthesis and respiration to warming and drought in tropical trees is currently very limited (Smith & Dukes, 2013; Huntingford *et al.*, 2013; Mercado *et al.*, 2018). Although photosynthesis and leaf dark respiration (R_d) are important components of the global carbon budget, data are scarce for tropical trees (Booth *et al.*, 2012; Atkin *et al.*, 2015; Scafaro *et al.*, 2017). No study yet has investigated their acclimation to warming and drought in

African tropical forests under ecologically realistic conditions. There is a large interest in the role of acclimation of physiological processes to environmental change in the ecosystem modelling community (Arneth *et al.*, 2010; Booth *et al.*, 2012; Slot & Kitajima, 2015; Mercado *et al.*, 2018). Better understanding of tropical tree responses of photosynthesis and leaf R_d to climate change is crucial for improved projections of carbon fluxes in a warmer climate by Earth System and Terrestrial Biosphere models. Moreover, it is important to increase the knowledge of how different plant groups may respond differently to warming for better understanding of how climate change affects tree community composition (Feeley *et al.*, 2013).

2.5. Aims and Hypotheses

The overall aim of this thesis is to improve the limited understanding of the climate change sensitivity of leaf carbon fluxes of tropical tree species, by providing mechanistic understanding of the physiological responses. This thesis examines whether photosynthesis and its underlying mechanisms (biochemical photosynthetic and respiratory processes, stomatal regulation) can acclimate to elevated growth temperature and seasonal drought. I used an elevation gradient approach with different designs in different studies: existing mature trees (Paper I); multispecies plantations named Rwanda TRopical Elevation Experiment (Rwanda-TREE), using either plants freely rooted in the soil (Paper II and III) or plants growing in pots with similar soil (Paper IV).

The specific papers of this thesis have the following aims and hypotheses:

Paper I:

The overall aim of this study was to investigate the climate change sensitivity of plant traits in mature tropical trees along an elevation gradient in Rwanda. The study explored the elevation patterns of tree physiological, structural and chemical traits and addressed the following hypotheses: (i) Leaf transpiration (E) decreases while A_n is relatively stable and water use efficiency increases with elevation. (ii) Leaf temperatures greatly exceed air temperatures in LS species, but less so in ES species with higher E. (iii) Nitrogen (N) limitation does not increase with elevation, as otherwise most commonly reported for tropical montane forests.

Paper II:

This study aimed to investigate to what extent ES and LS species acclimate their photosynthesis (photosynthetic capacity and A_n) and g_s to increased growth temperature and seasonal drought in the multispecies plantations elevation gradient experiment Rwanda-TREE. The study tested the following hypotheses: (i) Light saturated A_n at ambient growth temperature (A_{growth}) during non-drought conditions decreases with warming due to declines in g_s rather than biochemical photosynthetic capacity. (ii) Declines in photosynthesis with warming are more pronounced in LS than in ES species. (iii) The slope parameter of the stomatal conductance-photosynthesis model, g_1, increases with warmer growth environment and is smaller in LS compared to ES species. (iv) Declines in A_{growth} during late dry season are stronger at warmer sites with more pronounced drought.

Paper III

The overall aim of this study was to improve the understanding of the effects of elevated growth temperatures and seasonal drought on leaf R_d in tropical tree species grown in Rwanda-TREE. The hypotheses were: (i) Leaf R_d acclimates to growth temperature (i.e., to be reduced in warm-grown trees at a common measurement temperature). (ii) The thermal acclimation of R_d is partial, i.e. not strong enough to prevent increased R_d at prevailing nighttime temperatures under warmer growth conditions. (iii) Given strong control of sugar substrate availability on respiration, leaf R_d is lower during late dry season compared to early dry season, particularly at warmer sites with more severe drought. (iv) ES species exhibits stronger thermal acclimation of leaf R_d than LS species. (v) A_n and leaf nitrogen (N) are stronger predictors of interspecific variation and thermal acclimation of leaf R_d than leaf phosphorus (P) or leaf mass per area (LMA).

Paper IV

This study aimed to assess the thermal acclimation of A_n and its component processes in two tropical montane tree species grown in 11 liters pots at the three different sites of Rwanda-TREE. The study further evaluated to what extent these processes were linked to changes in leaf nutrient status and tree growth responses at different sites. The following hypotheses were tested: (i) The T_{opt} of A_{n}, V_{cmax} and J_{max} increase in a warmer climate, but the acclimation is only partial (i.e., approximately 0.5 °C per 1 °C of warming). (ii) Based on both least-cost and photosynthetic optimality theories, g_{s} and photosynthetic capacity (i.e., V_{cmax} and J_{max}) at a common temperature decrease with warming. (iii) Leaf R_{d} measured at a common leaf temperature shows strong downward acclimation to warming. (iv) Thermal acclimation of photosynthetic capacity and leaf R_{d} are tightly correlated and linked to leaf N.

3. Material and Methods

My research used an elevation gradient approach with different designs in different studies: existing mature trees of four species growing at five locations at different elevation (Paper I); multispecies plantations established at three sites at different elevation and vegetation zones in an elevation experiment (Rwanda-TREE), using either plants freely rooted in the soil (Paper II and III) or plants growing in pots with the same soil at all sites (Paper IV). For the Rwanda-TREE project, 20 species comprising both ES and LS species originating from Afromontane rainforest as well as transitional rainforest vegetation zones of Rwanda were planted at three sites along an elevation gradient (Figure 5). A step down slope in the elevation gradient represents a possible future warming scenario. Experiments and methodologies are described in details in each of the original studies forming this thesis. Here, a brief description is provided for sites, plant material, measurements and data analyses of the mature tree (Paper I), multispecies plantations (Paper II and III), and potted study (Paper IV).

3.1. Description of regional climate in Rwanda

Rwanda experiences moderate tropical climate owing to its high altitude, ranging from 900 m to 4,500 m above sea level. Overall, temperature decreases and precipitation increases with increasing elevation, but there is also an east-west gradient such that precipitation at a given elevation is lower further to the east (Figure 4). The mean annual temperature is related to altitude. Mean annual temperature exceeds 21 °C in east and southeast, while this falls below 15 °C at the highest altitudes (Ravelingen, 2001; Figure 4). Rwanda is characterized by large spatial and temporal variability in rainfall. The annual rainfall exceeds 1,600 mm in the montane regions while the eastern savanna and the central part are significantly drier, receiving less than 900 mm rainfall annually (Figure 4; Ravelingen, 2001). The main dry season is from June to August/September and the period with the heaviest rainfall is from March to May. It should be noted, however, that the duration and severity of the dry season is greater at lower elevation.

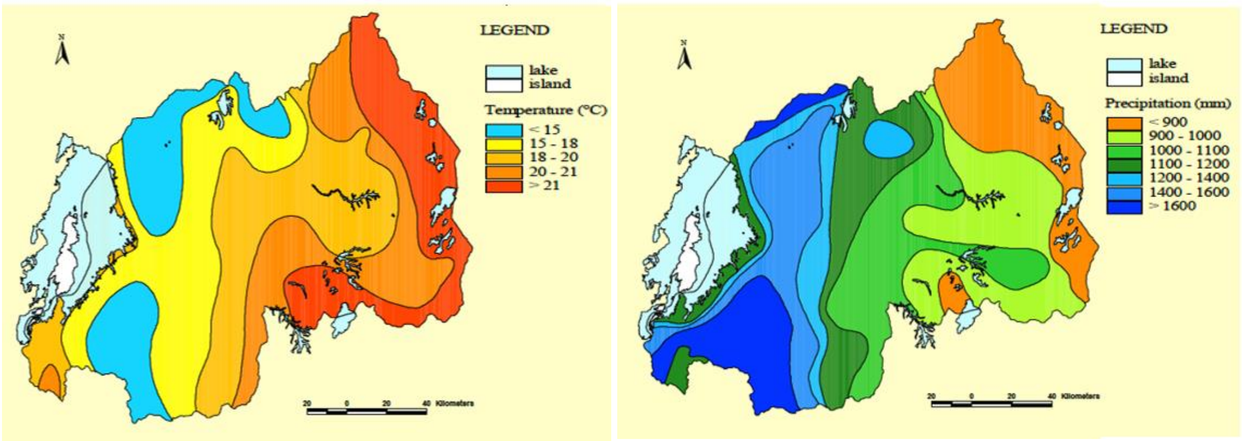


Figure 4. *Mean annual temperature (map to the left) and mean annual precipitation (map to the right) in Rwanda (source: Verdoot A. & Van Ranst E. (2003) with permission from Prof. Van Ranst).*

Both annual mean temperature records from Rwanda Meteorological Service and climate projections taken from the General Circulation Models (GCMs) used in the Coupled Model Intercomparison Project 3 (CMIP3) show an increase in temperature over time for different regions of Rwanda (GoR, 2011). Historically, there has been a trend towards increasing rainfall, but with the increase in potential evapotranspiration exceeding the increase in precipitation during the dry period (June to September) for the period of 1964-2010 (Haggag *et al.,* 2016). From the intermediate A1B scenario of CMIP3, temperature is projected to increase by 2.5 °C by 2050 and by 4 °C by 2080 for Rwanda (GoR, 2011). Moreover, the water deficit period in which potential evapotranspiration exceeds precipitation is projected to extend from the current 4 months to 10 months in some parts in the country (Haggag *et al.,* 2016).

3.2. Physiological responses to warming in mature tropical trees (Paper I)

Sites description and plant material

This study was carried out on mature trees, at five sites along an elevational gradient ranging from ~1700 m to ~2700 m in South and South-West Rwanda. The lowest and warmest site (Arboretum of Ruhande) is a forest plantation with mixed native and exotic tree species located at transitional tropical rainforest zone in southern Rwanda (2°36´55.2´´S, 29°44’E, 1638-1737 m elevation) (Nsabimana, 2009). The other four sites were located in Nyungwe National Park.

Nyungwe is a tropical montane rainforest (2°17´-2°50´S, 29°07´-29°26´E) with altitude ranging from 1600 to 2950 m (Gross-Camp *et al.,* 2012). Nyungwe covers 1013 km^2 and forms, together with the contiguous Kibira National Park in Burundi, the largest block of mid-elevation tropical montane forest remaining in Africa (Plumptre *et al.* 2002). Nyungwe forest is one of the top priority sites for conservation in the Albertine Rift due to the numbers of endemic and globally threatened species (Plumptre *et al.,* 2007). For further details on site descriptions, see Paper I. Data were collected from two ES and two LS species, which are abundant in Nyungwe and could mostly be found along the entire elevation gradient*: Syzygium guineense* (LS), *Carapa grandiflora* (LS), *Macaranga kilimandscharica* (ES), and *Polyscias fulva* (ES). The first three species together account for 42 % of the large trees (with diameters at breast height, DBH > 30 cm) in the forest (Plumptre *et al.* 2002).

Gas exchange measurements

Leaf gas exchange measurements were taken between 10:00-16:00 h during three measurement campaigns: two wet season campaigns in February-March 2017 and January-March in 2018 and one dry season campaign during September in 2017. This allowed for quantification of altitudinal patterns and the effect of natural seasonal drought on tree traits. Six trees per species and site were measured in each campaign, aiming at selecting trees with DBH of 15-40 cm. A 20 m long carbon fiber telescopic pole was used to access branches in the upper canopy and the measurements were done as soon as possible after the branch was cut (usually within 15 min) to minimize possible post-cut decreases in g_s. Leaf gas exchange instruments measured the leaf fluxes of CO_2 and water vapor to determine tree physiological traits such as A_n, g_s and E. Gas exchange measurements were done with a SC-1 porometer (Decagon devices Inc. Pullman, Washington USA) in campaign 1 and with a LI6400 (Li-COR, Inc. Lincoln, Nebraska USA) in campaigns 2 and 3. The porometer was evaluated against the LI6400 for inter-calibration and subsequent data adjustment.

Leaf temperature

Leaf temperature (T_{leaf}) measurements were taken for the same leaves measured for gas exchange using an infrared thermometer (Trotec BP10 IR, Trotec Laser GmbH, Ismaning, Germany). Thereafter, the leaf-to-air temperature difference ($T_{\mathrm{leaf}} - T_{\mathrm{air}}$) was standardized to a wind speed of 1 m s^{-1} (ΔT_{std}) to account for the influence of varying wind speed on T_{leaf} as follows:

The leaf boundary layer conductance for heat (g_{heat}) was calculated as

$$g_{heat} = 0.135 * \left(\frac{u}{d}\right)^{0.5} \qquad \text{(Equation 1)}$$

Values of g_{heat} were calculated both at measured wind speed (g_{heatobs}) and at a wind speed of 1 m s^{-1} (g_{heatstd}). The ΔT_{std} was then approximated from the ratio of these conductances and the observed T_{leaf}–T_{air} (ΔT_{obs}):

$$\Delta T_{std} = \Delta T_{obs} * \frac{g_{heatobs}}{g_{heatstd}} \qquad \text{(Equation 2)}$$

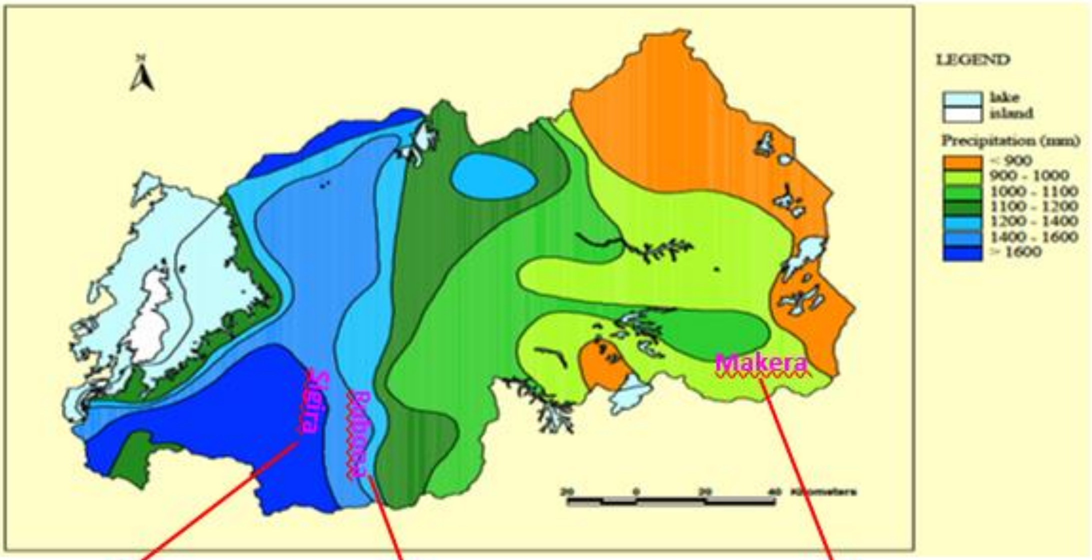
Photosynthetic photon flux density (PPFD) at leaf angle was measured using a photosynthetically active radiation sensor positioned adjacent to each leaf measured for T_{leaf}.

3.3. Photosynthesis and Respiration measurements in Rwanda-TREE plantations (Papers II and III)

Sites description and experimental design

Studies II and III were carried out on three half-hectare plantations established at three different sites along an elevation gradient in Rwanda, Central Africa in the Rwanda-TREE project (Figure 5). These sites are within ~ 250 km distance, and they exhibit large variations in elevation (1300 – 2400 m.a.s.l) and climate (Figure 5). The three sites differ in annual average daytime temperature, with values for the high-elevation (Sigira), intermediate-elevation (Rubona) and low-elevation (Makera) sites being 17.5, 22.5 and 23.8 °C, respectively, during the February 2018 to January 2020 period. Differences in average weekly maximum air temperatures were larger: 23.1, 28.5 and 31.2 °C. The sites also differed substantially in annual precipitation, decreasing progressively from Sigira (c. 2100 mm) to Rubona (c. 1600 mm) and Makera (c. 1050 mm). However, the relative distribution of precipitation over the year is similar at all sites, with highest rainfall in March–May and a dry period in June–August. Furthermore, the soil type differs across the three sites. The soil texture is clay to clay loam at Sigira, sandy clay to sandy clay loam at Rubona and sandy clay loam to clay loam at Makera. The three sites occur in different vegetation Zones; Afromontane rainforest (Sigira), Lake Victoria transitional rain forest (Rubona), and evergreen and semi-evergreen bushland and thicket (Makera) (Kindt *et al.,* 2014). A step down in elevation represents a possible climate change scenario.

At each site, the plantation is 50 m wide and 102.5 m long, with 18 plots of 15 x 15 m each and spaced by 2.5 m. In each plot, plants are spaced by 1.5 m, allowing 100 plants belonging to 20 different tree species with a replication of five plants. Seeds or cuttings of each tree species were collected from either montane rainforest or transitional rainforest locations and propagated in poly-pots in a nursery at the mid-elevation site (Rubona). Plants were transplanted, after 6 to 12 months in the nursery and having a height of ~10-75 cm (depending on species), into the soil at the three sites during December 2017 to January 2018. The position of plants in each plot was completely randomized across species. Two levels of nutrient supply (unfertilized and fertilized + limed) and three levels of water supply (low, medium and high, to mimic the precipitation levels at the three sites), were randomly applied across plots, in a factorial design with three plots of each nutrient and water level combination (Figure 5). Fertilized plots were not used for my studies and all plants were irrigated equally during first 1.5-year period to avoid water deficiency stress and allow successful plant establishment. However, the plots studied here were left without irrigation during the main dry season in 2019, with plants therefore being subject to natural seasonal drought from June through August in that year.



Sigira/Nyamagabe
S 2° 30′ 54″; E 29° 23′ 44″
Montane rain forest
2400 m. a. s. l.
17.5/23.8 ° C, 2100 mm

Rubona/Huye
S 2° 28′ 30″; E 29° 46′ 49″
Transitional rain forest
1600 m. a. s. l.
22.5/28.6 ° C, 1600 mm

Ibanda **Makera**/Kirehe
S 2° 6′ 31"; E 30° 51'16"E
Evergreen and semi-evergreen bushland and thicket
1300 m. a. s. l.
23.8/31.4 ° C, 1050 mm

Treatments:

	HW	MW	LW
LN	Control	Shelter -500 mm	Shelter -900 mm
HN	Fertilizer	Shelter -500 mm -& Fertil.	Shelter -900 mm -& Fertil.

Treatments:

	HW	MW	LW
LN	Irrigation +500 mm	Control	Shelter -400 mm
HN	Irrigation +500 mm & Fertil.	Fertilizer	Shelter -400 mm -& Fertil.

Treatments:

	HW	MW	LW
LN	Irrigation +900 mm	Irrigation +400 mm	Control
HN	Irrigation +900 mm & Fertil.	Irrigation +400 mm & Fertil.	Fertilizer

LN = low nutrient (control)
HN = high nutrient (fertilised)
LW = low water supply
MW = medium water supply
HW = high water supply

Figure 5. *Rwanda-TREE experimental sites location and schematic overview of the experimental design at three sites. The information about each site includes the names of research station/district, potential vegetation type, elevation, annual average daytime temperature, annual average daily maximum temperature and annual precipitation. The treatments at each site include low and high nutrient (LN, HN) and low, mid and high water input (LW, MW, and HW). Depending on the annual precipitation, irrigation or rain shelters are applied to obtain comparable water inputs at each site. The fertilization aims at reducing nutrient-related productivity limitations.*

Plant material

Twenty tropical tree species were selected, representing a range of species with different habitats of origin and different successional strategies. Afromontane species which are common in Nyungwe forest (Plumptre *et al.* 2002) included five ES species and five LS species. In addition, species occurring in Lake Victoria transitional rainforests of Rwanda included six ES species and four LS species (Table 1). The present thesis used 18 species (Table 1), with approximately equal representation of ES and LS species and montane rainforest and transitional rainforest species.

Table 1. *Tree species and their taxonomic families and successional identity.*

Scientific names	**Author**	**Family**
Early-successional species		
Afromontane rainforest species		
Bridelia brideliifolia	(Pax.) Fedde	Phyllanthaceae
Harungana montana	Spirlet	Hypericaceae
Macaranga kilimandscharica	Pax	Euphorbiaceae
Maesa lanceolata	Forsk.	Primulaceae
Polyscias fulva	(Hiern) Harms	Araliaceae
Lake Victoria Transitional Forest species		
*Albizia gummifera**	(J.F.Gmel.) C.A. Sm	Mimosoideae
Bridelia micrantha	(Hochst.) Baill.	Phyllanthaceae
Croton megalocarpus	Hutch.	Euphorbiaceae
Dombeya torrida	(Hochst.) Planchon	Malvaceae
Harungana madagascariensis	Lam. ex Poiret	Hypericaceae
*Markhamia lutea***	(Benth.) K.Schum.	Bignoniaceae
Late-successional species		
Afromontane rainforest species		
Afrocarpus falcatus	R.Br. ex Mirb.	Podocarpaceae

Carapa grandiflora	Sprague	Meliaceae
Faurea saligna	Harv.	Proteaceae
Prunus africana	(Hook.f.) Kalkman	Rosaceae
Syzygium guineense	(Wild.) DC.	Myrtaceae
Lake Victoria Transitional Forest species		
Chrysophyllum gorungosanum	Engl.	Sapotaceae
Entandrophragma excelsum	(Dawe & Sprague) Sprague	Meliaceae
*Ficus thonninghii***	Blume	Moraceae
*Newtonia buchananii**	Gilbert & Boutique	Mimosoideae

**Not studied in this thesis due to slow establishment.*

***These are not distinct representatives of their successional groups and have been recorded as both early- and late-successional species in previous studies.*

Gas exchange measurements

Measurements of leaf gas exchange were made in unfertilized plots in three different campaigns. The first campaign was conducted in wet season in November of 2018. The aim of this campaign was to assess thermal acclimation of photosynthesis and leaf R_d. During this campaign, light saturated A_n (at PPFD = 1800 μmol photons m^{-2} s^{-1}) was measured at 25 °C for ten ES- and six LS species, and leaf R_d was measured at 20 °C for the same species. The second and third campaigns were conducted in early-dry (May-June 2019, non-drought conditions) and late-dry seasons (August 2019), respectively, and the main purpose of these two campaigns was to investigate A_n at growth temperature and the seasonal drought effects on photosynthesis and foliar respiration. However, R_d was measured in only two Afromontane rainforest tree species, *Carapa grandiflora* (a LS species) and *Polyscias fulva* (an ES species) typically representing each successional group, in these campaigns (Paper III).

a. Net photosynthesis measurements and analysis

Photosynthesis measurements were made prior to R_d measurements, between 9:00 and 16:30 h using two portable photosynthesis systems, both with a 2 x 3 cm leaf chamber (LI6400, Li-Cor Inc., Lincoln, NE, USA). The temperature in the leaf chamber was controlled by setting the block temperature to 25 °C during the November 2018 campaign and to the ambient air temperature during May-June and August 2019 campaigns. Other LI6400 settings were: air flow rate of 400 μmol s^{-1}, CO_2 concentration of air entering the leaf chamber at 415 μmol mol^{-1} and PPFD of 1800 μmol m^{-2} s^{-1}. The branch of each measured leaf during the early-dry (May-June 2019) season campaign was labelled for subsequent measurements on a neighboring leaf during the late-dry (August 2019) season campaign. The drought effect was determined by comparing A_n values between the two campaigns. For more details, see Paper II.

Given the large number of species covered in study II and that measuring light-saturated A_n at varying intercellular CO_2 concentrations (C_i), so called A-C_i curves are quite time consuming, V_{cmax} (μmol m^{-2} s^{-1}) was estimated from measured A_n and leaf R_d (multiplied by 0.7 to account for light-inhibition) using the so-called one point method (De Kauwe *et al.,* 2016). This was done using November 2018 data where A_n was measured at 25 °C. Values of V_{cmax} determined with this method have been shown to correlate strongly with V_{cmax} determined from full A-C_i curves measurements, showing that A_n is typically Rubisco limited (i.e. V_{cmax}) at the current ambient CO_2 partial pressure (C_a) and saturating light (De Kauwe *et al.,* 2016).

b. Leaf dark respiration measurements and analysis

Leaf R_d measurements were taken after sunset between 18:30 and 22:30 h on the same day as photosynthesis measurements at all sites, using the same leaf gas exchange instruments. For all measurements, the following settings were used: air flow rate of 250 μmol s^{-1}, CO_2 concentration of air entering the leaf chamber at 410 μmol mol^{-1}, chamber block temperature at 20 °C, and the light source turned off. Before measuring each tree, an empty chamber measurement was made to allow for subsequent corrections for any potential leaks in the leaf chamber. Leaf R_d at nighttime temperature was estimated from R_d at 20 °C and extrapolation using a fixed Q_{10} (i.e., the quotient of increase in R_d for a 10 °C rise in leaf temperature). A Q_{10} value of 2.3 was used, based on previous published studies on tropical tree species (Atkin & Tjoelker, 2003; Weerasinghe *et al.,* 2014; Slot & Winter, 2017a). Measurements were done on the same branch during early- (non-drought) and late dry campaigns as above mentioned. For more details, see Paper III.

3.4. Photosynthesis in potted trees (Paper IV)

The pot experiment used the same sites and plant material as in the Rwanda-TREE project but was conducted on potted plants in a companion study. In this study, eight species were grown in 11-litre pots using soil from the Sigira site at all three sites, to eliminate soil as a possible confounding factor. The soil was classified as a Ultisols with clay texture with pH (KCl) = 3.3 ± 0.13 (mean ± SD); bulk density = 0.99 ± 0.13 g cm^{-3}; Organic C = 3.8 ± 0.6%; NH_4^+ & NO_3^- = 3.9 ± 1.1 g m^{-3} and available P = 1.2 ± 0.4 g m^{-3}.

Plant material

This study used one ES species *Harungana montana* (Spirlet) and one LS species *Syzygium guineense* (Wild.) DC. The two species are common canopy tree species in Nyungwe forest (Nyirambangutse *et al.,* 2017; Ziegler *et al.,* 2020). Seeds were grown in the nursery at Rubona site and after seedlings had established roots (with a mean height of 43 to 48 cm, for *S. guineense* and *H. montana*, respectively), they were transferred to 11 liters pots and eight pots of each species were randomly assigned to each of the three experimental sites in February 2018. The pots were buried in the ground to avoid unnatural diurnal soil temperature variation. Seedlings were fertilized during nursery cultivation but not afterwards. Seedlings were watered as needed to maintain a moist growth medium throughout the experiment. Seedlings were grown there for one year until harvest in January 2019.

Gas exchange measurements

Leaf gas exchange measurements were conducted in April-May 2018, approximately three months after placing pots at the experimental sites. Leaves developed under the new growth conditions at each site were measured using two portable photosynthesis systems (Li-Cor 6400, Li-Cor Inc., Lincoln., NE, USA). The A-C_i curves were conducted at PPFD of 1800 μmol photons

m^{-2} s^{-1}, air flow rate of 400 μmol s^{-1} and at five leaf temperatures (19, 25, 30, 35 and 40 °C). A neighboring leaf was covered by aluminum foil for at least 30 minutes and measured for R_d at 25 °C. For more details, see Paper IV.

Parameterization of photosynthesis models

The C_3 photosynthesis model developed by Farquhar *et al*. (1980) was used to estimate V_{cmax} and J_{max} from the A-C_i curves, using the " fitacis" function and the "bilinear" fitting method from the "plantecophys" R package (Duursma, 2015) in R version 3.5.2 (R development Core Team, 2018). Default temperature dependencies of the CO_2 compensation point in the absence of mitochondrial respiration (Γ^*) and the Michaelis-Menten constants for CO_2 and O_2 (K_c and K_o) were taken from Bernacchi *et al.* (2001). Apparent values of V_{cmax} and J_{max}, parameterized based on C_i are reported. Further details can be found in Paper IV.

3.5. Chemical and morphological traits

For all four studies, leaves were collected immediately following the gas exchange measurements. Three to five discs of 18 mm or 10 mm diameter were collected for subsequent determinations of leaf mass per area (LMA) and leaf nutrient concentrations. Leaf material was oven-dried at 70 °C to constant mass. Dried leaf samples were ground into a fine powder using a ball mill (model MM 301, Retsch: Hann, Germany). Three to four milligrams of dried powder were weighed into tin capsules and then run through an Elemental analyzer coupled to an Isotope Ratio Mass Spectrometer (20-22, Sercon Ltd., Crewe, UK) or (EA 1108; Fison Instruments, Rodano, Italy) to determine leaf C and N concentrations (Papers I-IV). Leaf P concentration was analyzed through elements inductively coupled plasma mass spectrometry (VG101 analysis, ACME Analytical Laboratories: Vancover, BC, Canada) (all Papers).

3.6. Statistical analyses

In Paper I, differences among sites and species in physiological traits were tested using two-way ANOVA while differences in T_{leaf}-T_{air} among species were tested using analysis of covariance with SPSS software (IBM SPSS statistics for Windows, Version 16.0, IBM

Corporation: Armonk, NY, USA). In Paper II and III, the effects of the warming (i.e. site), successional group and their interaction on A_n, g_s, V_{cmax} and R_d were tested using mixed effects ANOVA with site and successional group as main factors and species nested within successional groups as random factor. The effect of drought on the same variables was analyzed by repeated measures ANOVA with early and late dry season sampling as repeated measures. Function '*nlme*' of the R package (Pinheiro *et al.,* 2019), *emmeans* (Lenth 2019) and *multcomp* (Hothorn *et al.,* 2008) packages were used. In Paper III, the relationships between dependent (e.g. R_d) and independent (e.g. A_n, leaf N and P and LMA) were analyzed by a mixed-effect linear regression with site as a main factor and species as a random factor. In Paper IV, site comparisons of temperature response curves of V_{cmax}, J_{max}, g_s and A_n were made by one-way repeated-measures ANOVA using lmerTest R package. Further study-specific details are provided in each Paper. Effects were considered statistically significant at $p < 0.05$. All analyses were performed in R version 3.6.1 (R Core Team, 2019).

4. Results

4.1. Plant traits in mature trees along an elevation gradient (Paper I)

4.1.1. Physiological traits

Elevational trends in physiological traits differed between wet and dry seasons. During the dry season both g_s and A_n markedly increased with increasing elevation, while there was no clear trend in the wet season (Figure 6a, b, e, f). Rates of E mostly decreased with elevation in the wet season, while there was a strong increasing trend in the dry season (Figure 6c, d). These results indicate that atmospheric evaporative demand (i.e. VPD) control E during wet periods while stomatal control over E dominates under drier conditions (i.e. at lower sites during the dry period). Values of g_s, E, and A_n were generally higher in ES compared to LS species. Species differences were significant for g_s in both wet and dry seasons, but only during dry season for E (Figure 6a-d). Species differences in A_n were similar to those for g_s and E; decreasing in the order *P. fulva* (Pf; ES), *M. kilimandscharica* (Mk; ES), *S. guineense* (Sg; LS), and *C. grandiflora* (Cg; LS) (Figure 6).

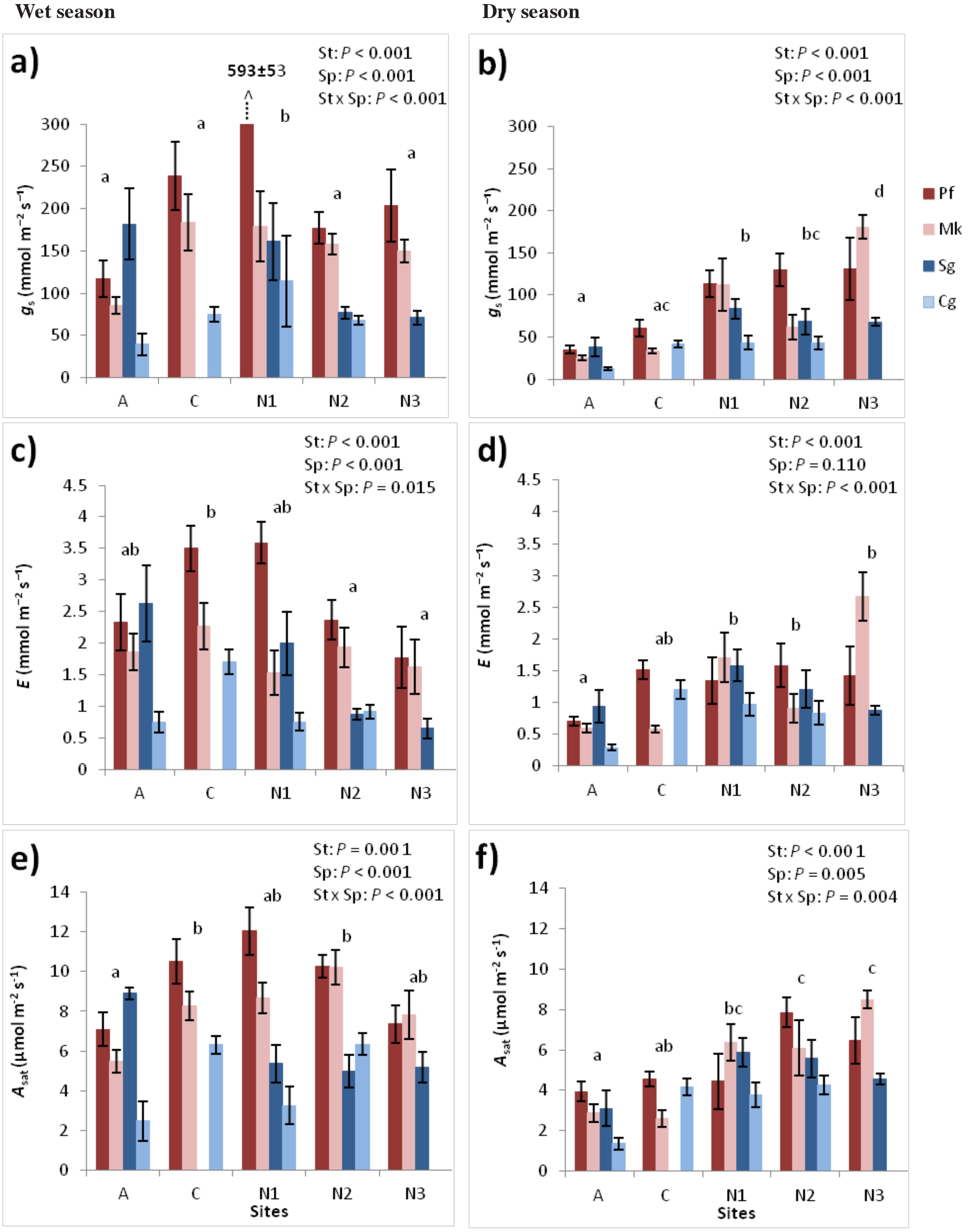


Figure 6. *Leaf stomatal conductance (g_s; a-b), transpiration (E; c-d) and light saturated net photosynthesis (A_n; e-f) of four species (Sp) at five sites (St) along an elevation gradient, measured during wet (a, c, e) and dry (b, d, f) seasons. Error bars show variation (SE) among trees within each species at each site (n = 6). P values for the effects of site (St), species (Sp) and their interaction (St x Sp) are shown in each graph. Significant overall differences among sites are indicated by different letters above the bars of each site. The order follows increasing elevation from left to right. Species abbreviations in the legend are based on first letters in genus and species. See Paper I for site abbreviations and descriptions. From* ***Paper I****.*

4.1.2. Leaf temperature

The leaf-to-air temperature difference (T_{leaf}–T_{air}) increased with radiation and was smallest in the ES species *Polyscias fulva* compared to other species, particularly at lower PPFD (Figure 7). For *P. fulva*, at radiation higher than 2000 μmol m^{-2} s^{-1}, T_{leaf} exceeded T_{air} by 3-5 °C while for the other three species; the average exceedance of T_{leaf} over T_{air} was 7-10 °C. *P. fulva* also had higher g_s and E than the other species, promoting leaf cooling (Figure 6). The slopes of the relationships between PPFD and T_{leaf}-T_{air} were significantly differed among species as shown by the ANCOVA test ($p = 0.001$).

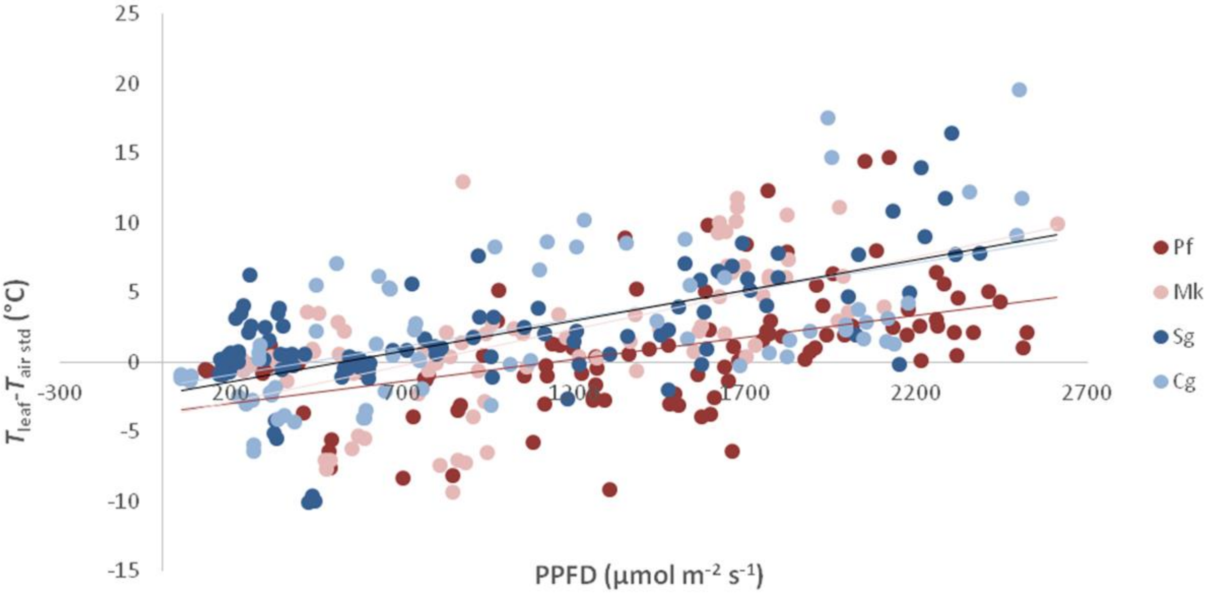


Figure 7. *Relationship between leaf to-air temperature difference (T_{leaf}-T_{air}) and photosynthetic photon flux density (PPFD) for four species in the wet season of 2017. Data are pooled across sites and each data point represents one leaf. The slopes of the relationships were markedly different among species according to the ANCOVA test ($p < 0.001$), being lowest in Polyscias fulva (Pf). Values of T_{leaf}-T_{air} were standardized to a wind speed of 1 m s^{-1}. Species are Polyscias fulva (Pf; ES), Makaranga kilimandscharica (Mk; ES), Syzygium guineense (Sg; LS) and Carapa grandiflora (Cg; LS). From* ***Paper I****.*

4.2. Thermal acclimation and seasonal drought effect on photosynthesis (Paper II)

There was a significant interspecific variation in photosynthesis at all sites and within both ES and LS groups (see Paper II). The shift in photosynthesis at warmer sites differed between successional groups (see below) but was not significantly related to species' elevation of origin. Therefore, species data were pooled together for each successional group.

4.2.1. Net photosynthesis under growth conditions

Light-saturated A_n at growth temperature (A_{growth}) and non-drought conditions significantly differed between sites ($p = 0.020$) and were higher in ES than in LS species ($p = 0.008$) (Figure 8). Also, there was a significant site by successional group interaction ($p = 0.008$), reflecting that A_{growth} declined at warmer sites in LS species but not in ES species. In LS species, A_{growth} was 12% and 30% lower at the mid- and lower-elevation sites (Rubona and Makera), respectively, compared to the high-elevation and coolest Sigira site (Figure 8). However, for ES species A_{growth} was similar at the warmest (Makera) and coolest (Sigira) sites. At all sites, rates of A_{growth} were higher in ES compared to LS species.

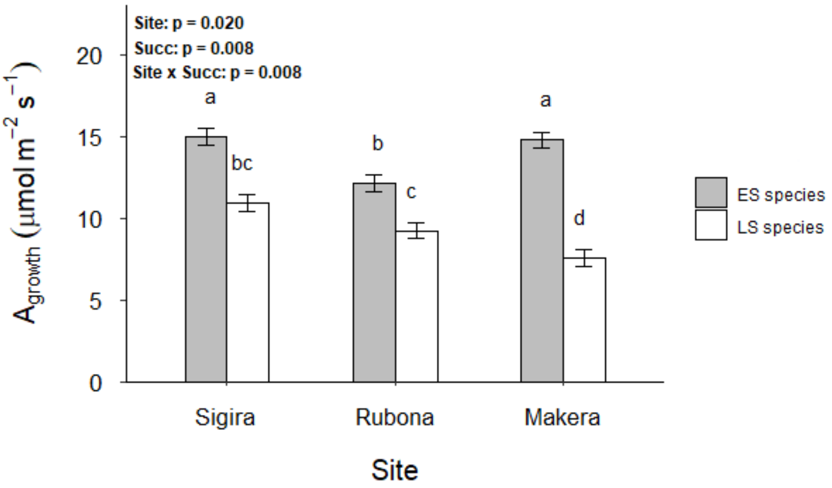


Figure 8. *Light saturated net photosynthesis measured at the ambient growth temperature (A_{growth}) and non-drought conditions (May-June 2019) for nine early-successional (ES) and seven late-successional (LS) species grown at Sigira (high-elevation), Rubona (mid-elevation) and Makera (lowest-elevation) sites in Rwanda-TREE. Means ± SE (n=7 or9 species). Different letters above bars represent significant differences ($p < 0.05$) according to Tukey's post hoc test. Statistical p values are shown for effects of sites, successional groups (Succ) and their interaction. From* ***Paper II****.*

4.2.2. Stomatal and photosynthetic capacity responses to temperature

To assess the underlying mechanisms of A_{growth} responses to elevated growth temperature under non-drought conditions, g_{s} was measured at growth temperature and V_{cmax25} was estimated from light-saturated A_{n} and leaf R_{d} measured at reference temperature. Stomatal conductance measured at ambient conditions was higher in ES compared to LS species at the high- and low-elevation sites but not at the intermediate site, Rubona, causing a near significant site by successional group interaction ($p = 0.061$). Photosynthetic capacity responses showed that overall, V_{cmax25} differed among sites ($p = 0.005$) and between successional groups ($p < 0.001$), but there was no significant site by successional group interaction ($p = 0.295$; Figure 9a). For both ES and LS species, values of V_{cmax25} were lowest at the warmest site (Makera). At all sites, ES exhibited higher V_{cmax25} than LS species (Figure 9a). Although no significant site by successional group interaction was found, the difference in V_{cmax25} between the warmest site and the coolest site (Sigira) was larger for LS species (31% lower at Makera) than for ES species (9% lower at Makera), as for A_{growth}.

When normalizing V_{cmax25} to leaf N (V_{cmax25N}) to assess whether the site or successional group effects on area-based V_{cmax25} were caused by decreased leaf N, results were mostly similar to those of area-based V_{cmax25}. There were significant main effects of both site ($p = 0.003$) and successional group ($p < 0.001$; Figure 9b). However, V_{cmax25N} values were highest at the mid-elevation site (Rubona) and not significantly different between the low- and high-elevation sites. This was due to lower levels of area-based leaf N at warmer sites, particularly at Rubona. Differences in leaf N thus explained a small part of the decline in area-based V_{cmax25} at the warmest site in LS species (31% lower at Makera compared to Sigira; Figure 9a), which was stronger than that for V_{cmax25N} (23%; Figure 9b).

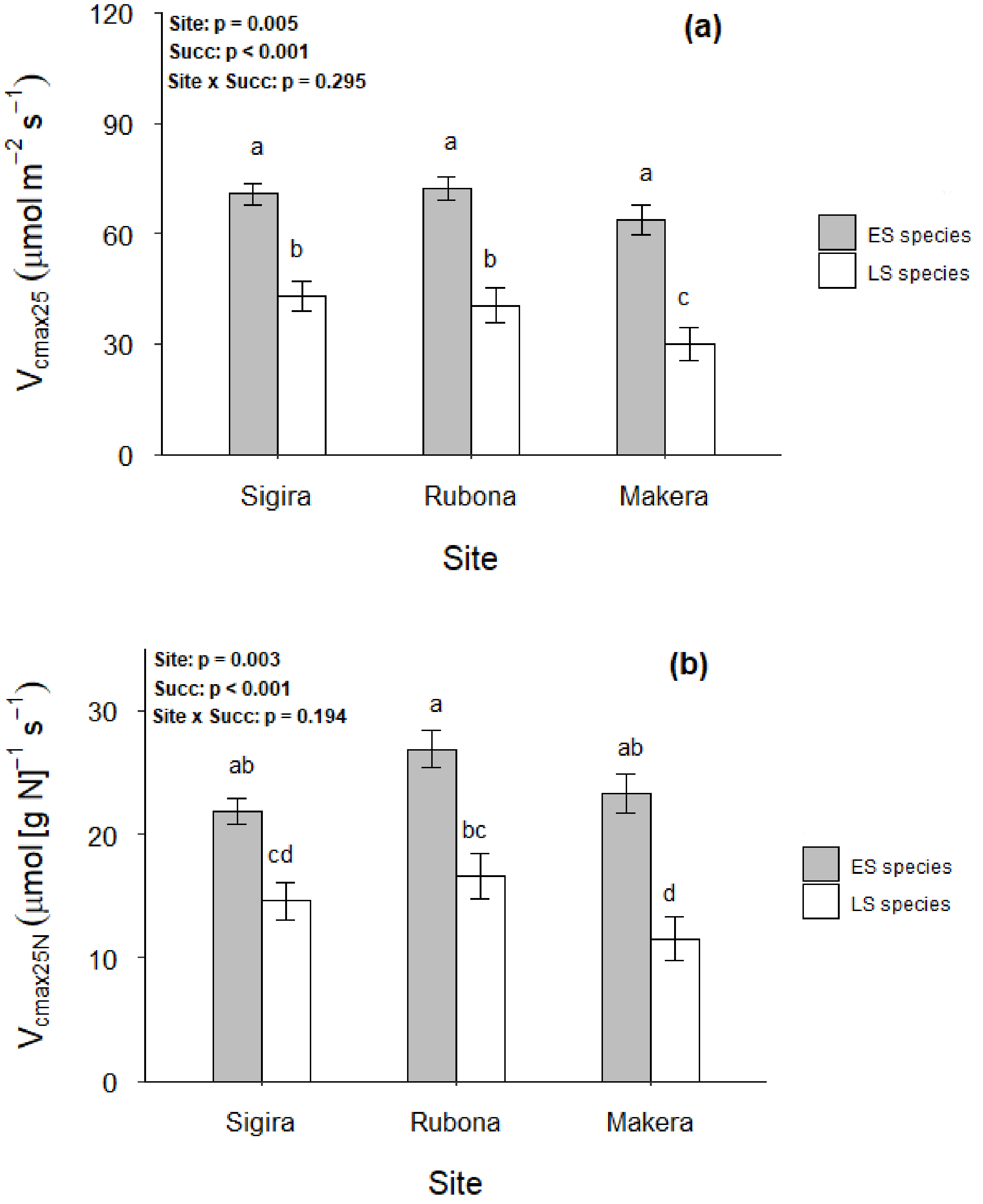


Figure 9. *Maximum rates of Rubisco carboxylation at a common leaf temperature of 25 °C (V_{cmax25}) expressed per unit leaf area (a) or per unit leaf N content (b) during non-drought conditions in November 2018 for early- (ES) and late-successional (LS) species grown at Sigira (high-elevation), Rubona (mid-elevation) and Makera (lowest-elevation) sites in Rwanda-TREE. Means ± SE (n = 5 or 9 species). Different letters on bars represent significant differences across sites and successional groups according to Tukey post hoc test ($p < 0.05$). Statistical p values are shown for effects of sites, successional groups (Succ) and their interaction. From* ***Paper II***.

4.2.3. *Slope parameter of the stomatal conductance-photosynthesis model, g_1*

The slope parameter of the stomatal conductance-photosynthesis model, g_1, did not differ either between sites or between successional groups and there was no interaction between effects of site and successional group (Figure 10). Values of g_1 were similar across all successional group by site combinations, with mean values ranging from 3.5 (± 0.76 SE) to 4.4 (± 0.77 SE). However, g_1 values varied greatly among individual species, ranging from 1.6 to 7.8 with an overall mean value of 4.15 across all 18 studied tree species. To some extent, the comparatively larger error bars for g_1 compared to g_s results can be attributed to lower tree replication for g_1 data, where only measurements from light-saturating ambient conditions (PPFD > 500 μmol m^{-2} s^{-1}) were considered (see Paper II).

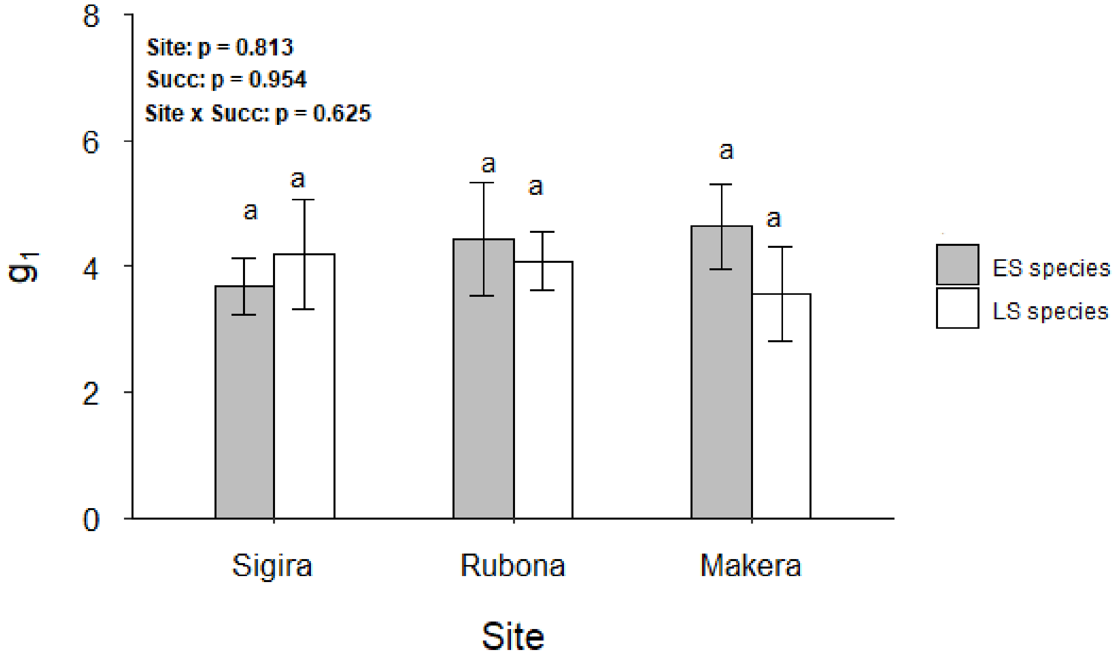


Figure 10. *Slope parameter of stomatal conductance-photosynthesis model (g_1 dimensionless) measured at ambient growth temperature during non-drought conditions (May-June 2019) for early-successional (ES) and late-successional (LS) species grown at Sigira (high-elevation), Rubona (mid-elevation) and Makera (lowest-elevation) sites in Rwanda-TREE. Means ± SE (n = 3-9). Different letters on bars represent differences between sites and successional groups according to Tukey post hoc test ($p < 0.05$). Statistical p values are shown for effects of sites, successional groups (Succ) and their interaction.*

4.2.4. *Seasonal drought effect on net photosynthesis*

Rates of A_{growth} were strongly reduced during late dry season at mid- and lower-elevation sites (Rubona and Makera, respectively) but not at the high-elevation, cooler site (Sigira) (Figure 11). This shows that trees at the montane site did not experience any drought stress during the approximately two-month long dry period. The A_{growth} rates during late compared to early dry season were 92 % lower at the warmest Makera site, 63 % lower at Rubona site, and 19% but non-significantly lower at Sigira site. The seasonal drought effect was similar for both ES and LS species and therefore Figure 11 shows results for data from both groups being pooled together.

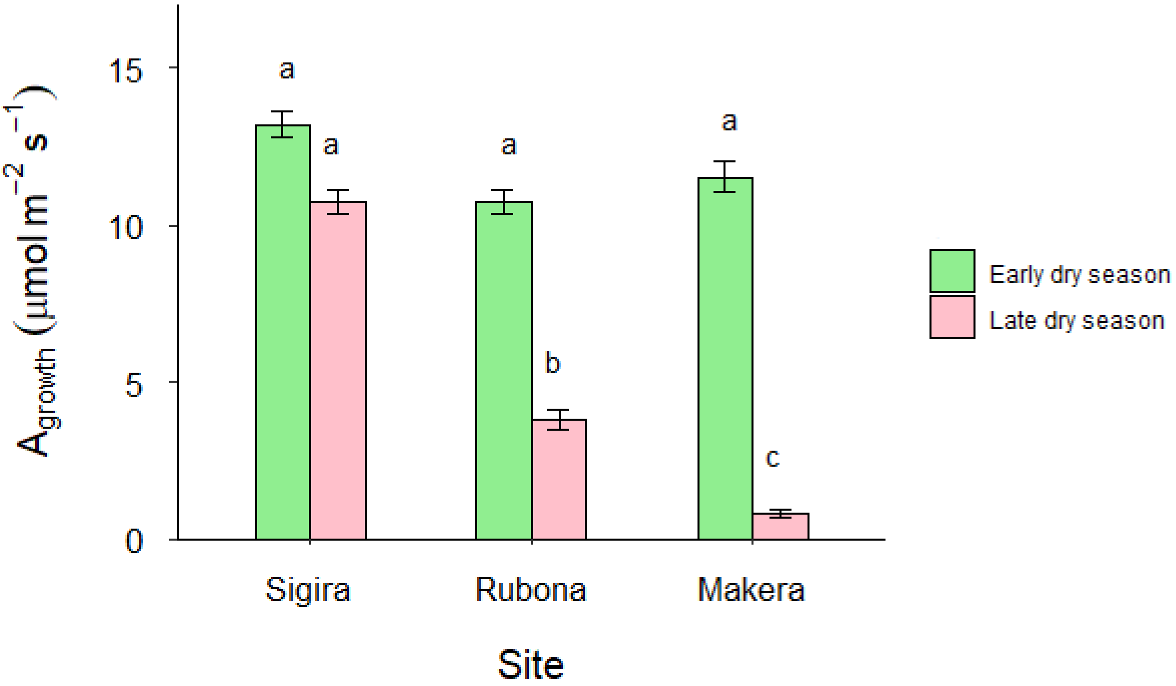


Figure 11. *Light saturated net photosynthesis measured at the ambient growth temperature (A_{growth}) during early and late dry season (May-June and August 2019) for early-successional (ES) and late-successional (LS) species grown at Sigira (high-elevation), Rubona (mid-elevation) and Makera (lowest-elevation) sites in Rwanda-TREE. Values are averaged across all 16 species at each site since response patterns were similar in early- and late-successional species. Means ± SE (n = 16). The ANOVA had a highly significant Site by Drought interaction ($p < 0.001$). Different letters on bars represent differences across sites and measurements campaigns according to Tukey post hoc test ($p < 0.05$). From **Paper II**.*

4.3. Thermal acclimation and seasonal drought effect on leaf dark respiration (Paper III)

4.3.1. Thermal acclimation of leaf R_d

Leaf R_d measured at a common leaf temperature of 20 °C (R_d20) acclimated to prevailing temperature in all 16 species such that it significantly decreased at sites with high growth temperature (Figure 12a). Rates of R_d20 were 36% lower at the intermediate elevation (Rubona) site and 47% lower at the lowest elevation (Makera) site compared to the highest elevation (Sigira) site. There was no significant difference between successional groups, neither in the magnitude of R_d20 or in its acclimation capacity. Moreover, leaf R_d20 normalized to leaf N (R_d20N) was still lower at intermediate and lower-elevation sites compared to Sigira (Figure 12b). The observed thermal acclimation of leaf R_d was not primarily driven by other measured leaf traits such as concomitant thermal acclimation of V_cmax, leaf N or leaf P (Paper II).

Estimated R_d20 at mean nighttime growth temperature (R_growth) was 8% (non-significantly) and 28% (significantly) lower at Rubona and Makera sites, respectively, compared to Sigira (Figure 12c). Similar R_growth between Sigira and Rubona, but lower R_growth at Makera mean that the strong thermal acclimation of R_d20 resulted in homeostasis of leaf R_d in trees at Rubona and over-compensation in trees at Makera (i.e., lower R_growth than in Sigira).

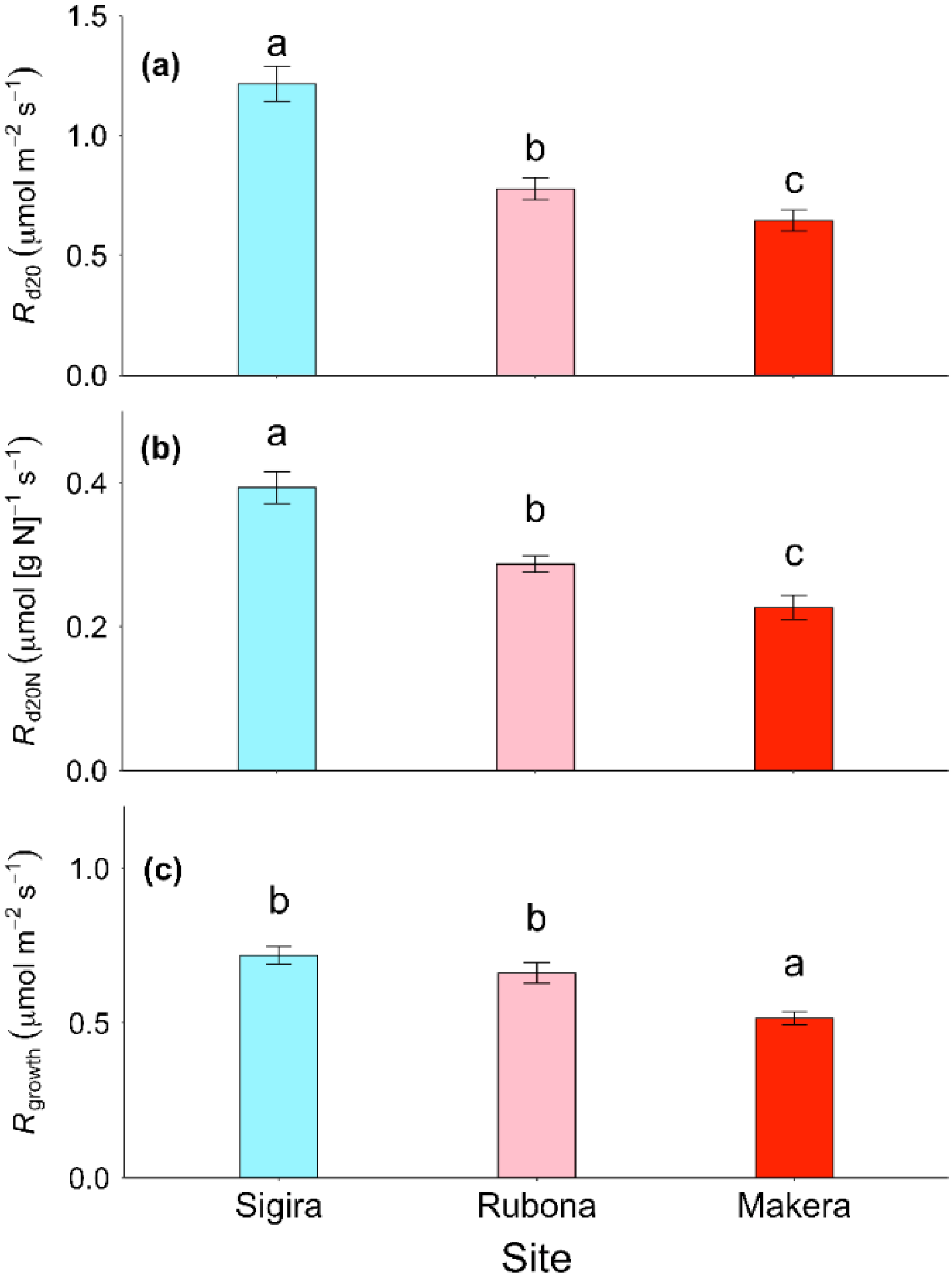


Figure 12. *Leaf dark respiration measured during the wet season (November 2018) averaged across all 16 species at each site. Leaf dark respiration at a common leaf temperature of 20 °C (R_{d20}) (a); R_{d20} normalized to total leaf N content (R_{d20N}) (b); leaf dark respiration at site-specific nighttime growth temperature (R_{growth}) (c). Colors represent different sites (high-elevation Sigira site = blue; mid-elevation Rubona site = pink; low-elevation Makera site = red). Means ±SE. n = 16. From* ***Paper III****.*

4.3.2. Relationship between interspecific variation in leaf R_d and other leaf traits

Interspecific variation in leaf R_{d20} was to a smaller or larger extent related to variation in other measured leaf traits. There were positive relationships between leaf R_{d20} and A_n, leaf N and leaf P, but not with LMA (Figure 13). The positive relationship was strongest for A_n (adjusted R^2 = 0.78), compared to leaf N (adjusted R^2 = 0.62) and P (adjusted R^2 = 0.53). These R^2 represent the proportion of variations explained by the whole model that takes into account differences in intercepts between sites and successional groups. While the slopes of these relationships were similar among sites for leaf N and P, they significantly differed for A_n, declining from high-elevation Sigira site to low-elevation Makera site (Figure 13). Residuals from the relationship between A_n and R_{d20} were not explained by variation in either leaf N or P.

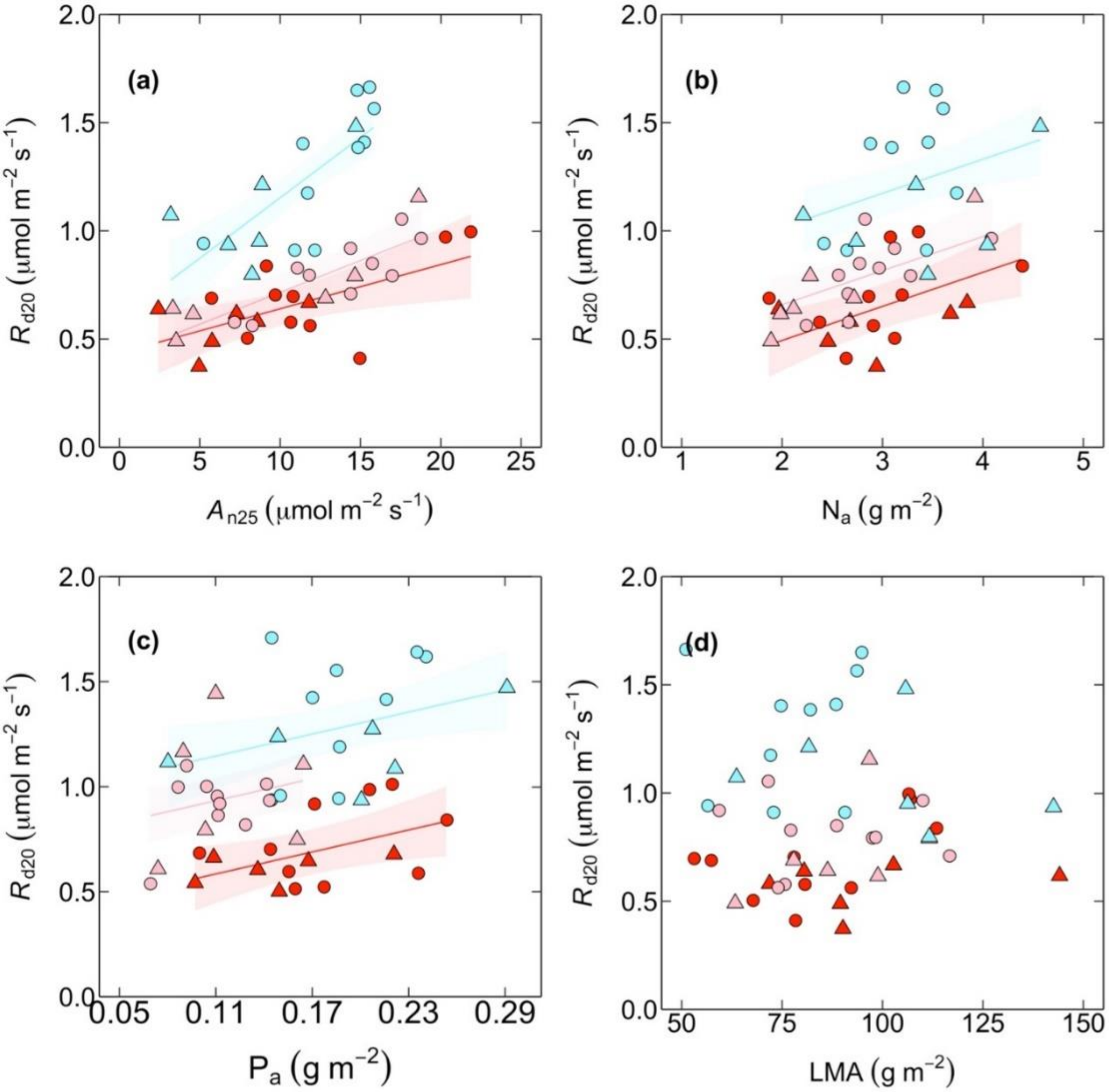


Figure 13. *Leaf respiration measured at 20 °C (R_{d20}) as a function of light-saturated net photosynthesis at 25 °C (A_{n25}; $R^2 = 0.27$, $R^2 = 0.26$ and $R^2 = 0.21$ for the high-elevation Sigira site, mid-elevation Rubona site and low-elevation Makera site, respectively) (a), area-based leaf nitrogen (N_a; $R^2 = 0.037$, $R^2 = 0.16$ and $R^2 = 0.097$) (b), area-based leaf phosphorus (P_a; $R^2 = 0.045$, $R^2 = 0.11$ and $R^2 = 0.28$) (c), and leaf mass per area (LMA; $R^2 = 0.023$, $R^2 = 0.029$ and $R^2 = 0.068$) (d). Symbols represent successional groups (early-successional species = circle; late-successional species = triangle). Colors represent different sites (high-elevation Sigira site = blue; mid-elevation Rubona site = pink; low-elevation Makera site = red). Each data point represents the average value of measured trees in each species at each site (n = 3-5). From* ***Paper III****.*

4.3.3. Drought effect on leaf R_d

Leaf R_d measured at 20 °C (R_{d20}) was decreased at the end of seasonal drought in the two species where drought effects on R_d were studied (Figure 14). The reduction was strongest in trees at the coolest high-elevation site and in *Polyscias fulva*, the ES species. Specifically, in *P. fulva*, dry season reduced leaf R_{d20} by 56%, 36% and 37% at Sigira, Rubona and Makera sites, respectively, while in *C. grandiflora*, dry season significantly reduced R_{d20} at Sigira only, by 36%. Site differences in R_{d20} were large at the beginning of the dry season (i.e. at non-drought conditions) but considerably smaller and not statistically different towards the end of the dry season. For R_d at prevailing nighttime temperatures, this implies rather similar rates under non-drought conditions but increased R_d at warmer and drier sites late during the dry season.

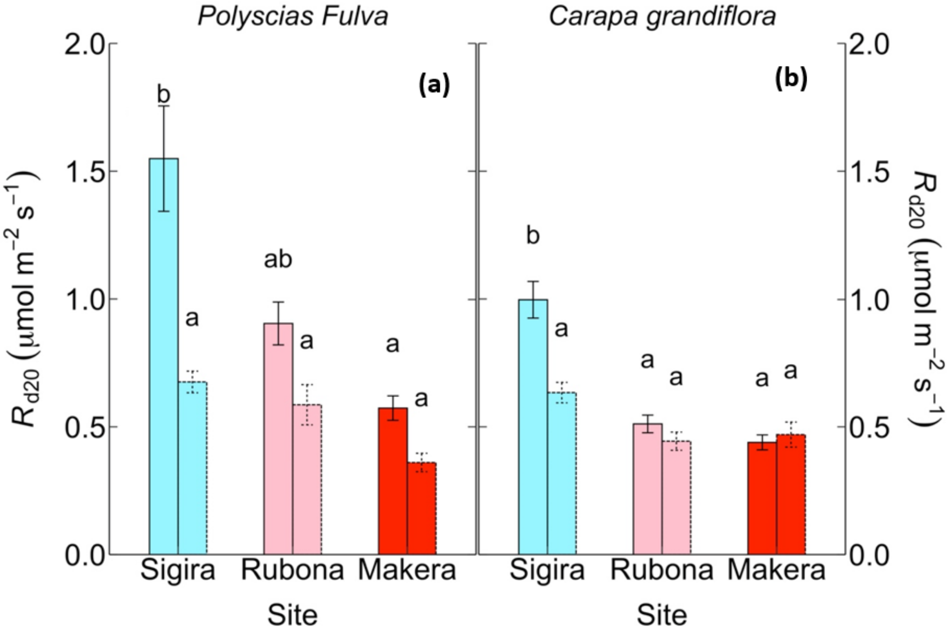


Figure 14. *Leaf dark respiration measured at a common leaf temperature of 20 °C (R_{d20}) at both early- and late-dry season in Polyscias fulva (an early-successional species) (a) and Carapa grandiflora (a late-successional species) (b). Bar lines represent measurement campaigns (early-dry season = solid; late-dry season = dotted). Colors represent different sites (high-elevation Sigira site = blue; mid-elevation Rubona site = pink; low-elevation Makera site = red). Means ± SE. Different letters on bars represent differences across sites and measurement campaigns according to Tukey post hoc test ($p < 0.05$). n = 9 for Sigira site, and n = 5-6 for Rubona and Makera sites. From* ***Paper III.***

4.4. Thermal acclimation of photosynthesis in potted tree seedlings (Paper IV)

Paper IV investigated two montane tree species with contrasting successional strategies (ES: *Harungana montana*; LS: *Syzygium guineense*) grown in 11 liter-pots with soil from Sigira at all three sites of the Rwanda-TREE project. The study investigated the instantaneous temperature responses of A_n, V_{cmax} and J_{max}, including their T_{opt}; the thermal optimum of A_n (T_{optA}), the thermal optimum of V_{cmax} (T_{optV}), the thermal optimum of J_{max} (T_{optJ}), and how these were affected by growth temperature. Also, R_d at 25 °C was explored.

The response of A_n to short-term variation in leaf temperature at different sites exhibited somewhat different patterns between the two studied species (Figure 15a, b). For both sites and species, A_n was approximately constant between 18 and 25 °C and declined above this temperature range. In *H. montana*, A_n was condiderably higher between 18-30 °C at the high-elevation site compared to mid-and low-elevation sites, but dropped substentially at leaf temperatures above 30 °C to realize comparable net CO_2 assimilation rates to the other two sites (Figure 15a). However, *in S. guineense*, A_n rates decreased at leaf temperatures above 25 °C, but A_n rates were similar among sites throughout the entire measuring temperature range (Figure 15b). In the two studied species, T_{optA} did not significantly increase despite of a 7.4 °C temperature difference in mean daytime temperature between the coolest and warmest site during the four months period (February-May 2019) preceding and during the gas exchange measurements campaign. There were small but statistically non-significant shifts in T_{optA}, averaging 0.34 and 0.16 °C per 1 °C increase in daytime mean growth temperature across the two warmer sites for *H. montana* and *S. guineense*, respectively.

The shape of the temperature response curve of V_{cmax} was not significantly altered by rising growth temperature in any of the species (Figures 15c,d; $p = 0.87$ and $p = 0.98$ for *H. montana* and *S.guineense*, respectively). As for T_{optA}, there were small but statistically non-significant shifts also in T_{optV}. These averaged 0.35 and 0.22 °C per 1 °C increase in daytime mean growth temperature across the two warmer sites for *H. montana* and *S. guineense*, respectively.

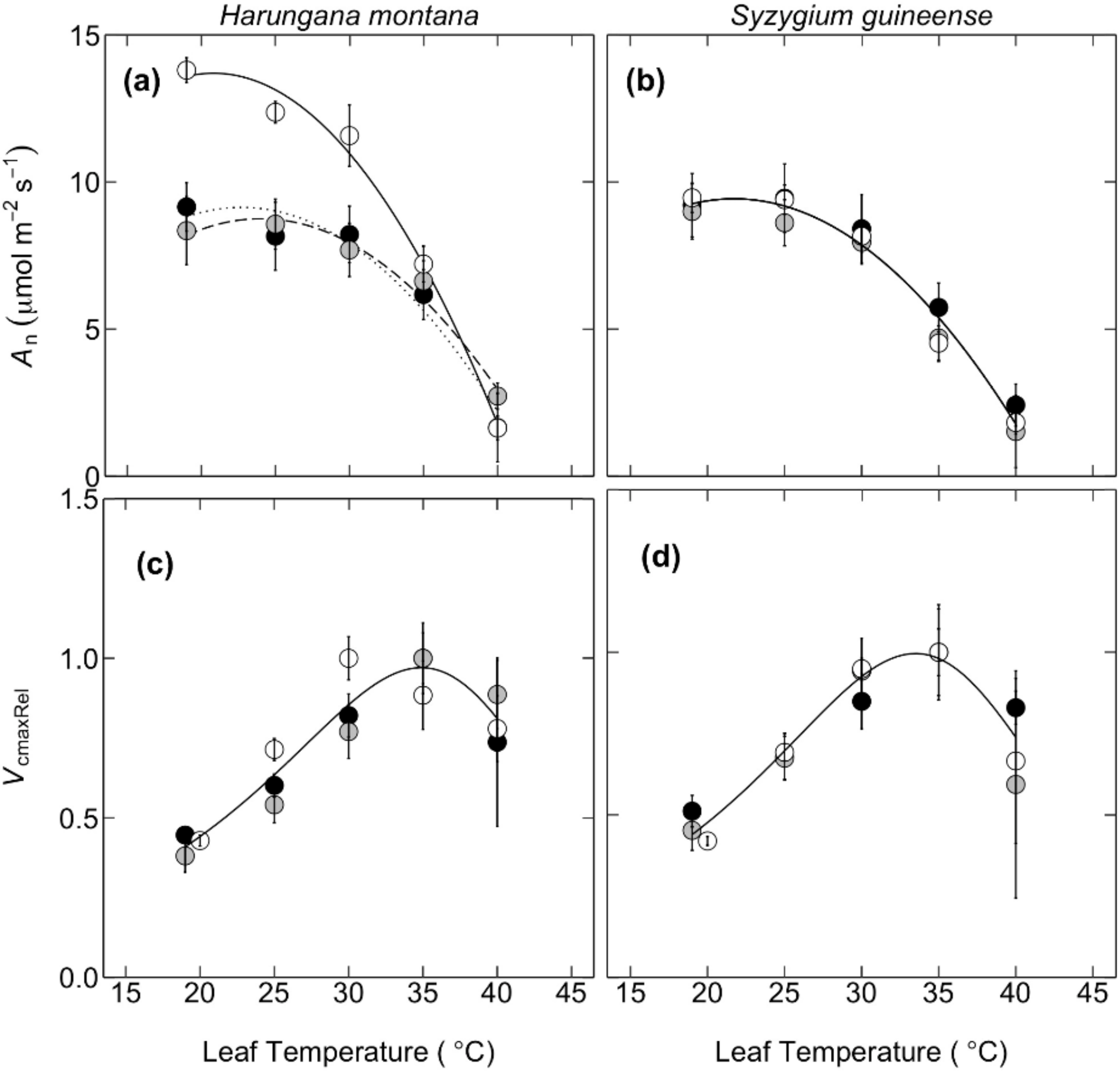


Figure 15. *Temperature responses of net photosynthesis (A_n; a-b) and relativized maximum carboxylation rate of Rubisco ($V_{cmaxRel}$; c-d) in Harungana montana (a, c) and Syzygium guineense (b, d) grown at different sites. Lines represent regression lines for different sites (high-elevation Sigira = solid; intermediate-elevation Rubona = dashed; low-elevation Makera = dotted lines). Colors represent different sites (high-elevation Sigira = white, intermediate-elevation Rubona = grey; low-elevation Makera = black). Means ± SE. n = 3-5. From* ***Paper IV****.*

The relationship between thermal acclimation of leaf R_{d25} and photosynthetic capacity (V_{cmax25} and J_{max25}) was explored. When data were pooled across species and sites, rates of R_{d25} were positively related to V_{cmax25} and J_{max25} (Figure 16), indicating a coordinated thermal acclimation between respiration and photosynthesis.

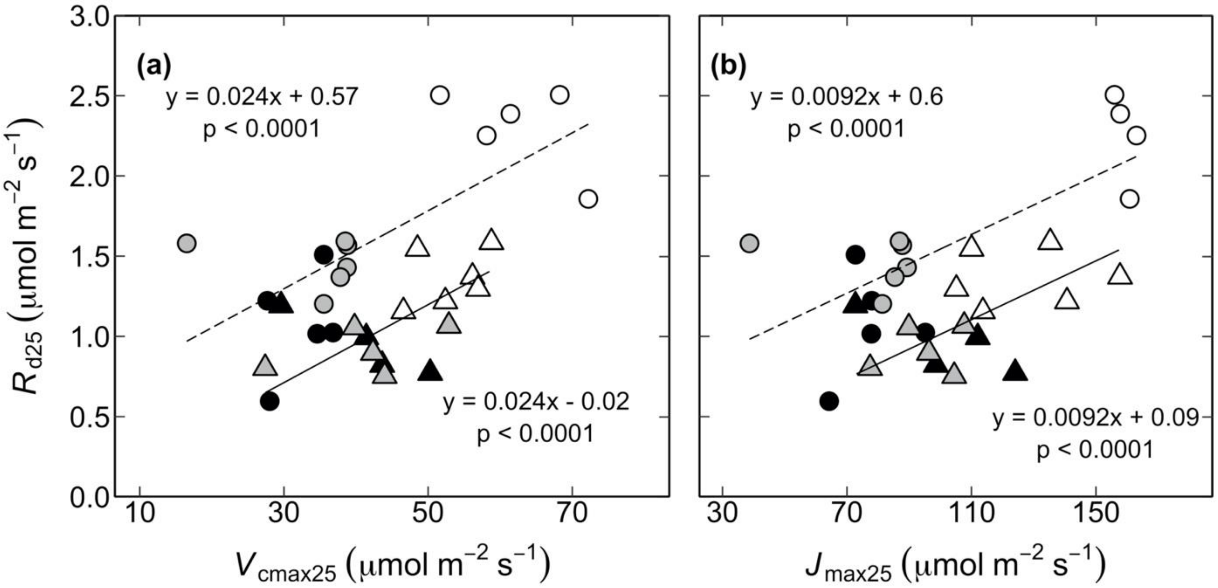


Figure 16. *Relationship between foliar respiration and photosynthetic capacity. Foliar dark respiration rate (R_{d25}), maximum carboxylation rate of Rubisco (V_{cmax25}), maximum photosynthetic electron transport rate (J_{max25}) measured at 25 °C. Lines represent simple line regression for different species (Harungana montana = dashed, circle; Syzygium guineense = solid, triangle. Colors represent different sites (high-elevation Sigira = white; intermediate-elevation Rubona = grey; low-elevation Makera = black). Data points represent measured seedlings for each of the two species. Adjusted R^2 is 0.58 for both a and b. From* ***Paper IV****.*

5. Discussion

5.1. Plant traits in mature trees along an elevation gradient (Paper I)

Physiological traits

In the wet season *E* mostly decreased with elevation while g_s, *E* and A_n did not systematically change (Figure 6). In the dry season, however, g_s, *E* and A_n all increased with elevation. This observed difference in physiological traits relationship with elevation between wet and dry seasons indicates that atmospheric evaporative demand (i.e. VPD) control *E* during wet periods while stomatal control over *E* dominates under drier conditions (i.e. at lower sites during the dry period). These observations are consistent with earlier studies in tropical lowland forests in Borneo (Kumagai *et al.,* 2005), Panama (Meinzer *et al.,* 1995) and central Amazonia (Malhi *et al.,* 2002). It is not surprising that values of g_s, *E* and A_n were generally higher in ES compared to LS species, in agreement with earlier studies on tropical trees (e.g. Dusenge *et al.,* 2015; Nogueria *et al.,* 2004). This result suggests that leaf transpiration and CO_2 uptake of tropical montane forests may decline in a warmer climate with more pronounced dry periods.

Leaf temperature

The leaf-to-air temperature difference (T_{leaf}–T_{air}) was smallest in the ES species *Polyscias fulva* compared to the other three species (Figure 7). This species also had higher g_s and *E* than the other species (Figure 6). This result is consistent with earlier controlled warming experiments indicating less warming sensitivity in ES compared to LS species (Cheesman *et al.,* 2013; Slot *et al.,* 2016) as well as a common garden experiment with seedlings in Rwanda (Vårhammar *et al.,* 2015) which indicated that LS species have higher T_{leaf} than ES species with higher *E*. The present study corroborates the findings of the latter seedling study by showing that also in mature trees, species with lower g_s and *E* (which is typical in LS species) have higher T_{leaf} than species with higher g_s and *E* (which is typical in ES species). Heat-induced declines in A_n on hot days are thus likely to be larger in LS compared to ES species, regardless if they have lower optimum temperatures of photosynthetic biochemistry (Slot *et al.,* 2016) or not (Vårhammar *et al.,* 2015).

5.2. Thermal acclimation and seasonal drought effect on photosynthesis (Paper II)

Net photosynthesis under growth conditions

Light-saturated A_n at growth temperature (A_{growth}) and non-drought conditions was strongly decreased at warmer site in LS but not in ES species (Figure 8; $p = 0.008$), suggesting that ES species may have a photosynthetic advantage over LS species under climate warming. The result agrees with recent observations of tropical LS species being more negatively affected by warming than ES species in both controlled-environment chamber experiments (Cheesman & Winter, 2013; Slot & Winter, 2018) and field experiments (Li *et al.,* 2020; Carter *et al.,* 2020). Poor photosynthetic performance of LS species under warmer conditions may be exacerbated by their higher leaf temperatures compared to ES species due to low transpiratory cooling and poor heat dissipation of large leaves, as shown in previous seedling studies on tropical tree species in Rwanda (Vårhammar *et al.,* 2015; Ntawuhiganayo *et al.,* 2020). Such effects are not well captured by instruments measuring gas exchange in leaf chambers with fans (such as the LI6400 used here), causing high leaf boundary conductance and, thus, small leaf to air temperature differences. The negative warming effects on A_{growth} in LS species observed here may therefore be an underestimation of the effects present in the field, outside the leaf chamber.

Stomatal and photosynthetic capacity responses to temperature

Warming did not significantly affect g_s. The lack of indication of g_s declines with higher growth temperatures (and VPD) may be explained by long-term adjustments to facilitate increased water uptake and transport in trees grown in a warmer climate with higher VPD, as sometimes observed before (Marchin *et al.,* 2016). However, several indoor chamber studies (Drake *et al.,* 2015; Wu *et al.,* 2018; Fauset *et al.,* 2019) and one forest understorey experiment (Carter *et al.,* 2020) with tropical trees reported decreased g_s with warming. It is not clear why our result was different from these studies, but stronger hydraulic adjustments of root systems in the field-grown plants of our study may play a role.

Similarly to A_{growth}, also V_{cmax25} decreased at the warmest site (Figure 9a). This finding was partially in agreement with the recent meta-analysis study indicating V_{cmax25} declines in warm-grown plants (Wang *et al.,* 2020). However, our results conflict with previous studies on tropical trees (Scafaro *et al.,* 2017; Crous *et al.,* 2018; Fauset *et al.,* 2019; Carter *et al.,* 2020) as well as with several earlier global meta-analyses (Kattge & Knorr, 2007; Way & Oren, 2010; Kumarathunge *et al.,* 2019) reporting no significant change of V_{cmax25} with warming. Clearly, more research is needed to explore how warming affect photosynthetic capacity in tropical trees.

Slope parameter of the stomatal conductance-photosynthesis model, g_1

Neither warming nor successional group significantly affected g_1 (Figure 10), in good agreement with a previous study on 21 African tropical tree species (Hasper *et al.,* 2017). These results contrast with global meta-analysis showing that g_1 values are smaller in plant species with more conservative water use strategy (Lin *et al.,* 2015). More conservative water use is presumably found in LS (lower g_s) compared to ES (higher g_s) species, but these groups exhibited similar g_1. The reason for the lack of patterns of g_1 with growth temperature or successional strategy is unclear. Although lack of g_1 acclimation simplifies modelling, more research on this is required to increase the reliability of predictions of tropical forest canopy-atmosphere gas exchange in a changing climate.

Seasonal drought effect on net photosynthesis

Rates of A_{growth} were strongly reduced during late dry season at mid- and lower-elevation sites but not at the high-elevation, cooler site (Figure 11). At warmer sites, a combination of higher evaporative demand and somewhat longer dry seasons (plus lower soil water holding capacity at the intermediate elevation Rubona site; Paper III) together resulted in considerable drought stress during the late dry season. The decreased A_n towards the end of the dry period at the two warmer sites are in agreement with several studies on tropical tree species, e.g. in semi-deciduous forest trees at a rain forest–savanna transition in South Amazon (Miranda *et al.,* 2005) and in tropical rainforests of central Amazon (Santos *et al.*, 2018), Bolivia (Doughty *et al.*, 2015) and French Guiana (Stahl *et al.*, 2013). The results highlight the strong reduction in leaf-level photosynthesis under warmer and drier conditions. This is very important given the intensification of dry seasons with large exceedance of evapotranspiration compared to projected precipitation for Rwanda in the future (Haggag *et al.,* 2016). This implies that canopy fluxes of CO_2 during the dry season will likely be strongly decreased in a future climate, for both ES and LS stands.

5.3. Thermal acclimation and seasonal drought effect on leaf dark respiration (Paper III)

Thermal acclimation of leaf R_d

Leaf R_d measured at a common leaf temperature of 20 °C (R_d20) acclimated to prevailing temperature in all 16 species such that it significantly decreased at sites with high growth temperature (Figure 12a). The acclimation of R_d was complete in Rubona (i.e., similar R_growth as in Sigira) and over-compensatory in Makera (i.e., lower R_growth than in Sigira; Figure 12c).

Previous studies have demonstrated that leaf R_d at a given temperature is frequently downregulated in plants grown under warmer conditions, but typically not to an extent that prevents increased R_d at prevailing growth temperatures, i.e. partial thermal acclimation (Atkin & Tjoelker, 2003; Slot & Kitajima, 2015; Reich *et al.,* 2016; Smith & Dukes, 2017). Our finding of complete or even over-compensatory acclimation suggests that tropical tree species acclimate leaf R_d more strongly to warming than most trees from temperate and boreal forests, which dominate previous studies (Slot & Kitajima, 2015; Reich *et al.,* 2016; Smith & Dukes, 2017). This strong thermal acclimation of leaf R_d in tropical tree species compared to species in other biomes may be related to contrasting effects of warming on photosynthesis (and thus substrate availability for respiration) in trees from different biomes. Moderate warming usually stimulates photosynthesis more in temperate and boreal ecosystems than in tropical ecosystems (where it often declines) (Liang *et al.,* 2013; Slot & Winter, 2018; Reich *et al.,* 2018). This, in turn, is likely because tropical species are operating closer to their thermal optimum of A_n compared to temperate and boreal species (Huang *et al.,* 2019).

Relationship between interspecific variation in leaf R_d and other leaf traits

Interspecific variation in leaf R_d20 was significantly related to variation in A_n, leaf N and P, but not with LMA (Figure 13). The relationship was strongest for A_n. This is consistent with earlier observations of positive relationships of R_d with A_n (Atkin *et al.,* 2005; O'Leary *et al.,* 2019), leaf N (Ryan, 1995; Atkin *et al.,* 2005 Rowland *et al.,* 2017) and leaf P (Meir *et al.,* 2001; Rowland *et al.,* 2017). However, the results do not support earlier observations of positive relationship between LMA and leaf R_d (e.g. Meir *et al.,* 2001; Rowland *et al.,* 2017). The strong dependence of leaf R_d

on photosynthesis is probably driven by carbohydrate supply from photosynthesis, which is the main source of substrates for respiration metabolism (O'Leary *et al.,* 2017, 2019).

Drought effect on leaf R_d

Leaf R_d measured at 20 °C (R_d20) was reduced at the end of seasonal drought in the two species where drought effects on R_d were studied (Figure 14). Site differences in R_d20 were large at the beginning of the dry season, being lower at warmer sites, while rates did not statistically differ towards the end of the dry season. This implies that R_d at prevailing nighttime temperatures were rather similar under non-drought conditions but considerably higher at warmer and drier sites during the late dry season. This could reflect an increased need for carbohydrates to support hydraulic repair at sites with more pronounced drought, as indicated in previous studies (Atkin & Macherel, 2009; Brodersen & McElrone, 2013; Rowland *et al.,* 2015).

5.4. Thermal acclimation of photosynthesis in potted tree seedlings (Paper IV)

Warming effect on temperature sensitivity of net photosynthesis and its underlying biochemical processes

In the two studied species, T_optA did not significantly increase despite of a 7.4 °C difference daytime mean growth temperature between the coolest and warmest site (considering the four-months period preceding and during the gas exchange measurements campaign). This suggests a limited capacity (absent or weak) of photosynthesis to acclimate to warmer growth temperatures in these tropical montane rainforest tree species. The non-significant positive shifts in T_optA (0.34 and 0.16 °C per 1 °C warming for *H. montana* and *S. guineense*, respectively) are lower than the value previously observed in a tropical lowland study (0.47 °C per 1 °C) (Slot & Winter, 2017a) and in global meta-analyses dominated by temperate and boreal tree species (0.55-0.62) (Yamori *et al.,* 2014; Kumarathunge *et al.,* 2019; Way, 2019). These results thus suggest weaker thermal acclimation capacity of T_optA in tropical montane species compared to most previous studies on temperate and boreal tree species. The poor acclimation capacity observed here may partly explain the high sensitivity of upland tree species to warming along Andean tropical elevation gradients during the past few decades (Duque *et al.,* 2015; Fadrique *et al.,* 2018).

Relationship between thermal acclimation of foliar dark respiration and photosynthetic capacity

Rates of R_{d25} were positively related to both V_{cmax25} and J_{max25} (Figure 16). This suggest that thermal acclimation of R_d was strongly driven by thermal acclimation of photosynthetic capacity, consistent with the optimality theory of photosynthetic capacity recently proposed by Wang *et al.* (2020), which stipulates that thermal acclimation of R_d should closely follow that of V_{cmax} in order to maintain optimal CO_2 assimilation with efficient use of resources in a given environment. This thermal acclimation in leaf respiration can, in turn, be achieved via several biochemical processes including reduction in Cytochrome C Oxidase (COX) content, a key central respiratory protein (Rashid *et al.,* 2020a), decrease in mitochondrial density (Armstrong *et al.,* 2006), or changes in some intermediates glycolysis and tricarboxylic acid cycle (Rashid *et al.,* 2020b).

6. Conclusions and Outlook

6.1. Conclusions

Overall, this thesis studied physiological responses to warming and drought in a broad range of tropical tree species. The data were collected from three types of experiments, all with the elevation gradient approach: one study on existing mature trees of four common tree species growing at five locations along a 1700-2700 m elevation gradient (Paper I), a multi-species plantation experiment with 5400 trees of 20 species and from the same plant material grown at three sites with elevations at 2400, 1600 and 1300 m (Paper II and III) and a study with potted trees grown at the same three sites (Paper IV). The three experimental designs used here complete each other to achieve both high ecological realism and a high degree of certainty when attributing plant responses to warming rather than confounding effects of other environmental factors. The studies on mature trees and large plantations contribute valuable ecological realism for reliable projections of tropical forests performance under warmer and drier climate. Covering many species provides important information on interspecific variation and differences in responses between successional groups. Overall, observed contrasting photosynthetic warming responses between ES and LS species suggest shifts in tree species composition in tropical forests in a warmer world, to the disadvantage of LS species. Moreover, the strong thermal acclimation of leaf respiration in all studied tree species should be accounted for to avoid overestimation of the impact of global warming on autotropic respiration in tropical forests. This research is useful for global change ecology and climate modelling. Moreover, the knowledge gained contributes to national and regional priorities for climate resiliency and biodiversity conservation.

These are the main conclusions from each paper:

Paper I demonstrated that during the dry season, g_s, E and A_n were reduced at low-elevation sites where drought was more pronounced, while patterns were absent or opposite (for E) in the wet season. These results of pronounced seasonality in altitudinal patterns suggest that tropical tree water use and CO_2 uptake will be substantially reduced if dry seasons become more pronounced in a warmer climate. The leaf-to-air temperature difference was smallest in the ES species *P. fulva*, which also had the highest stomatal conductance and transpiration.

Paper II showed strong decline in A_n rates (at prevailing growth temperature during wet season) at the warmest site in LS species, but not in ES species. Also, higher rates of A_n and V_{cmax25} were obtained in ES compared to LS species. Drought strongly reduced A_n at warmer sites but not at the coolest site and this response was similar in both ES and LS species. The results suggest contrasting responses of photosynthesis to warming between LS and ES species under non-drought conditions, and strong declines in A_n rates for both LS and ES species during the dry season in a warmer climate with more pronounced seasonal droughts.

Paper III reported strong reduction in R_d rates at elevated growth temperatures in both ES and LS species. The observed complete or over-compensatory acclimation of leaf R_d has been so far less commonly reported in the literature, dominated by boreal and temperate tree studies. This observed strong downregulation of R_d may be related to responses of photosynthesis, which typically increases with warming in boreal and temperate species but not in tropical species (where it often declines). Also, the study showed that drought reduced R_d and this effect differed between both species and sites.

Paper IV demonstrated that T_{opt} of A_n and V_{cmax} did not significantly increase with warming. These results indicate limited or no capacity of the T_{opt} of net photosynthesis and its underlying biochemical processes to acclimate to warming in tropical trees. The observed weak or absent acclimation capacity may partially explain the high sensitivity of upland tree species to warming during the past few decades reported from Andean elevation gradients. However, photosynthetic capacity and leaf R_d both adjusted downwards under warming, in a coordinated manner.

6.2. Outlook

The data presented in my thesis form a unique dataset, with photosynthetic and leaf R_d responses to temperature and drought investigated in a broad range of tropical tree species with different growth strategies using an elevation gradient approach. While previous physiological studies on warming responses of tropical trees were mostly conducted on small plants in controlled conditions, I studied trees grown freely rooted (except in Paper IV) under ecologically realistic conditions. This provided an opportunity to reduce the knowledge gaps on tree physiological responses to temperature and drought, which are key knowledge gaps in global change ecology as well as ecosystem and climate modelling.

From a modelling point of view, there is evidence that including information on thermal acclimation and/or adaptation of photosynthesis to growth temperature improved the ability of global vegetation models to accurately predict ecosystem-level primary production (Mercado *et al.,* 2018). However, in the most recent global meta-analysis study investigating the adjustments of photosynthesis to increased growth temperature (Kumarathunge *et al.,* 2019), species from tropical montane forests were poorly represented. One of my findings was declined A_n and photosynthetic capacity at warm sites in LS but not ES species, offering novel information on differential warming acclimation capacity of species with contrasting growth strategies. Another key finding was the strong reduction in leaf-level photosynthesis under warmer and drier conditions. This is very important given the intensified dry seasons with large exceedance of evapotranspiration compared to precipitation projected for Rwanda (Haggag *et al.,* 2016). This implies that canopy fluxes of CO_2 during the dry season will likely be strongly decreased in a future climate. Moreover, the finding that the thermal optima of A_n and its underlying biochemical processes did not significantly shift with warming suggest that vegetation models should not generalize the partial thermal acclimation observed in studies dominated by temperate and boreal species for tropical montane rainforests tree species. My finding of strong thermal acclimation of leaf respiration in tropical montane tree species has important implications for the projection of future tropical biosphere-atmosphere interactions, to avoid overestimation of the impact of global warming on autotrophic respiration in tropical forests. Vegetation models should also consider the tight coordination of thermal acclimation of leaf respiration and photosynthetic capacity when predicting feedback between terrestrial vegetation and climate. Finally, my thesis facilitates improved representation of African montane tropical trees in global vegetation models by providing information on their physiological responses to temperature and drought.

The results of my thesis have implications for forestry in Rwanda and the region beyond. With respect to results on photosynthesis, some LS species may not be particularly suitable for tree plantation efforts in light of their stronger warming sensitivity. For instance, this is the case for LS species such as *Carapa grandiflora* and *Entandrophragma excelsum*. It may be that they would do better as understorey species, but that is rare in plantations, at least in agroforestry. On the other hand, the higher warming sensitivity of LS species imply that they are particularly important to protect and promote for the conservation of biodiversity and other ecosystem services in a changing climate. Species diversification is among the guiding principles of the strategic plan for the forest sector in Rwanda, and part of the country's commitment to the Bonn Challenge (GoR, 2015). On the contrary, many ES species in my thesis showed similar photosynthesis rates between the highest (or control) and the lowest elevation sites. If coming studies show that the growth and survival rate of these species also respond well to warmer climate, they can be suitable to tree plantations efforts in different regions of Rwanda. This would serve as a long-term process for recovering ecological integrity and enhanced social well-being in areas with degraded land. Species diversification with inclusion of native tree species enhances numerous ecological benefits, particularly in agroforestry, by controlling erosion, providing fodder and improving soil fertility.

My findings of temperature and drought effects on tree physiological processes have important implications not only for Rwandan forestry, but also for central African forests in general. A recent study predicted a warming- and drought-induced long-term future decline in the carbon sink of the Congo basin (Hubau *et al.,* 2020). Also, a recent study on temperature sensitivity of tropical forests across a pantropical network of permanent plots showed declines in carbon gain driven by high daytime rather than by high nighttime temperatures (Sullivan *et al.*, 2020). My photosynthetic data showing poor performance of LS species under warmer climate and strong declines in net photosynthesis by intensified seasonal drought for both ES and LS species provide physiological understanding and support of these large-scale responses, suggesting strong climate change sensitivity of Central-East African tropical forests.

Moving forward to the recommendations of future studies, since measurements of A-C_i curves are time consuming and given the broad range of species covered in my doctoral thesis, it was not possible to do such measurements. Therefore, further studies to quantify photosynthetic capacity in these species from the direct measurements of A-C_i curves would be valuable. Moreover, studies capturing how water (irrigation, rainout shelters) and nutrient treatments affect thermal acclimation of both photosynthesis and leaf R_d in Rwanda-TREE project are recommended for increased applicability across areas with varying precipitation and fertility. In addition, drought effects on R_d was tested for two species only. Further studies to investigate and quantify the interactive effects between seasonal drought and growth temperature on leaf R_d in a broad range of species belonging to both ES and LS groups are recommended. In addition, the results that photosynthesis is more sensitive to high temperature in LS compared to ES species is worth exploring further in other types of tropical forests.

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