

Suitability of native tree species across regions of Rwanda in relation to climate sensitivity and ecosystem services

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2025

This thesis is submitted in fulfilment of the requirements for the award of the Degree of Doctor of Philosophy under double degree program between the University of Rwanda and the University of Gothenburg, Sweden. The degree in biological sciences will be awarded by the University of Rwanda, School of science, Department of Biology, and the degree in Natural sciences, specialising in Environmental sciences will be awarded by the University of Gothenburg. The thesis will be publicly defended on 27 November 2025 at 09:00 CET, 10:00 in Rwanda at the University of Rwanda, College of Science and Technology, plus online webinar that shall be communicated by the time of the defence.

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Declaration

I, Bonaventure Ntirugulirwa, declare that this thesis titled “Suitability of different native tree species across regions of Rwanda in relation to climate sensitivity and ecosystem services is the outcome of my own PhD by research, except where specifically acknowledged.

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Date 2025-10-27

ISBN 978-91-8115-519-8 (PRINT)
ISBN 978-91-8115-520-4 (PDF)
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Printed by Stema, Borås, Sweden

Dedication

To my wife Olga Victorovna Ntirugurirwa

To my mother Saveline Rivamunda

*To my sons Serge Bonaventurovitch Ntirugurirwa and Daniel Bonaventurovitch
Ntirugurirwa*

To my brother Pascal Hitimana

To my sisters

Acknowledgement

My heartfelt gratitude goes to the Rwanda Agriculture and Animal Resources Development Board (RAB) for selecting me as candidate for PhD studies and for granting me time to do the research, and avail three sites to establish research experiments. My thankfulness goes particularly to the RAB former Director General (DG) Dr. Patrick Karangwa, Dr. Mark Bagabe and Dr. Daphrose Gahakwa, to DG of Rwanda forestry Authority (RFA) Dr. Concorde Nsengumuremyi, to the Research Division Manager of RFA Dr. Ivan Gasangwa for their moral assistance and material assistance. I express my thanks to the University of Rwanda (UR) and the University of Gothenburg (GU) for offering me the double degree program which I followed to conduct my PhD studies. I thank the GU that allowed me to stay in Gothenburg for my PhD double degree program, whereby I profited from short courses, physical meetings with my supervisors, field, and laboratory activities. My gratitude also goes to Per Adolf Larssons Scholarship Fund for the stipend fees that allowed me to stay in Gothenburg University. I am also deeply grateful to the Swedish Research Councils VR and Formas for funding the Rwanda TREE project, within which this thesis was conducted.

My special gratitude goes to my main Supervisor Prof. Göran Wallin for accepting me as a PhD student and for his comments and feedbacks, field trips to Rwanda, important courses and conferences, moral support, encouragement and stimulating discussions that have guided me all over my work. Furthermore, I thank Göran Wallin for organizing my frequent travels to and from Gothenburg and arranging for my accommodations.

I address many thanks to my co-supervisor Prof. Johan Uddling for his supporting reviews, comments, encouragement, important courses, seminars related to my PhD studies. I would like also to express my gratitude to my co-supervisor Prof. Donat Nsabimana and Dr. Eric Mirindi Dusenge for their important comments and advice on my PhD studies.

I would like to express my sincere gratitude to my examiner, Prof. Håkan Pleijel, for his valuable insights and guidance.

My heartfelt thanks also go to the staff at the University of Gothenburg, especially Prof. Henrik Aronson, Prof. Cornelia Spetea, and Dr. Lasse Tarvainen, all from the Department of Biological and Environmental Sciences, for their support during my stay at the university.

I am grateful to Sven Toresson, Ylva Heed, Karin Johansson, Linnéa Wallgren, Carl Svensson and Minna Panas for their various support and friendship during my stay in Gothenburg. I am deeply grateful to the field staff of the Rwanda TREE Project Experiment-Kayindo Gelace, Nyirawenda Josephine, Sibomana Athanase, and Munanira Emmanuel—for their dedicated monitoring of the research sites at Sigira, Rubona and Ibanda Makera. I also thank my colleagues Zibera Etienne, Bambe Jean Claude, Bahati Elyse Ntawuhiganayo, Gakwerere Nkuba Epaphrodite, Dr. Myriam Mujawamariya, Dr. Aloysie Manishimwe, Dr. Olivier Jean Leonce Manzi, and Dr. Maria Wittemann for their valuable comments and encouragement.

My sincere thanks go to Bigirimana Mao Elie and Gasirikare Louis for their constant field support, and to my brother Hitimana Pascal for reviewing my thesis and offering helpful advice. I am also grateful to Etienne Hagumigara, Dr. Jean Damascene Ndayambaje and Dr. Jean Damascene Ntawukuriryayo for their moral support throughout my PhD studies.

Abstract

Our ability to select native tree species for forest restoration and ecosystems services in tropical areas is limited by insufficient knowledge of tree growth, survival and climate sensitivity. This thesis aims to enhance the understanding of the suitability of tree species from highland tropical forest in current and future climates across Rwanda's agro-ecological regions through three experiments and one literature study. Two experiments with young trees were established at three sites along an elevation gradient (2400 to 1300 m a.s.l., temperature difference of 5.4 °C): one involving multispecies plantations of 20 species and another with potted trees of two species planted in the same soil at all sites. A third experiment, conducted in the Ruhunde Arboretum (~1700 m a.s.l.) studied shade tolerance of six species. All experiments included a mix of early (ES) and late (LS) successional species, with the multispecies plantations containing species with dominant distribution in different vegetation types and elevations (transitional rainforest at 1600 – 2000 and montane rainforest at > 2000 m a.s.l.). The literature study assessed the suitability of 81 native tree species to different potential natural vegetation systems of east Africa and their contributions to different ecosystem services. The results from the multispecies plantation experiment showed that warming stimulates early tree growth in most early-successional species, particularly those originating from transitional rainforests. In contrast, several late-successional species, especially from higher elevations, did not respond or grew slower and had higher mortality at warmer sites. Findings from the potted tree experiment, although only limited to two species, aligned with results from the multispecies plantations, indicating that warming and not soil differences was the primary explanation of the observed site differences in tree growth in the larger study. In warmer climates, total biomass increased in the ES species without altering biomass allocation. In contrast, in the LS species, only root mass increased at warmer sites. The shading experiment revealed that dense canopy conditions significantly reduced the total tree biomass differently between species. However, under open sky, late-successional (shade-tolerant) species grew equally well as early-successional (shade-intolerant) species, suggesting tree growth differences in the elevation gradient were not due to species differences in light tolerance. The literature study of East African tree species showed clear relationships between elevation, climate, and species traits. Wood density increases as precipitation decreases, which it does with decreasing elevation. Among selected species, most provide multiple ecosystem services: 83% medicinal, 79% construction, 68% fuel, 58% edible, 56% cultural and 53% supporting and 31% regulating. The experimental studies suggest that in a warmer climate, higher-elevation and late-successional species may face increased competition from lower-elevation and early-successional species. When combined with findings from the literature, these results indicate that climate change will likely decrease the provisioning of ecosystem services specific to some late-successional species, as well as the biodiversity and carbon storage of Afromontane forests.

Key words: Native trees, Elevation gradient, Tree growth and mortality, Afromontane rainforest, Transitional rainforest, Successional group.

List of papers

Papers and manuscripts included in the thesis:

Paper I. **Ntirugulirwa B.**, Zibera, E., Nkuba E., Manishimwe, A., Nsabimana, D., Uddling, J. & Wallin, G. (2023). Thermophilization of Afromontane Forest stands demonstrated in an elevation gradient experiment. *Biogeosciences*, 20, 5125–5149, <https://doi.org/10.5194/bg-20-5125-2023>

Paper II. Dusenge, M.E., Wittemann M., Mujawamariya, M., Ntawuhiganayo, E. B., Zibera, E., **Ntirugulirwa, B.**, Way D. A., Nsabimana, D., Uddling, J. & Wallin, G. (2021). Limited thermal acclimation of photosynthesis in tropical montane tree species. *Global change biology*, 27, 4860-4878. <https://doi.org/10.1111/gcb.15790>

Paper III. Ntawuhiganayo, E.B., Uwizeye, F.K., Zibera, E., Dusenge, M.E., Ziegler, C., **Ntirugulirwa, B.**, Nsabimana, D., Wallin, G. & Uddling, J. (2020). Traits controlling shade tolerance in tropical montane trees. *Tree Physiology* 40, 183-197. <https://doi.org/10.1093/treephys/tpz119>

Paper IV. **Ntirugulirwa, B.**, Zibera, E., Nsabimana, D., Uddling, J. & Wallin G (2023) Selection of native tree species for multifunctional landscapes supporting ecosystem services in agro-ecological regions of Rwanda. (*Manuscript*).

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

Co-authored papers with me as co-author that are not included in the PhD thesis:

Manzi O.J.L., Wittemann M., Dusenge M.E., Habimana J., Manishimwe A., Mujawamariya M., **Ntirugulirwa B.**, Zibera E., Tarvainen L., Nsabimana D., Wallin G., and Uddling J. (2024). Canopy temperatures strongly overestimate leaf thermal safety margins of tropical trees. *New Phytologist* 243, 2115–2129. <https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.20013>

Wittemann, M., Mujawamariya, M., **Ntirugulirwa, B.**, Uwizeye, K.F., Zibera, E., Manzi, O.J.L., Nsabimana, D., Wallin, G., Uddling, J. (2024). Plasticity and implications of water-use traits in contrasting tropical tree species under climate change. *Physiologia Plantarum*, 2024;176:e14326. <https://onlinelibrary.wiley.com/doi/10.1111/ppl.14326>.

Mujawamariya, M., Wittemann, M., Dusenge, E.M., Manishimwe, A., **Ntirugulirwa, B.**, Zibera, E., Nsabimana, D., Wallin, G., Uddling, J. (2023). Contrasting warming responses of photosynthesis in early- and late-successional tropical trees. *Tree Physiology*, 43, 1104–1117, <https://doi.org/10.1093/treephys/tpad035>

Manishimwe, A., **Ntirugulirwa, B.**, Zibera, E., Nyirambangutse, B., Mujawamariya, M., Dusenge, M.E., Bizuru, E., Nsabimana, D., Uddling, J., Wallin, G. (2022) Warming responses of leaf morphology are highly variable among tropical tree species, *Forests*, 13, 219; <https://doi.org/10.3390/f13020219>

Wittemann, M., Andersson, M.X., **Ntirugulirwa, B.**, Tarvainen, L., Wallin, G., Uddling, J. (2022) Temperature acclimation of net photosynthesis and its underlying component processes in four tropical tree species. *Tree physiology*, 42 1188-1202. <https://doi.org/10.1093/treephys/tpac002>

Tarvainen, L., Wittemann, M., Mujawamariya, M., Manishimwe, A., Zibera, E., **Ntirugulirwa, B.**, Ract, C., Manzi, O.J.L., Andersson, M.X., Spetea, C., Nsabimana, D., Wallin, G., Uddling, J. (2021) Handling the heat - photosynthetic thermal stress in tropical trees, *New Phytologist*, 233, 236-250. <https://doi.org/10.1111/nph.17809>

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

Table of contents

Declaration.....	ii
Dedication.....	iii
Acknowledgement	iv
Abstract.....	v
List of papers.....	vi
Papers and manuscripts included in the thesis:.....	vi
Co-authored papers with me as co-author that are not included in the PhD thesis:	vi
Table of contents.....	vii
List of figures.....	ix
List of Tables	ix
List of symbols and abbreviations	x
1 General introduction	1
1.1 Tropical forests and their threats	3
1.2 Forest futures: secondary succession, plantations and species composition	5
2 Literature review.....	8
2.1 Climate change and sensitivity of tropical trees	8
2.2 Temperature and drought sensitivity of tropical trees and forests.....	10
2.3 Drought sensitivity	10
2.4 Climate-Proofing Forests: Tree Species Selection for the Future	11
2.5 Elevation gradient and warming effects on tree physiology.....	13
3 Key knowledge gaps and research needs.....	13
4 Aims and hypotheses	15
5 Material and methods.....	17
5.1 Overview of the studies and used plant material	17
5.2 Experimental sites	20
5.3 Weather and soil conditions at experimental sites.....	21
5.4 Experimental design	21
5.5 Measurements.....	23
5.6 Selection of native tree species suitable in different regions of Rwanda with respect to climate change sensitivity – literature review (Paper IV).....	25
5.7 Statistical analyses.....	25
6 Results.....	26
6.1 Warming responses of tree growth and mortality in the mixed tree plantations (Paper I).....	26
6.2 Warming responses of growth and biomass allocation of potted trees (Paper II)	29

6.3	Responses of growth and biomass allocation to different degrees of shade (Paper III)..	30
6.4	Tree stand composition (Paper I).....	31
6.5	Photosynthesis, respiration, and stomatal conductance (Paper II and III).....	33
6.6	Selection of native tree species suitable in different regions of Rwanda with respect to climate change sensitivity – literature review (Paper IV).....	36
7	Discussion.....	38
7.1	Growth responses to warming (Paper I, II)	38
7.2	Response to shade (Paper III).....	40
7.3	Mortality responses to warming (Paper I)	41
7.4	Tree stands composition (Paper I)	42
7.5	Multifunctionality of tree species (Paper IV)	42
7.6	Study limitations.....	43
8	Implication and recommendations.....	44
8.1	Forest Restoration and Climate Adaptation.....	44
8.2	Technical Recommendations.....	45
8.3	Scientific Recommendations	45
8.4	Policy Recommendations	45
8.5	Recommendation of species	45
9	Conclusions.....	46
10	References.....	47

List of figures

Figure 1. Conceptual figure - environment, biodiversity, ecosystem services	2
Figure 2. Outline of three experiments	17
Figure 3. Topographic map of Rwanda showing experimental sites.....	18
Figure 4. Natural elevation ranges for the species used in the three experiments	20
Figure 5. Map of the plot design at each site within the elevation gradient	22
Figure 6. Examples of changes in stem height and relative over 2 years	27
Figure 7. Base diameter, tree height, number of stems and tree mortality at different sites in the elevation gradient	28
Figure 8. The effect on tree stem height versus effect on base diameter.....	29
Figure 9. Total plant biomass and its allocation in <i>Harungana montana</i> and <i>Syzygium guineense</i>	30
Figure 10. Total biomass, relative growth rate (RGR) and biomass allocation of species in the Potted tree shade experiment.....	32
Figure 11. Fractions of basal area for different species groups at planting and after 2 years.	32
Figure 12. Gas exchange responses to temperature in <i>Harungana montana</i> and <i>Syzygium guineense</i>	34
Figure 13. Leaf dark respiration measured at 25°C (R_{d25}) in <i>Harungana montana</i> and <i>Syzygium guineense</i>	34
Figure 14. Light-saturated net CO ₂ assimilation (A_n), maximum rates of photosynthetic carboxylation (V_{cmax}), electron transport (J_{max}), $J_{max}:V_{cmax}$ ratio and stomatal conductance (g_s) of six tropical tree species grown under open, sparse canopy and dense canopy	35
Figure 15. Relationship between average tree traits and environments of species from 11 different potential vegetation types in Rwanda.....	37

List of Tables

Table 1. Total forest area and plantation forest area by world region and subregion.....	4
Table 2. Area of forest types in Rwanda in 2019.....	8
Table 3. Distribution of tree species forest plantations in Rwanda.....	8
Table 4. Taxonomy of species and their main forest type (FT) of origin, classification into successional group (SG), native distribution,.....	19
Table 5. Weather and other characteristics of experimental sites for the warming experiment in an elevation gradient and the potted tree - shade experiment..	22

List of symbols and abbreviations

AfriTRON	African Tropical Rainforest Observatory Network
A_n	Net photosynthesis
BA_{abs}	Absolute basal area
BA_{frac}	Fractional basal area
C	Carbon
C_i	Intercellular CO ₂ concentration
D	Diameter of tree
DBH	Diameter at breast height
ES	Early-successional species
FAO	Food and Agriculture Organisation
g_s	Stomatal conductance for water vapour (mmol H ₂ O m ⁻² s ⁻¹)
GtCO ₂	Gigatons of carbon dioxide
h	Total height of tree
IPCC	Intergovernmental Panel on Climate Change
J_{max}	Maximum rate of photosynthesis (μmol m ⁻² s ⁻¹)
LCP	Light compensation point
LMA	Leaf mass per area (g m ⁻²)
LS	Late-successional species
LVTf	Lake Victorian transitional forest
MAT	Mean annual temperature
N	Nitrogen
NNP	Nyungwe National Park
PNV	Potential Natural Vegetation
PPFD	Photosynthetic photon flux density (μmol photons m ⁻² s ⁻¹)
R_d	Leaf dark respiration rate (μmol CO ₂ m ⁻² s ⁻¹)
RGR	Relative growth rate
Rwanda TREE	Tropical Elevation Gradient Experiment in Rwanda
SI	Shade-intolerant species
ST	Shade-tolerant species
T_{air}	Air temperature (°C)
TMF	Tropical Montane Forest
T_{optA}	Optimum temperature for net photosynthesis (°C)
V_{cmax}	Maximum velocity of Rubisco carboxylation (μmol m ⁻² s ⁻¹)
VECEA	Vegetation and Climate change in East Africa
VPD	Vapor pressure deficit (kPa)

1 General introduction

Forests play a fundamental role in sustaining life by providing a wide range of ecosystem services such as goods (e.g. timber, firewood, food and medicine), support functions (e.g. genetic resources, habitat for biodiversity, soil formation), regulating functions (e.g. water flow, erosion control, filtration of nutrients and pollution) and cultural benefits (e.g. recreation, aesthetic, spiritual and religious values; Millennium Ecosystem Assessment, 2005). These services are essential not only for sustaining the livelihood of billions of people, but also for preserving global biodiversity and regulating key biogeochemical cycles, particularly water and carbon cycles, which significantly influences the global climate and potentially mitigate global climate change (Cone et al., 2013; Joy & Death, 2013; Pan et al., 2011; Publicover et al., 2021). Climate is closely linked to the global carbon cycle, as the fluxes of carbon between the atmosphere, hydrosphere, and terrestrial biosphere regulate atmospheric CO₂ concentrations, a greenhouse gas trapping outgoing infrared radiation. This alters Earth's energy balance and drives large-scale climate dynamics (Cox, et al., 2000; Houghton 2003; Masson-Delmotte et al., 2021).

Terrestrial ecosystems have served as a major net carbon sink, removing an average of approximately 10 gigatons of CO₂ (Gt CO₂, corresponding to 2.7 Gt carbon) per year over the past four decades (IPCC, 2021). Despite considerable interannual variations, forest alone account for about 5.5±8.1 Gt CO₂ annually of this sink, highlighting their importance in the global carbon cycle (Gibbs et al., 2025). Forests also play a key role in the hydrological cycle by regulating the balance between evapotranspiration and runoff (Sheil, 2018). Thus, in areas which largely depend on natural precipitation for agriculture, regional forest cover is essential in the regulation of water availability (FAO, 2021). While, forests help regulate the climate, they are also shaped by it, as climate conditions affect forest health, species composition, and geographical distribution (Gibson et al., 2011; Ramsfield et al., 2016).

The climatic and environmental requirements for tree growth vary significantly, with temperature and precipitation being the primary drivers. Trees respond to environmental conditions through their structural and functional traits, such as wood density, leaf mass per area (LMA), maximum tree height, rooting depth, and leaf phenology, which collectively shape both the landscape structure and regional biodiversity. These traits, in turn influences the ecosystem services that forests provide (Lavorel et al., 2011), as illustrated in Figure 1.

Climate is the dominant factor determining forest distribution at global and continental scales (Pan et al., 2013), largely influenced by latitude, altitude, and proximity to the sea, collectively defining broad ecosystem types, or biomes, such as tropical forests. Local forest structure and composition are further shaped by topography, soil properties, species interactions, and disturbance regimes (Pan et al., 2013). Within the tropical forest biome, diverse woodland types exist—including montane rainforests, lowland rainforests, and seasonal forests with distinct dry periods—often with transitional forms in between. Understanding how these forests respond to rapid shifts in temperature and precipitation is key to predicting their resilience and future under climate change (Millar et al., 2007).

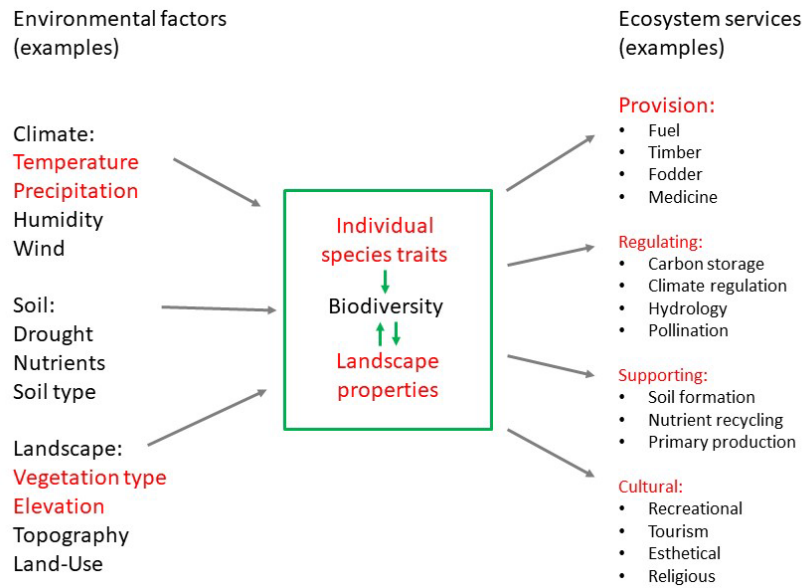


Figure 1. Conceptual figure representing how biodiversity is influenced by environmental factors, the landscape and species properties which influence the provision of ecosystem services. Factors and services marked in red are particularly discussed in this thesis.

In light of the pressing challenges posed by deforestation and climate change, there is an urgent need for comprehensive studies regarding how trees in the African tropical highland forests can be restored, how they respond to various climate change scenarios, and the ecosystem services they can provide. Many African nations have demonstrated strong commitments to large-scale restoration initiatives, such as the Bonn Challenge, which aims to restore 150 million hectares of degraded and deforested land by 2020 and 350 million hectares by 2030 (Cuni-Sanchez et al., 2021). Rwanda is among the nations committed to the Bonn Challenges, with national policies, emphasize biodiversity conservation, sustainable wood supply, and climate resilience (Ministry of Lands and Forestry, 2018). Achieving these goals requires the identification of climate-resilient native species well-suited to local conditions, along with the adoption of diverse site-specific restoration approaches rather than reliance on exotic monocultures. Aligning species selection with national forest and climate policies will help build adaptive restoration models that support both ecological integrity and community well-being (e.g. Mansourian and Berrahmouni, 2021).

This study will explore the growth and mortality of trees from this biome, examining shifts in tree community composition as well as how different species contribute to ecosystem services. By understanding these dynamics, the research aims to inform strategies for selecting resilient species for tree plantations, ensuring sustainable forestry practices that can withstand future climate uncertainties and support local livelihoods and conservation efforts. The suitability of planting a tree species in a certain location is dependent on how well it is adapted to the environment and the demand for ecosystem services of that site. The assessment of the relationship between the livelihood perspective and the global perspective of ecosystem services, was therefore based on the conceptual model in Figure 1 linking: (i) environmental

requirements; (ii) plant traits and (iii) ecosystem services. Particular attention is given to environmental factors such as temperature, precipitation, vegetation type, and elevation.

1.1 Tropical forests and their threats

Tropical forests are among the most productive ecosystems on Earth, estimated to account for more than one-third of the terrestrial gross primary productivity (Pan et al., 2024) and contain one-half of carbon stored in terrestrial vegetation (Erb et al., 2018). Therefore, small changes in productivity and carbon storage within the tropical forest biome can potentially lead to major global impacts on global greenhouse gas concentrations with implications for the climate (Lewis, 2006). In addition to their impact on climate, tropical forests host at least two-thirds of the terrestrial species diversity and provide significant benefits through the provision of economic goods and services (Bradshaw et al., 2009; França et al., 2020; Gardner et al., 2009; Lewis 2006; Nair, 2007; Seymour & Busch 2016; Singh & Sharma 2009). However, deforestation and climate change threaten these values, posing a critical risk to climate stability, biodiversity and provisions of ecosystem services (Fearnside, 1999; Mooney et al., 2009; Ometto et al., 2022; Sintayehu, 2018).

1.1.1 Deforestation

According to the FAO's Global Forest Resources Assessment (2020), more than 420 million hectares of forest were lost to deforestation between 1990 and 2020, with over 90% of this loss occurring in tropical regions. However, due to afforestation and natural forest regrowth — e.g., on abandoned agricultural land — the net reduction in global forest area was smaller, amounting to approximately 177 million hectares (Table 1). While annual deforestation rates declined over the period, this positive trend slowed in the past decade. However, forest loss in Africa continued to increase, whereas Asia recorded the largest net forest gain between 2010 and 2020, but with considerable variation among countries (FAO, 2020). It is imperative that we address this issue to ensure the provision of forest services to future generations. Commercial agriculture (primarily cattle ranching and cultivation of soya bean and oil palm) comprised 40% of tropical deforestation between 2000 and 2010 while local subsistence agriculture accounted for 33%. The dominant drivers of deforestation vary by region: large-scale cattle ranching and soybean production in South America, commercial agriculture in Asia, and subsistence farming and local market-oriented agriculture in Africa (Jayathilake et al., 2021; Masolele et al., 2024). Despite these losses, some primary tropical forests transition into secondary forests through natural regeneration or plantation establishment on abandoned land, helping to mitigate some of the biodiversity and ecosystem services losses (Chazdon, 2014).

Tropical montane forests (TMFs), typically found at elevations above 1,000 meters above sea level (though definitions may vary), are ecologically important ecosystems that offer vital services such as water regulation, carbon storage, and habitat for unique and often endemic species. Although they represent only around 8% of the total pan-tropical forest area (Spracklen & Righelato, 2014), TMFs are increasingly at risk due to deforestation. In eastern Africa, TMFs and their transitional zones comprise much of the remaining old-growth forest (Cuni-Sanchez et al., 2021), making them a key focus of this thesis.

Table 1. Total forest area and plantation forest area ($\times 1000$ ha) by region and subregion between 1990 and 2020, including annual changes in forest and plantation area, the percentage of plantation forest relative to total forest area, and the proportion of exotic species in plantations as of 2020 (compiled from FAO 2020).

Region/Subregion	Total forest			Planted forest				
	Area (1000 ha)		% net change	Area (1000 ha)		% annual change	forest area	% exotic species
	1990	2020		1990	2020			
Eastern and Southern Africa	346 034	295 778	-14.5	6 161	7 139	0.5	2.4	74
Northern Africa	39 926	35 151	-12.0	1 383	1 983	1.4	5.6	50
Western and Central Africa	356 842	305 710	-14.3	956	2 269	4.6	0.7	74
Total Africa	742 801	636 639	-14.3	8 500	11 390	1.1	1.8	70
East Asia	209 906	271 403	29.3	57 483	98 139	2.4	36.2	31
South and Southeast Asia	326 511	296 047	-9.3	12 949	31 469	4.8	10.6	40
Western and Central Asia	48 976	55 237	12.8	3 757	5 621	1.7	10.2	5
Total Asia	585 393	622 687	6.4	74 188	135 230	2.7	21.7	32
Europe excl. Russian Fed.	185 369	202 150	9.1	41 743	55 004	1.1	27.2	
Russian Fed.	808 950	815 311	0.8	12 651	18 880	1.6	2.3	
Total Europe	994 319	1 017 461	2.3	54 394	73 884	1.2	7.3	77
Caribbean	5 961	7 889	32.3	479	851	2.6	10.8	32
Central America	28 002	22 404	-20.0	74	391	14.3	1.7	18
North America	721 317	722 417	0.2	22 596	45 785	3.4	6.3	2
Total North and Central America	755 279	752 710	-0.3	23 149	47 027	3.4	6.2	4
Total Oceania	184 974	185 248	0.1	2 784	4 812	2.4	2.6	78
Total South America	973 666	844 186	-13.3	7 046	20 245	6.2	2.4	97
World	4 236 433	4 058 931	-4.2	170 061	292 587	2.4	7.2	44

Historically, most deforestation occurred in lowland tropical forests, but tropical montane forests (TMFs) are now facing equally severe and in some areas, more rapid loss (Barlow et al., 2016; Brancalion et al., 2019). Drivers of TMF loss include conversion to agriculture, logging, and expansion of monoculture plantations (e.g., tea, coffee, palm oil), leading to biodiversity loss and degraded ecosystem services (Edwards et al., 2019; Koh & Wilcove, 2008; McDonald et al., 2020; Montero et al., 2024; Sodhi et al., 2010; Vanbergen & Insect Pollinators Initiative, 2013; Vandermeer et al., 2010). Although some abandoned land regenerates, secondary forests are often less diverse, ecologically complex and contain less carbon than original montane forests (Hernandez Marentes et al., 2022; Nyirambangutse et al., 2017; Santoro et al., 2023).

In Africa, approximately 5% of TMF cover was lost between 2001 and 2018, with the greatest absolute losses in the Democratic Republic of Congo, Uganda, and Ethiopia (Cuni-Sanchez et al., 2021). In relative terms, Mozambique and Côte d'Ivoire experienced especially severe declines, losing over 20% of their remaining TMF area during this period.

1.1.2 Climate change impacts

Tropical forests are threatened not only by deforestation, but also from global warming which alter key growth-regulating factors such as temperature, precipitation, and soil moisture (Wagner et al., 2014). These climate driven changes potentially impact growth, mortality and thus also forest structure, species composition, and ecosystem functioning (Clark et al., 2016;

Dale et al., 2001; Grimm et al., 2013; Lindner et al., 2010; Menezes-Silva et al., 2019; Weber and Flannigan, 1997). High temperatures potentially reduce tree growth rates (Anderegg et al., 2015; Clark et al., 2003; Feeley et al., 2007; Vlam et al., 2014) and, tropical species are predicted to further shift their geographical distributions towards cooler latitudes and elevations (Thuiller, 2007) leading to range contractions and potential local extinctions, especially among high-elevation specialists (Chen et al., 2011; Fadrique et al., 2018; Feeley et al., 2013). TMFs are particularly vulnerable due to their climatic sensitivity and restricted elevational ranges. Changes in cloud cover and moisture availability may further disrupt these ecosystems, reducing their capacity to store carbon and support biodiversity (Helmer et al., 2019 & 2025; Still et al., 1999). At higher elevation, increased temperature leads to increased growth but with lower competitiveness of high-elevation species and species that were previously abundant at lower, hotter elevations will shift towards cooler latitudes and high elevation. Such changes are determined thermophilisation (Feeley et al., 2020).

1.2 Forest futures: secondary succession, plantations and species composition

Disturbances in tropical forests — such as logging, agricultural expansion, fire, and hurricanes — have significantly altered successional dynamics and species composition, and some of these changes are expected to be further intensified by climate change (Anderson-Teixeira et al., 2013; Brodie et al., 2012; Dale et al., 2001; Lewis, 2006; Malhi et al., 2014; McDowell et al., 2020). These shifts often favour early-successional (Pioneer) species, which can hinder or delay the recovery of old-growth forest characteristics. Effective restoration strategies must therefore account for forest successional processes, species ecological traits and their resilience to future climate conditions (Chazdon, 2008; Lewis et al., 2015). Understanding these interactions is key to supporting biodiversity and ecosystem function in a changing climate.

Following severe natural or anthropogenic disturbances, forests undergo successional transition that influence their resilience, with trajectories differing between primary or secondary forests (Contreras-Hermosilla, 2000; Hilmers et al., 2018). Finegan (1996) identified three main successional stages in forest recovery. The first stage involves the colonisation of herbs, shrubs, and climbers, and early-successional tree species. In the second stage, short-lived early-successional trees dominate the canopy of secondary forests. The third stage, characterised by primary forests, is dominated by long-lived late-successional species thriving in minimally disturbed ecosystems. The primary forest still cover about 1.1 billion ha (34% of the world's forests) but have declined by over 80 million hectares between 1990 and 2020 (FAO, 2020).

Secondary forests, which regenerate after disturbance, feature a more dynamic structure, typically composed of three canopy layers: canopy, sub-canopy, and understory. The understory serves as a recruitment pool for species that eventually move into the upper layers (Peña-Claros, 2003). These forests are initially dominated by early-successional species — fast-growing, light-demanding trees with low wood density. However, they generally store less carbon than forests dominated by late-successional species, which characterize old-growth or primary forests (Landau, 2004; Nyirambangutse et al., 2017; Swaine & Whitmore, 1988). The late-successional species are often slow-growing with high wood density and shade tolerant, which has been explained by two main hypotheses: (i) the carbon gain and (ii) stress tolerance

hypotheses (Valladares & Niinemets, 2008). The carbon gain hypothesis suggests that tolerance arises from traits enhancing carbon acquisition and minimizing loss in low light, such as high photosynthetic quantum yield, low respiration and light compensation point (LCP), low leaf mass per area (LMA), and greater biomass allocation to light-capturing structures (Baltzer & Thomas 2007; Givnish, 1988; Kitajima, 1994; Lusk & Pozo 2002; Niinemets 2006; Luttge, 2008; Valladares & Niinemets, 2008). In contrast, the stress tolerance hypothesis links shade tolerance to traits conferring resistance to biotic and abiotic stress, including high defence compound levels, wood density, and LMA (Gommers et al., 2013; Kitajima 1994;). Both hypotheses likely contribute to explaining shade tolerance.

Over time, successional shifts in species composition from early- to late successional species will influence ecosystem services such as carbon storage and water regulation, thereby affecting the forest's role in climate mitigation. Secondary forests characterised by natural regeneration now make up much of the remaining native vegetation in many tropical regions and are expanding globally (Chazdon, 2014; Malhi et al., 2014). However, it remains unclear whether climate change will promote or hinder this expansion.

Planted forests, in contrast to secondary forests, are composed of trees that have been established through planting and/or deliberate seeding, with planted or seeded trees making up more than 50 percent of the growing stock at maturity (FAO, 2012). Globally, planted forests covered approximately 294 million hectares, accounting for 7% of the world's forest area in 2020 (Table 1; FAO, 2020). Between 1990 and 2020, Asia recorded the highest portion of planted forest area, whereas Africa as a continent still has relatively low share of planted forest (Table 1).

Planted forests are composed of both native and exotic tree species, often established for timber production. Globally, 44% of plantations are dominated by exotic tree species but there is significant regional variation – for example plantations in sub-Saharan Africa contain an average of 74% exotic species (Table 1). These are typically fast-growing tree species valued for roundwood quality. In contrast, native species are less used, partly due to perception of slower growth (Carnus et al., 2006; Payn et al., 2015; West, 2014). However, recent efforts increasingly promote native species to enhance biodiversity, ecosystem services, and climate resilience (Bremer & Farley, 2010; Galhena et al., 2013; Thomas et al., 2014). Native species plantations tend to resemble natural forests more closely and support richer biodiversity (Brockerhoff et al., 2008; Stephens & Wagner, 2007). Multi-species native plantations may also be more resilient to stressors and beneficial for surrounding agriculture (Aguirre-Gutiérrez et al., 2022; Brasier, 2008; Sena et al., 2014; Woodcock et al., 2017) and improved hydrological performance (Reed et al., 2020). However, the broader adoption of native species remains limited due to knowledge gaps on their climate tolerance, and growth performance, scarcity of quality planting material, and perceived risk of planting failures under changing conditions – factors that encouraged reliance on well-tested exotic species (Aitken et al., 2008; Forrester et al., 2005; Thomas et al., 2014). Nonetheless, native species are increasingly recognized for their dual value in timber production and biodiversity conservation, and for their potential in climate change adaptation and mitigation (Thomas et al., 2014).

Rwanda is a typical example of a country where exotic species dominate planted forests. Most forest products, fuelwood, timber, and building poles, are sourced from plantations, woodlots, and agroforestry, as natural forests are protected as national parks or reserves (Nduwamungu, 2011). Since the 1970s, the government has invested heavily in tree planting, primarily using fast-growing exotic species to protect fragile landscapes, buffer natural forests, and meet rising demand for wood products. Many of these plantations were established with external support from institutions such as the World Bank, African Development Bank, European Union, and several European countries (Nduwamungu, 2011). *Eucalyptus* species dominate these plantations, while native species have been largely undervalued and underused (Mugabowindekwe et al., 2022; Ndayambaje et al., 2013). Recent surveys by the Ministry of Environment (2019) show that forests cover about 30.4% of Rwanda's land area, with planted forests making up 53.5% (16% of national land) and natural montane forests about 18.1% (5.5%). The remaining forest cover consists of wooded savannah and bamboo vegetation (Table 2). Despite their smaller extent, natural montane forests have been estimated to store significantly more carbon, 51.4% of above-ground carbon, compared to just 9.9% in planted forests, contributing to an estimated 14.3 ± 2.8 Tg of above-ground carbon stocks on a national scale (Mugabowindekwe et al., 2022).

The Southern Province of Rwanda has the largest area of planted forests. In addition to various *Eucalyptus* species, other commonly planted exotics include *Pinus patula*, *Cupressus lusitanica*, *Acacia melanoxylon*, *A. mearnsii*, *Callitris* spp., *Grevillea robusta*, *Casuarina* spp., *Cedrela serrata*, *Alnus acuminata*, *Maesopsis eminii*, *Senna spectabilis*, *Senna siamea*, *Leucaena leucocephala*, and *Calliandra calothyrsus* (Table 3; Mihigo, 1999; Nduwamungu, 2011). In contrast, only a few native species—such as *Croton megalocarpus*, *Afrocarpus falcatus*, *Markhamia lutea*, and *Polyscias fulva*—have been planted in significant numbers.

To address this imbalance, the Rwandan government has committed to promoting native tree species in its plantation programs (Ministry of Lands and Forestry, 2017). However, there is limited knowledge on the ecological suitability of many native species across Rwanda's diverse agro-ecological zones. There is an urgent need for information on species performance under current and projected climate conditions, especially in the context of increasing temperatures and more frequent droughts.

This strategy is now embedded in national reforestation policies, which set targets to include 30% native trees and 20% fruit trees in annually plantations (Ministry of Natural Resources, 2014; Ministry of Lands and Forestry, 2017). However, progress is constrained by knowledge gaps that hinder effective, climate-resilient species selection and their capacity to deliver key ecosystem services under future climate scenarios. Bridging these gaps is essential for informed, adaptive forest management.

Table 2. Area of forest types in Rwanda in 2019. Compiled from Ministry of Environment (2019).

Forest type	Forest area (ha)					Total
	Province Name					
	Kigali city	East	North	South	West	
Bamboo	133	135	144	62	141	613
Planted forest	12 379	64 649	73 791	132 683	103 924	387 425
Natural montane forest		7 085	11 740	43 014	69 012	130 850
Wooden savannah		161 832		10	1	161 843
Total	12 641	274 630	85 688	177 537	174 199	724 695

Table 3. Distribution of tree species forest plantations in Rwanda by ownership type in 1990 (Mihigo, 1999)

Tree species	Plantation area							
	Ownership							
	State ^a		Institutional ^b		Private ^c		Total	
	ha	%	ha	%	ha	%	ha	%
<i>Eucalyptus</i> spp.	30 600	50	69 370	70	61 040	70	161 010	65
<i>Pinus patula</i>	18 360	30	9 910	10	4 360	5	3 230	13
<i>Cupressus lusitanica</i>	4 900	8	7 930	8	8 720	10	21 550	9
<i>Acacia melanoxydon</i>	4 280	7	6 940	7	–	–	11 220	5
<i>Callitris</i> spp.	1 830	3	2 970	3	–	–	4 800	2
<i>Grevillea robusta</i>	–	–	–	–	4 360	5	4 360	2
<i>Casuarina</i> spp.	1 230	2	1 980	2	–	–	3 210	1
Others	–	–	–	–	8 720	10	8 720	3
Total	61 200	100	99 100	100	87 200	100	247 500	100

^aState forests include all forest plantations established through government or donor-funded projects, as well as those planted on government land during national tree-planting days and communal work activities.

^bInstitutional forests are those owned by such institutions as churches, educational institutions, and local districts

^cPrivate plantations include individual woodlots and plantations by individuals, private enterprises such as tea factories

2 Literature review

2.1 Climate change and sensitivity of tropical trees

Human-driven climate change, primarily caused by the burning of fossil fuels and large-scale land-use changes such as deforestation, is resulting in widespread environmental impacts (IPCC, 2021). While the most pronounced warming is expected in boreal regions, tropical areas are projected to experience a rise in the frequency, length and intensity of extreme weather events, including heatwaves, storms, and droughts (Diffenbaugh et al., 2017; Perkins-Kirkpatrick & Gibson, 2017). Since the pre-industrial period (1850–1900) until 2020, the global average temperature has risen by 1.09°C and is expected to further increase, reaching 1.4°C to 4.4°C by 2100, depending on CO₂ emission scenarios (IPCC, 2021).

Forest growth responses to climate change will likely vary significantly across biomes and forest types (Hansen et al., 2001). In boreal regions, forests may experience modest increases in growth, particularly where moderate warming extends the growing season, improves

temperature conditions for photosynthesis, and enhances overall productivity (D'Orangeville et al., 2018; Reich et al., 2022). In these regions, coniferous tree species often show increased productivity under warming scenarios (Briceño-Elizondo et al., 2006; Bugmann et al., 2001; Lasch et al., 2002). In contrast, tropical and subtropical forests, though expected to experience less warming than higher latitudes, may be more vulnerable to temperature increases due to their adaptation to historically stable thermal conditions (Doughty and Goulden, 2008; Ghalambor et al., 2006; Janzen, 1967). This thermal specialization may limit their capacity for acclimation compared to plants from more seasonal regions (Crous et al., 2022; Cunningham and Read, 2002; Way and Oren, 2010) and temperatures in these regions are likely to surpass the optimal range for photosynthesis more frequently, leading to reduced growth potential (Mau et al., 2018). In addition, tropical regions are projected to face increasingly frequent and severe drought events over the 21st century (Chadwick et al., 2016; Malhi et al., 2008). Climate models suggest that the tropics will undergo a combination of warming and drying, accompanied by more extreme heat, drought, and heavy rainfall (Allan and Soden, 2008; Cusack et al., 2016; Giorgi et al., 2014; Joetzjer et al., 2013). The Coupled Model Intercomparison Project Phase 6 (CMIP6) provides the latest generation of global climate model simulations, offering standardized experiments for historical climate reconstructions and future climate projections under different socioeconomic and emissions pathways (Eyring et al., 2016). Using the CMIP6 projection under the SSP2-4.5 scenario, which represents an intermediate “middle-of-the-road” development pathway where greenhouse gas emissions peak mid-century before gradually declining. However, the reductions are not fast enough to meet the Paris Agreement’s 1.5 °C or 2 °C targets. By 2100, this pathway results in a radiative forcing of 4.5 W/m² and associated increase in global mean temperatures of approximately 2.4°C. By contrast, the SSP5-8.5 scenario represents a fossil fuel–intensive, high-emissions pathway. Under this scenario, radiative forcing is projected to reach 8.5 W/m² by 2100, leading to more extreme warming up to 4.4 °C (Ayugi et al., 2021; IPCC 2021).

In Rwanda, the average temperature increased by approximately 0.33°C per decade between 1964 and 2010 (Haggag et al., 2016). CMIP6-based projections indicate further warming in Rwanda compared to the reference period 1995-2014: by mid-century (2040-2059), mean temperatures are expected to rise by about 1.3°C under SSP2-4.5 and 1.8°C under SSP5-8.5 scenarios. By the late century (2080–2100), projected increases reach approximately 2.2°C for SSP2-4.5 and 4.1°C for SSP5-8.5 (World Bank Group, 2025).

These changes in temperature will likely reduce photosynthesis and growth of both trees and agriculture crops, lower aboveground biomass, increase tree mortality and may alter species composition, ultimately diminishing net primary productivity (NPP) and the tropical forest carbon sink (Austin et al., 2020; Manzi et al., 2025; Pau et al., 2018; Vårhammar et al., 2015; Yu et al., 2021). However, rising atmospheric CO₂ levels may at least partially offset these impacts by enhancing photosynthesis and growth, a phenomenon known as CO₂ fertilization, which could increase NPP by average of 16% (5-20%) per 100 ppm (Norby et al., 2005; Piao et al., 2013). The net effects of climate change on tropical forests therefore remain uncertain.

2.2 Temperature and drought sensitivity of tropical trees and forests

Recent studies show that warming and drying trends have weakened the Amazon carbon sink over a few decades (Brienen et al., 2015), with similar signs now emerging in the Congo Basin (Hubau et al., 2020). El Niño years further amplify these effects, reducing tree growth and increasing mortality across tropical regions (Baumann et al., 2021 & 2022; Clark et al., 2003; Lewis et al., 2011; Rifai et al., 2018). Heat and drought often co-occur and interact, intensifying stress on trees (Baumann et al., 2021 & 2022; Jung et al., 2017; Zhao et al., 2013). However, the specific impact of warming remains unclear due to this co-variation (Docherty et al., 2022; Piao et al., 2020). While drought effects are well-studied through rain exclusion experiments (da Costa et al., 2010; Meir et al., 2014), large-scale warming experiments are lacking, limiting predictions about tropical carbon sink resilience.

2.2.1 Warming sensitivity of tropical trees and forests

Global meta-analyses indicate that warming generally stimulates photosynthesis and growth in cooler biomes but tends to reduce tropical tree growth (Crous et al., 2022; Lin et al., 2010; Way and Oren, 2010). However, responses in the tropics are variable — ranging from positive to negative — depending on species and location. This variation may be linked to differences in species native temperature ranges and the intensity of the warming treatments, with positive responses being more likely in species from cooler origins exposed to moderate warming. Also, the successional strategy of the trees may influence the sensitivity to warming.

Previous studies suggest that late-successional species are more sensitive to warming than early-successional species (Cheesman and Winter, 2013; Mujawamariya et al., 2023; Slot and Winter, 2018; Tarvainen et al., 2022; Vårhammar et al., 2015). Part of the reason can be that late-successional species, tend to have large leaves that dissipate heat poorly, and exhibit low transpiration cooling. These traits increase their vulnerability to heat stress, especially affecting photosynthesis negatively (Tarvainen et al., 2022) and this can be translated into lower growth rates.

2.3 Drought sensitivity

Drought significantly reduces tree growth in tropical forests, mainly through two mechanisms: carbon starvation caused by sustained stomatal closure and hydraulic failure due to strong negative pressure in the water conducting xylem tissue (McDowell et al., 2018; McDowell & Allen, 2015). Larger trees in tropical forests are especially vulnerable, with prolonged droughts leading to heightened mortality rates and a subsequent decline in above-ground carbon storage (De Meira Junior et al., 2020). An analysis of 100 long-term plots across six African countries, conducted through the AfriTRON network, found substantially decline in CO₂ uptake during the 2015–2016 El Niño. However, despite record heat and drought, old-growth tropical forests remained a net carbon sink (Bennett et al., 2021). These findings suggest that intact African tropical forests, mostly dominated by late-successional species, despite reductions in CO₂ uptake may be relatively resilient to extreme climate events. Some studies indicate that early-successional species are more vulnerable to drought than late-successional species (Pineda-García et al., 2013; Rahman et al., 2019). Their higher transpiration rates, lower embolism resistance, faster growth rate, lower water use efficiency and often shallower roots contribute

to higher drought mortality of early-successional species (Aleixo et al., 2019; Bennett et al., 2015a; Craine et al., 2012; da Costa et al., 2010; Feng et al., 2017; Funk et al., 2013; Meakem et al., 2018; Nepstad et al., 2007; Rowland et al., 2015). Soft wood in early-successional species further correlate with reduced resistance to hydraulic stress (Van Gelder et al., 2006), while denser wood in late-successional species typically are associated with higher tolerance to drought (Phillips et al., 2010; Poorter et al., 2010; Santiago et al., 2004; Meinzer, 2003). Further research is needed to clarify the contrasting responses of late-successional and early-successional species to warming and drought.

2.3.1 Implications for forest dynamics

Warming may have less immediate impact on high-elevation species still below their thermal limits, but it can give lower-elevation species a competitive advantage, driving upslope shifts in species distributions. This shift may disadvantage cooler-adapted species, as already observed in both montane forest in Andes and Africa (Cuni-Sanchez et al., 2024; Duque et al., 2015; Fadrique et al., 2018). However, due to the combined and variable impacts of warming and drought among early- and late-successional tropical trees the net effects remain unclear. Some studies find late-successional species more heat-sensitive (Mujawamariya et al., 2023; Tarvainen et al., 2022), while others report greater drought vulnerability in early-successional species (Aleixo et al., 2019; Feng et al., 2017). These mixed responses (Cheesman & Winter, 2013; Rahman et al., 2019) suggest that climate change could alter successional trajectories, species composition, and forest structure in different directions, with potential consequences for biodiversity and carbon storage. Such changes may have important implications for forest dynamics under changing climatic conditions (Aguirre-Gutiérrez et al., 2022; Feeley et al., 2012; Hu et al. 2024). Understanding this difference is critical in the perspective of the predicted rising frequency and intensity of droughts forecasted by climate models. Being fast-growing and short-lived, early-successional species may contribute to faster carbon uptake but lower long-term carbon storage (Aleixo et al., 2019; Nyirambangutse et al., 2017). The contrasting results show that large trees typically associated with late-successional stages, often show greater vulnerability to drought compared to smaller individuals (Meinzer et al., 1999; Nepstad et al., 2007; Phillips et al., 2010; Stahl et al., 2013; Uriarte et al., 2016). Similarly, large trees showed reduced growth during years with severe dry seasons, suggesting that water availability limits whole-tree carbon assimilation and storage making them more vulnerable to disease, or to carbon starvation (Phillips, et al., 2010). However, exceptions exist; for example, some large trees may access deeper soil moisture, which can buffer them against drought stress (Chitra-Tarak et al., 2021; Padilla et al., 2007)

2.4 Climate-Proofing Forests: Tree Species Selection for the Future

As described above, tropical forests play a key role in ecosystem functioning and human well-being but face serious threats such as deforestation, degradation, over-exploitation, monocultures, and climate change, with many species struggling to cope with rising temperatures (Hubau et al., 2020). Selecting tree species that tolerate heat and drought is essential to maintain ecosystem services and ensure forest resilience. Climate-proofing forests

demand a balance of ecological, economic, and practical factors to prioritize productive, resilient species.

2.4.1 Planted forest

Large-scale reforestation is gaining attraction for climate mitigation and CO₂ sequestration, supported by initiatives like the UN Decade on Ecosystem Restoration (Strassburg et al., 2020). However, poorly planned projects risk undermining biodiversity, resilience, and local livelihoods (Reed et al., 2016 & 2020). Traditional ecological knowledge (TEK), often excluded from reforestation planning, can inform better species selection and long-term sustainability (Reyes-García et al., 2019).

Planted forests worldwide include both exotic and native species, typically established through reforestation and afforestation efforts. Species selection is shaped by local conditions — such as climate and soil properties — as well as plantation goals, including timber, pulp, fuelwood production, erosion control, water regulation, recreation, and biodiversity conservation (Yang, 2009). Important selection criteria include growth rate, wood quality, pest and disease resistance, planting material availability, and long-term climate adaptability. While exotic species can thrive under a wide range of environmental conditions and support timber industries, their spread often threatens biodiversity, native ecosystems, and ecosystem service provision (Hartley, 2002; Mack et al., 2000). In addition to the lower support of local biodiversity, the exotic species may become invasive. Such examples are different *Pinus* species, that have become significant environmental challenges in regions like South Africa, New Zealand, and Australia (Pauchard et al., 2004; Richardson et al., 2008).

A way to better support different ecosystem services is to select native multipurpose trees (NMTs) which offer a wide range of benefits. They provide food, medicine, firewood, fodder, and income, while improving soil fertility, reducing erosion, retaining moisture (Leakey & Akinnifesi, 2008), and sequestering carbon (Atiojio et al., 2014).

2.4.2 Challenges and Regional Gaps

Despite their advantages, adoption of NMTs is hindered by limited knowledge of cultivation techniques, germination and growth performance, and climate sensitivity (Aitken et al., 2008; Leakey & Akinnifesi, 2008). Research has focused largely on West and Southern Africa, leaving the Albertine Rift (Rwanda, Burundi, DRC, Uganda) under-studied. In Rwanda, exotic species like *Eucalyptus* dominate, though some farmers use native species from surrounding forests (Bigirimana et al., 2012). While exotic trees have been historically favoured for reforestation in the tropics (Sands, 2013), recent studies show a preference for NMTs due to their broader benefits (Katayi et al., 2023). Both conservationists and policy makers are increasingly promoting native species to enhance ecosystem services, biodiversity, and resilience to environmental stressors (Bremer & Farley, 2010; Thomas et al., 2014).

2.5 Elevation gradient and warming effects on tree physiology

Understanding tree resilience to climate change requires insight into how temperature and moisture stress affect tropical species. Elevation gradients provide a useful approach to gain better understanding of how temperature influences trees under global warming (Malhi et al., 2010). Lower elevations are typically warmer and drier, while higher elevations are cooler and often wetter. Studies along elevation gradients may therefore offer valuable insight into how species and ecosystems may respond to a future warmer and drier climate (Sundqvist et al., 2013). The temperature shifts are however, accompanied by co-varying environmental factors such as cloud cover, solar radiation, vapor pressure deficit (VPD), wind exposure, and humidity (Metcalf et al., 2025). Together, these variables shape the microclimate, influencing species distribution, physiological stress, and ecosystem responses to warming (De Frenne et al., 2021; Lembrechts et al., 2019; Zellweger et al., 2018). A key challenge in using elevation gradients to study warming effects is species turnover (Sundqvist et al., 2013; Pescador et al., 2015; Gibson-Reinemer et al., 2015): different elevations host different species composition, making it difficult to separate differences in tree traits and functioning caused by adaptation from physiological acclimation (Freeman et al., 2018).

To improve our understanding of how warming impacts tropical tree physiology and functioning, more standardized, controlled studies are needed (Cavaleri et al., 2015; Chung et al., 2013; Slot & Winter (2016). Specifically, experiments should involve the same genotypes of tree species planted across elevation gradients. Such research would allow for clearer insights into physiological acclimation and community responses to global climate change (Sundqvist et al., 2013). Future studies should also consider differences among early-successional and late-successional species, as well as species native to different elevation ranges. Understanding these dynamics is essential for predicting species survival, growth patterns, and plant-climate feedback under future climate. Continued research also needs to identify plant traits for selecting native tree species based on their climate resilience, ecosystem service provision, and to develop management guidelines that support multifunctional landscapes and food security and support resilient restoration aligned with Rwanda's Forest Policy (Ministry of Lands and Forestry 2017 & 2018)

3 Key knowledge gaps and research needs

Projected increases in temperature and shifts in rainfall patterns are expected to affect the adaptability of tree species, their capacity for carbon storage and sequestration, and overall species competitiveness—ultimately altering tree community composition in tropical rainforests (Bonal et al., 2016). However, there is still limited knowledge altering how native tree species respond to climate warming, particularly in terms of their productivity, carbon stocks (Cuni-Sanchez et al., 2021; Lázaro-Lobo et al., 2025; Nyirambangutse et al., 2017; Salinas et al., 2021), suitability under ongoing climate change, and their contribution to key ecosystem services. In addition, field-based studies examining the response of native

Afromontane tree species to projected temperature increases, particularly those conducted along elevation gradients, remain scarce.

Earlier research along tropical elevation gradients have mainly focused on describing differences in trees and ecosystem traits within existing natural systems (Malhi et al., 2010), offering limited insight into tree acclimation potential or changes in community composition under rapid climate change. While the effects of climate change on tree growth and survival have been studied in intact forest monitoring plots (Chazdon et al., 2005; Clark et al., 2003; Clark, 2004; da Costa et al., 2010; Feeley et al., 2007; Lewis et al., 2009; Phillips et al., 2008 & 2010), few field-based experiments have tested tropical trees of the same genotype across varying temperatures, such as those found along elevation gradients. Some studies have shown that native species respond differently to temperature shifts across ecological settings (Körner, 2007; Malhi et al., 2010), yet the potential for native species to migrate into Afromontane habitats remains poorly understood. Common garden experiments have assessed the suitability of individual tree species (Pollastrini, 2020; Roloff et al., 2007; Showers, 2010; Walentowski et al., 2017), but often without evaluating their adaptability across different climatic regions or their broader ecosystem service contributions. Additional studies have explored species selection for urban environments (Li et al., 2011; Percival & Fraser, 2001; Percival et al., 2002, 2006; Yang, 2009) or abandoned farmland (Meng et al., 2021), while transplant experiments (e.g., Tito et al., 2021) typically focus on a single species and do not assess broader suitability across ecological gradients or ecosystem service impacts.

Furthermore, while some factors are known—such as limited availability of planting material, slower early growth of some native tree species, and a preference for fast-growing exotic species—there is still limited comprehensive understanding of the full range of ecological suitability, their ecosystem services, and institutional barriers that hinder the wider adoption of native species in Rwanda’s plantation programs. More research is needed on their traits to identify suitable species for specific locations, which could enhance land use management, increase yields, and strengthen climate resilience. While some studies have assessed crop adaptability across Rwanda’s agro-ecological zones (Verdoodt & van Ranst, 2003), most focus on native fruit trees or exotics, e.g., Bigirimana et al. (2016) on eight species and Zaongo et al. (2004) on seven *Eucalyptus* species. However, broader studies on native tree suitability across ecological regions are lacking. Since the 1970s, exotic species have been promoted through government and donor programs, while native species received less attention and investment (Ndayambaje et al., 2013). Recent policies to support native species remain unfulfilled, partly due to limited knowledge of their environmental requirements and climate resilience.

Tree species selection should consider ecosystem service contributions (provisioning, regulating, supporting, cultural) and environmental factors (elevation, climate, soil). Long-term suitability under future climate scenarios must also guide species choice (Yang, 2009), which is essential for forest productivity, biodiversity, and climate adaptation and mitigation.

4 Aims and hypotheses

The overall aims of this thesis project were to assess how common tropical upland tree species native to Central and East Africa:

- (i) will respond to warming considering their adaptation to different successional stages and elevation origin (Papers I -III),
- (ii) will contribute to different ecosystem services (Paper IV).

These aims were addressed in four papers: three of which are experimental studies (see Figure 2), while the fourth entails an analysis of literature data. While especially papers II and III encompass broader aims than this thesis, only the parts directly relevant to the thesis aims and hypotheses are treated here.

Paper I

The aim was to assess the effect of a warmer climate on tree growth and mortality and how this may affect tree community composition. Mixed-species plantations composed of 20 native tree species with contrasting successional strategies and climate origin, established along an elevation gradient, were used to test the following hypotheses:

- H1 Tree growth responses to a warmer climate are more positive (or less negative) in early than in late-successional tree species.
- H2 The warmer climate at lower elevation decreases tree growth in species with their central distribution in montane rainforests (> 2000 m a.s.l.) while it stimulates growth of species predominantly occurring in transitional rain forests (< 2000 m a.s.l.).
- H3 Mortality increases in a warmer climate, and this is more pronounced in high-elevation and late-successional species compared to lower-elevation and early successional tree species.
- H4 Interspecific variation in growth and mortality responses leads to altered tree community composition in a warmer climate, favouring lower-elevation and early-successional tree species.

Paper II

The aim was to explore how growth and photosynthesis of two tropical trees species respond to a warmer climate using the same elevation gradient as in in Paper I but with trees potted in uniform soil across all sites. The following specific hypothesis were tested:

- H1 Growth responses of potted trees agree with those grown in local soil - confirming responses to warming in the mixed-species plantations in Paper I.
- H2 Net photosynthesis rates are higher at the warmer site, particularly in early-successional species.

Paper III

The aim was to explore how photosynthesis, growth and biomass allocation in Afromontane species with contrasting shade tolerance respond to different radiation regimes (open sky, sparse or dense canopies). The study explored different traits to test the following hypothesis:

- H1 Shade tolerant species have a whole-plant biomass allocation strategy that maximizes light interception when grown in the understory, i.e., higher relative investment into branches and leaves.
- H2 Shade tolerant species have physiological leaf traits that allow for a more favourable leaf carbon balance in a low-light environment, i.e., lower respiration and light compensation point (LCP).
- H3 Shade tolerant species have leaf traits that cause high leaf temperature (i.e., low transpiration rates and large leaf size) and consequently high physiological heat stress under direct sun exposure.

The design of the study also allowed to evaluate how well late-successional species cope with high radiation and thus test the hypothesis that:

- H4 late-successional species are less tolerant to high radiation than early-successional species.

The last hypothesis is particularly relevant, as both successional groups in Paper I and II are planted under open sky.

Paper IV

The objectives of this study were:

- O1 To assess native tree species suitability for plantation in different climatic regions in Rwanda, considering both projected climate change and multi-functionality in agricultural landscapes.
- O2 To assess the contributions of different native tree species to different ecosystem services

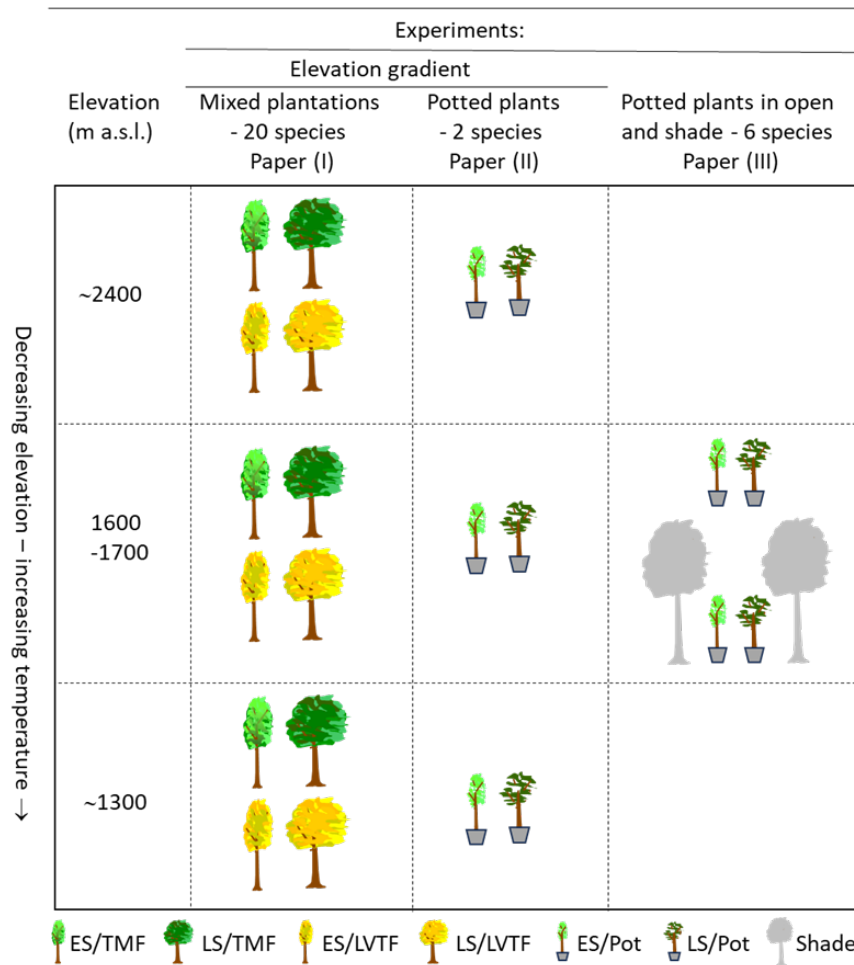


Figure 2. Outline of the three experiments using tree species of different origin (TMF, tropical montane rainforest > 2000 m a.s.l.; LVTF, Lake Victoria transitional rain forest, 1600-2000 m a.s.l.) and successional groups (ES, early-successional; LS, late-successional). The manipulation factors are elevation, soil (planted in local soil or in pots with soil from a common site) and openness (with and without shade). The species in the different experiments are shown in Table 4.

5 Material and methods

5.1 Overview of the studies and used plant material

The thesis comprises three complementary experimental studies (Figure 2) and one literature analysis, described in this section. Two experimental studies were undertaken at three sites (Figure 3) within the Tropical Elevation Experiment in Rwanda (www.rwandaTREE.com): (i) employing a mixed plantation of 20 native tree species planted in local soil (hereafter referred to as the *mixed tree plantation (- warming experiment)*; Paper I), and (ii) utilizing potted trees of two species (hereafter referred to as the *potted tree - warming experiment*; Paper II). The third experiment was conducted at one site using potted trees of six species grown under varying degrees of shade (hereafter referred to as the *potted tree - shade experiment*; Paper III). The species used in the two potted studies were a subset of those used in the mixed tree plantation - warming experiment (Table 4). In the *literature review*, an analysis was conducted on 81 tree species identified as potential components of Rwanda's natural vegetation (Paper IV). These species were systematically characterized based on various criteria such as climatic

regions, specific traits unique to each species, and the ecosystem services they can provide. The species used in the experimental studies were a subset of those used in the literature study.

The tree species included in the experiments were selected to represent important and common species in two eastern and central African forest types: tropical montane forest (TMF >2000 m a.s.l.) and Lake Victoria transitional forest (LVTF 1600–2000 m a.s.l.); see Figure 4 for species elevation ranges. From each forest type, species representing both early-succession (ES) and late-succession (LS) strategies were selected. In the mixed tree plantation experiment, species from all four groups were included in the following quantities: 5 ES/TMF, 5 LS/TMF, 6 ES/LVTF, and 4 LS/LVTF. The other experiments focused on early and late-successional species in the following quantities: 1 early-successional and 1 late-successional species in the Potted Tree - Warming Experiment, and 3 early-successional/shade intolerant and 3 late-successional/shade-tolerant species in the Potted Tree - Shade Experiment. All species are native to Eastern and Central Africa, with some Afrotropical and a few endemics to the Albertine rift. Eight of the species were among the 20 most common tree species in Nyungwe national park (NNP; Plumptre et al., 2002).

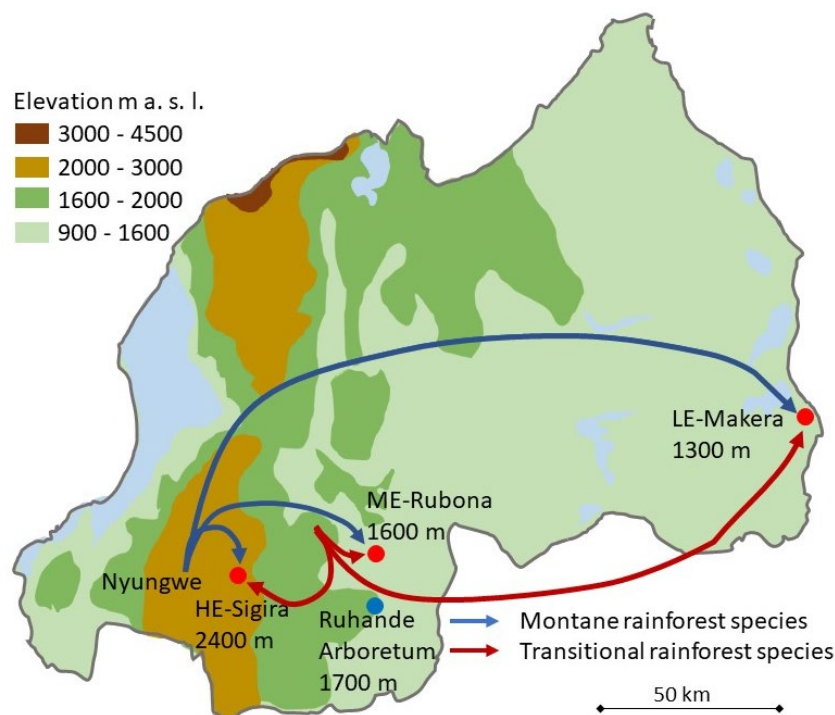


Figure 3. Topographic map of Rwanda showing the location of the Rwanda TREE sites (red dots) and the Ruhande arboretum (blue dot). The blue and red lines show the transfer of species origin from the Nyungwe montane rain forest (> 2000 m a.s.l.) and from the transitional rainforest (1600-2000 m a.s.l.), respectively to the Rwanda TREE sites. The studies in paper I and II were conducted at Sigira, Rubona and Makera sites, while the study in paper III was conducted at Ruhande arboretum.

Table 4. Taxonomy of species and their main forest type (FT) of origin, classification into successional group (SG), native distribution, classification into plant functional type, and in which paper they are studied. TMF, tropical montane forest (~ > 2000 m a. s. l.); LVTF, Lake Victoria transitional forest (~ 1600 - 2000 m a. s. l.); SG, successional group (ES, early, LS, late).

Code	Scientific name and author ¹	Family name ¹	FT ²	SG	Distribution ³	Plant Functional Type ⁴	Papers
Afa	<i>Afrocarpus falcatus</i> (Thunb.) C.N.Page	Podocarpaceae	TMF	LS	Eastern and Southern Africa	Evergreen	I
Agu	<i>Albizia gummifera</i> (J.F.Gmel.) C.A.Sm.	Fabaceae	LVTF	ES	Eastern and central Africa	Semi-deciduous	I
Bbr	<i>Bridelia brideliifolia</i> (Pax) Fedde	Euphorbiaceae/ Phyllanthaceae	TMF	ES	Eastern and Southern Africa	Semi-deciduous	I
Bmi	<i>Bridelia micrantha</i> (Hochst.) Baill	Euphorbiaceae/ Phyllanthaceae	LVTF	ES	Sub-Sahara Africa	Semi-deciduous	I
Cgo	<i>Chrysophyllum gorungosanum</i> Engl	Sapotaceae	LVTF	LS	Pantropical Africa mountains	Evergreen	I
Cgr	<i>Carapa grandiflora</i> Sprague	Meliaceae	TMF	LS	Albertine Rift and west Africa	Evergreen	I,III
Cme	<i>Croton megalocarpus</i> Hutch.	Euphorbiaceae	LVTF	ES	Pantropical Africa	Semi-deciduous	I,III
Dto	<i>Dombeya torrida</i> (J.F.Gmel.) Bamps, Synonym: <i>Dombeya goetzenii</i> K.Schum.	Sterculiaceae/ Malvaceae	LVTF	ES	East Africa mountains	Semi-deciduous	I,III
Eex	<i>Entandrophragma excelsum</i> (Dawe & Sprague) Sprague	Meliaceae	LVTF	LS	East Africa mountains	Evergreen	I,III
Fsa	<i>Faurea saligna</i> Harv	Proteaceae	TMF	LS	Eastern and Southern Africa	Evergreen	I
Fth	<i>Ficus thonningii</i> Blume	Moraceae	TMF	LS*	Pantropical	Semi-deciduous	I
Hma	<i>Harungana madagascariensis</i> Lam. ex Poir	Hypericaceae	LVTF	ES	Pantropical Africa	Semi-deciduous	I
Hmo	<i>Harungana montana</i> Spirlet	Hypericaceae	TMF	ES	Albertine Rift	Semi-deciduous	I, II
Mki	<i>Macaranga kilimandscharica</i> Pax	Euphorbiaceae	TMF	ES	East Africa mountains	Semi-deciduous	I
Mla	<i>Maesa lanceolata</i> (Henriq.) F. White	Myrsinaceae/ Primulaceae	TMF	ES	Sub-Sahara Africa and Madagascar	Semi-deciduous	I
Mlu	<i>Markhamia lutea</i> (Benth.) K.Schum	Bignoniaceae	LVTF	ES	Paleotropical	Evergreen	I
Nbu	<i>Newtonia buchananii</i> (Baker) G.C.C.Gilbert & Boutique	Fabaceae	LVTF	LS	Eastern and central Africa	Semi-deciduous	I
Paf	<i>Prunus africana</i> (Hook.f.) Kalkman	Rosaceae	TMF	LS	Sub-Sahara Africa and Madagascar	Evergreen	I
Pfu	<i>Polyscias fulva</i> (Hiern) Harms	Araliaceae	TMF	ES	Pantropical Africa	Semi-deciduous	I, III
Sgu	<i>Syzygium guineense</i> (Willd.) DC.	Myrtaceae	TMF	LS	Sub-Sahara Africa and Madagascar	Evergreen	I, II, III

¹Taxonomy information from the World Flora Online WFO (2024-01-31) at <http://www.worldfloraonline.org/>. For family names, both classic and Angiosperm Phylogeny Group (APG III) system are given when applicable; ²Forest type follows the Potential Natural Vegetation's by Kindt et al. (Kindt et al., 2014); ³ WFO (2024-01-31) at <http://www.worldfloraonline.org/>; ⁴ Semideciduous species drop variable amounts of leaf depending the severity of drought, but are rarely completely defoliated. Deciduousness information is from personal observation at experimental sites, or from various sources such as Fisher & Killmann (2008), useful tropical plants, world flora online and Mozambique flora webpages. The classification of species into successional groups delivered from various studies conducted in Rwanda, Ethiopia, Tanzania and Uganda as indicated in supplementary Table S4 of Paper I and associated list of references.

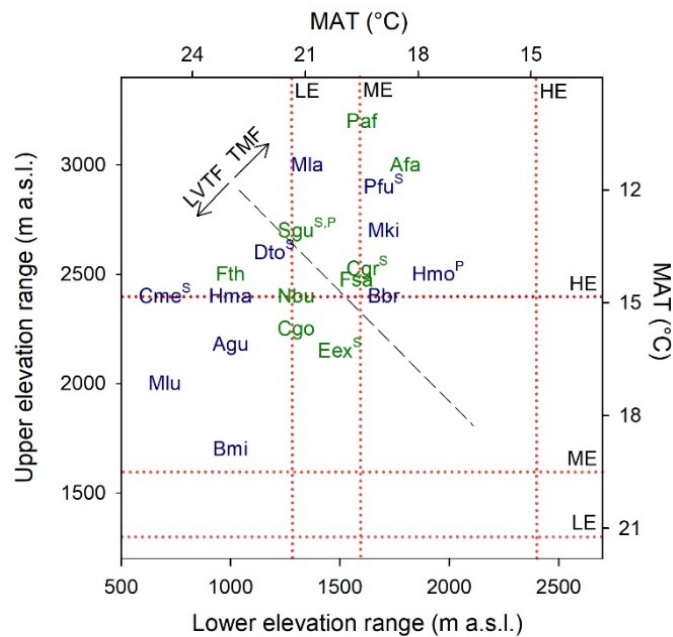


Figure 4. Commonly observed natural elevation ranges for the species used in the three experiments outlined in Figure 2. All species are used in the mixed tree plantation – warming experiment, while the species abbreviations with uppercase P and S are used in the potted tree – shade experiment (Paper II) and the potted tree warming experiment (Paper III), respectively. The diagonal dashed black line separates the species originating from the tropical montane forest (TMF) and the Lake Victoria transitional forest (LVTF). The elevation of the experimental sites (high – HE/Sigira; mid – ME/Rubona; low – LE/ Makera) are indicated by the dotted red lines. Species codes in blue and green are early- and late-successional species, respectively. MAT, mean annual temperature. For full species names, see Table 4 and more details, see paper I.

5.2 Experimental sites

The mixed tree plantations and potted tree – warming experiments were established as a field experiment along an elevation gradient in Rwanda. The high-elevation site (HE; 2400 m a.s.l.) is located at Sigira in Nyamagabe district (2°30'54" S; 29°23'44" E). The mid-elevation site (ME; 1600 m a.s.l.) is located at Rubona agricultural research station in Huye district (2°28'30" S; 29°46'49" E), c. 43 km south-east from Sigira site whereas the low-elevation site (LE; 1300 m a.s.l.) is located at Ibanda Makera in Kirehe district (2°6'31"S 155 ;30°51'16" E), hereafter denoted Makera (Table 4). The sites were located in different zones of Potential Natural Vegetation (Kindt et al., 2014): HE in the Afromontane tropical rainforest, referred to as the TMF or montane forest zone; ME in the Lake Victoria transitional rainforests, referred to as LVTF or transitional forest and LE in the evergreen and semi-evergreen bushland and thicket. Although many of the selected species are distributed in both montane and transitional forest, the HE site (Sigira) is considered as the control site in this experiment since today's remaining natural forests are predominantly montane and all species except one can be found at >2000 m elevation (Figure 4). Furthermore 18 out of 20 species used in the mixed tree plantation warming experiment naturally grow in the neighbouring NNP, ranging from 2950 down to 1600 m a.s.l. (Fischer and Killmann, 2008; Nyirambangutse et al., 2017). With the HE sites as control, the ME (Rubona) and LE (Makera) sites represent two different warming scenarios.

5.3 Weather and soil conditions at experimental sites

Ambient air temperature, relative humidity, precipitation, and solar radiation were recorded from start of the experiments at all sites at frequency of 30 minutes (Table 4). The mean annual temperatures (MAT), mean daytime temperature and extreme temperatures (expressed as 99%ile) at the different sites within the mixed tree plantations and potted tree – warming experiments were 14.6/17.1/23.1°C at HE-site, 20.0/22.4/28.4 °C at ME-site, and 20.6/24.0/31.2°C at LE-site (Table 5). The corresponding temperatures at Ruhande Arboretum where the potted tree -shade experiment was conducted, were 19.5/21.1/24.1 °C. The sites along the elevation gradient exhibit substantial differences in mean annual precipitation (MAP), with a progressive decrease from the HE-site (Sigira, approximately 2100 mm) to the ME-site (Rubona, approximately 1700 mm) and the LE-site (Makera, approximately 1100 mm). Despite this, the relative seasonal distribution of precipitation was consistent across all sites, with the highest rainfall occurring from March to May and a dry period typically lasting for about two months from June to August. Solar radiation levels were comparable at the ME and LE sites, whereas the HE-site received slightly less radiation, possibly due to higher cloudiness. At the Arboretum, the long-term annual precipitation was approximately 1200 mm, although this varied by several hundred millimeters between years (Table 5).

The Sigira (HE) site is located in a region dominated by ultisols with patches of inceptisols (Nzeyimana et al., 2014) developed on quartzite schist, mica schist, schist, and granite as parent material (Verdoodt Ann, 2003). The Central-South region, where Rubona (ME) and Ruhande Arboretum (located in Central-South region) are located is dominated by oxisols (Nzeyimana et al., 2014) also known as ferralsols (Nsabimana et al., 2009; Rwibasira et al., 2021) developed from Precambrian phyllitic rocks seated in the roof of a granite batholith leading to red brown ferrallitic soil (Moeyersons, 2003) whereas the South-East region, where Ibanda Makera (LE) is located, is dominated by entisols with patches of oxisols, inceptisols and vertisols (Nzeyimana et al., 2014). The soil texture along the elevation gradient varied also across sites. At the high-elevation (HE) site, the mineral topsoil consisted of 36% sand, 20% silt, and 44% clay; at the mid-elevation (ME) site, 56% sand, 6.5% silt, and 37% clay; and at the low-elevation (LE) site, 41% sand, 26% silt, and 33% clay (Paper I). Soil pH (water) was 4.2 at the HE site and increased by approximately one unit with each step down the gradient and at the Ruhande Arboretum it averaged to 5 (Paper I; Nsabimana et al., 2008).

5.4 Experimental design

5.4.1 Mixed tree plantation – warming experiment

Before establishing plantations, all existing vegetation was cleared, and large roots were extracted. Each site was divided into 18 plots, each 15 m x 15 m, with 2.5 m paths between them, covering a total area of 50 m x 102.5 m (Figure 5). Within each plot, 100 trees of 20 different species were planted with a 1.5 m x 1.5 m spacing and randomly positioned. This setup prepared the experiment for a full factorial experimental design, testing three water levels and two fertility levels across three replicates of each treatment combination. However, during the first two years of the experiment covered in this thesis, no treatment was applied. Instead, all 18 plots were used as replicates. Initial watering, irrespective of the subsequent planned

water treatment, was provided as needed until September and November 2019 when water and nutrient treatments commenced. Trees were propagated from seeds, cuttings, or seedlings, in poly-pots in a nursery at Rubona research station (near the ME site) in 2017. After 6 to 12 months in the nursery the trees were transplanted to the sites at the turn of the year 2017 and 2018, when the experiment commenced. Further details on tree propagation and initial sizes are provided in Paper I supplementary tables.

Table 5. Weather and other characteristics of experimental sites for the warming experiment in an elevation gradient (mixed tree plantations and potted trees) and the potted tree - shade experiment. Weather data are annual mean \pm SD. Rwanda TREE (Papers I & II). ESBT, Evergreen and semi-evergreen bushland and thicket, LVTF, Lake Victoria transitional forest, TMF, Tropical montane forest. MAT, mean annual temperature, T day, temperature at daylight, MAP, mean annual precipitation (give at three time), VPD day, daytime vapor pressure deficit calculated from air temperature and relative humidity, PPFD, photosynthetic photon flux density.

	Warming experiments			Shade experiment
	Makera	Rubona	Sigira	Arboretum
Paper	I, II	I, II	I, II	III
Potential vegetation	ESBT	LVTF	TMF	LVTF
Latitude	S 2°6'31"	S 2°28'30"	S 2°30'54"	S 2°36'55"
Longitude	E 30°51'16"	E 29°46'49"	E 29°23'44"	E 29°44'54"
Elevation (m a.s.l.)	1300	1600	2400	1700
MAT (°C)	20.6 \pm 0.1	20.0 \pm 0.0	15.2 \pm 0.1	19.5 \pm 0.2
T day (°C)	24.0 \pm 0.3	22.4 \pm 0.1	17.1 \pm 0.19	21.1 \pm 0.1
T 1%ile (°C)	10.9 \pm 0.8	13.4 \pm 0.2	10.9 \pm 0.3	16.0 \pm 0.5
T 99%ile (°C)	31.2 \pm 0.4	28.4 \pm 0.4	23.1 \pm 0.4	24.1 \pm 0.2
MAP (mm) ¹				1037 \pm 172
MAP (mm) ²	1106 \pm 33	1672 \pm 136	2144 \pm 61	1414 \pm 346
MAP (mm) ³				1192 \pm 207
VPD - day (kPa)	1.14 \pm 0.03	1.03 \pm 0.01	0.51 \pm 0.03	1.02 \pm 0.04
PPFD day ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	740 \pm 31	764 \pm 62	611 \pm 66	733 \pm 25

¹June 2013–May 2017; ²Feb 2018 –Jan 2020; ³Average 2006 to 2021 (2-year gaps). Data from Paper I and II, III.



Figure 5. Map of the plot design at each site within the elevation gradient, here represented by the high elevation site at Sigira. Trees from all 18 plots were included in the studies of the thesis, but before the treatment was started.

5.4.2 Potted tree - warming experiment

This study, conducted as a within-elevation gradient experiment, utilized the same batch of plant material grown in 11-liter pots using soil from the Sigira site across the three experimental sites to eliminate soil variation as a factor. The soil of the main plot, from where the soil to the pots were taken, was classified as an Ultisol with clay texture with pH (KCl) = 3.3 ± 0.13 (mean \pm SD); bulk density = 0.99 ± 0.13 g cm⁻³; Organic C = $3.8 \pm 0.6\%$; NH₄⁺ and NO₃⁻ = 39 ± 11 g m⁻³ and available P = 18 ± 4 g m⁻³. Eight species were grown in pots with a replication of 8 at each site, however, the study presented in the thesis include only two abundant tree species in Nyungwe: the early-successional *Harungana montana* and the late-successional *Syzygium guineense*. Seedlings were transplanted into pots after establishing roots and were randomly assigned to experimental sites in January 2018. After one year of growth, the seedlings were harvested in January 2019. Throughout the study, seedlings were watered to maintain soil moisture, with watering frequency adjusted based on differences in annual precipitation across sites. At the high-elevation site, watering occurred twice a week, while at the intermediate and lowest elevation sites, watering was conducted daily, with each plant receiving 2 liters of water per day.

5.4.3 Potted tree – shade experiment

Six montane tree species were selected to represent common species in Nyungwe montane rain forest, including both shade-tolerant (ST) and shade-intolerant (SI) types. The shade-tolerant species are among the 20 most common in Nyungwe and are more abundant in late-successional stands. They include *Carapa grandiflora*, *Entandrophragma excelsum*, and *Syzygium guineense*. The shade-intolerant species are more abundant in early-successional stands and include *Croton megalocarpus*, *Dombeya torrida*, and *Polyscias fulva*. Plants were cultivated from seeds collected in Nyungwe and transplanted into plots at the Arboretum, where they were subjected to different radiation regimes. Plants were randomly distributed to nine different plots in the Arboretum, differing in overstorey leaf area index and canopy light transmittance (Paper III; Table 1). These nine plots were divided into three radiation regimes: three open plots, three plots with the overstorey consisting of rather sparse canopies of early-successional species (*D. torrida*, *C. megalocarpus* and *Prunus africana*), and three plots with the overstorey consisting of dense canopies of later-successional species (*C. grandiflora*, *S. guineense*. and *Magnistipula butayei*). Each species had six replicate seedlings in each plot, totalling 324 seedlings across all radiation regimes. Regular irrigation was provided to ensure soil water availability, with varying frequencies based on the radiation regime and season. Monthly health inspections were conducted, resulting in 21 seedlings dying during the experiment. All plants were harvested after one year.

5.5 Measurements

5.5.1 Mixed tree plantations - warming experiment (paper I)

Tree stem height (*h*) and diameter (*D*) were measured every three months for the first two years after the planting in December 2017/January 2018, resulting in 8 censuses. *D* was measured using calipers, while *h* was measured with a stick or telescopic pole for larger trees. Only the

main stem of species with multiple stems was regularly measured (~trimonthly), with the average number of living stems also noted. Dead or weakened trees were recorded at each census. For trees below and above 250 cm in height, D was measured at stem base and breast height, respectively. Parallel measurements of both were taken after reaching 250 cm and three years later to develop species-specific functions to estimate stem base diameter (D_{base}). Outliers were identified as approximately >20% deviation from the line connecting previous and subsequent measurement. All flagged outliers were cross-checked with field notes to ensure that no valid data were incorrectly removed. Confirmed outliers or missing values were replaced with interpolated values which correspond to <1.5% of D_{base} and <0.5% of h recordings. Relative growth rates (RGR) for D_{base} and h were calculated using standardized equations, accounting for initial size variations among species and sites (see Papper I). Community composition was assessed by comparing basal area (BA) of different species groups (four groups representing two successional strategies and two elevation origins), with BA ($\text{cm}^2 \text{ m}^{-2}$) calculated as the sum of cross-sectional stem area per ground area, normalized for differences in living and dead individuals.

5.5.2 Potted trees – warming experiment (paper II)

Gas exchange measurements were conducted between April 23, 2018, and May 25, 2018, approximately three months after pot placement at experimental sites. A healthy leaf from five seedlings per species at each of three sites (totalling 30 leaves and plants) was measured using a portable photosynthesis system. Light-saturated net CO_2 assimilation rates (A_n) were measured at various intercellular CO_2 concentrations (C_i), creating A - C_i curves. Measurements were taken at a set photosynthetic photon flux density (PPFD) and varying leaf temperatures. Parameters like maximum Rubisco carboxylation efficiency (V_{cmax}) and maximum photosynthetic electron transport (J_{max}) were estimated from these curves using the photosynthesis model developed by Farquhar et al. (1980). Temperature responses of A_n , V_{cmax} , and J_{max} were fitted using nonlinear functions. Leaf structural and chemical analyses, including leaf dry mass per unit area (LMA) and leaf nitrogen content, were conducted after gas exchange measurements. At the time of plantation, the total dry mass of the two species was measured based on initial harvests of eight seedlings per species, randomly selected from the same populations as the potted seedlings. Seedlings were then grown at the sites for 1 year until harvest in January 2019. After one year, trees were harvested and separated into root, stem, and leaf components for dry mass determination and compared to the initial biomass.

5.5.3 Potted trees – shade experiment (paper III)

Monthly stem growth and health monitoring from May 2015 to April 2016 involved measuring seedling height and stem base diameter. For the final measurement, stem diameter at middle and top was also recorded to calculate stem volume accurately. 18 dead seedlings were replaced, with new plants used for physiological measurements but excluded from biomass analyses. Gas exchange measurements were conducted in February-April 2016 using a leaf gas exchange instrument, with parameters such as light saturated net photosynthesis (A_n) photosynthetic capacity (V_{cmax} , J_{max}) and quantum yield, stomatal conductance and dark respiration determined. Leaf trait measurements included leaf temperature and LMA. The trees were harvested at end of the experiment, with biomass divided into root, stem, branch, petiole,

and leaf fractions and dried at 70°C to determine the dry mass of each fraction. Biomass based RGR was determined by comparing the final biomass with the biomass of initially harvested trees.

5.6 Selection of native tree species suitable in different regions of Rwanda with respect to climate change sensitivity – literature review (Paper IV)

In this study, 81 tree species native to Rwanda, known for their various uses, were examined. These species were selected from a previous study on Vegetation and Climate Change in East Africa (VECEA), which identified Potential Natural Vegetation (PNV) in several East African countries (Kindt et al., 2014). The PNV classification was based on climatic adaptations of species, indicating what could potentially be the natural vegetation in specific areas. From the 255 species identified as PNV in Rwanda, 81 were chosen to represent different vegetation types, reflecting the topo-climatic variation in the country.

The selected species were associated with different vegetation classifications, including Agro-ecological regions, actual flora vegetation types, and the PNV classification. The geographical distribution of these species corresponded to specific regions within Rwanda, such as Afromontane rainforest, Lake Victoria transitional forest, and bushland areas. Most selected species belonged to Afromontane rainforest and Lake Victoria transitional forest types.

The study assessed species suitability for planting based on environmental requirements, plant traits, and ecosystem services. Data on elevation, precipitation, tree height, fruit size, and wood density were analysed across different PNVs. Species suitability was evaluated considering their adaptability to environmental conditions and their potential contributions to ecosystem services, including provision, supporting, regulating, and cultural services. Multifunctionality of tree species was determined based on their contributions to various ecosystem service categories.

5.7 Statistical analyses

To evaluate the findings from the various studies on tropical trees, a range of statistical methods was applied across the four studies. A summary of these methods is presented below. Results in paper I-III are reported as means \pm SE with significance was set at $p < 0.05$. The statistical analysis were conducted using SigmaPlot 12.5; SPSS 22.0-28.0 and R version 3.6.3.

5.7.1 Paper I

The effects of site and species on growth traits (e.g., base diameter, height, mortality, relative growth rates) were tested using two-way ANOVA with site and species/species group as fixed factors. Basal area was analysed using a two-way split-plot design, accounting for four species groups, two forest types, and two successional types within each plot, with species groups treated as within- and sites as between-subject factors. Post-hoc Tukey's tests followed significant interactions. Normality (Shapiro-Wilk) and homogeneity of variance (Levene's test) were evaluated, and data violating assumptions were excluded or corrected (e.g., Greenhouse-Geisser adjustment for sphericity).

5.7.2 Paper II

Site differences in photosynthetic parameters (e.g., biomass, V_{cmax} , J_{max} , g_s , A_n) were analysed using Welch's t-test, one-way ANOVA, and mixed-effects models (nlme package in R). Repeated measures ANOVA accounted for individual trees as random effects.

5.7.3 Paper III

Effects of radiation regime on shade-tolerance traits were analysed using ANOVA, with radiation as a fixed factor and species and plot as random factors. Plots were nested within radiation regimes and plant replication for each species inside each plot was six. Species-by-radiation interactions were the main focus, while simple one-way ANOVAs assessed radiation effects within species.

5.7.4 Paper IV

Linear and non-linear regressions, along with Chi-square tests, were used to examine relationships among vegetation types, topo-climatic variables, traits, and ecosystem services. Categorical data were simplified into binary classes. Analyses violating Chi-square assumptions (e.g., low cell counts) were excluded.

6 Results

The thesis is based on three complementary experimental studies and one literature analysis designed to explore the interspecific variation in temperature responses of African highland tree species and its implications for tree community composition in a warmer climate and tree species suitability in different regions of Rwanda.

6.1 Warming responses of tree growth and mortality in the mixed tree plantations (Paper I)

The response to warmer climate (i.e. the lower elevation sites compared to the high elevation site) varied among species. This is exemplified in Figure 6, where four distinct responses are shown: (i) increased growth with warming observed at both mid and low elevation sites (*Bridelia bridelifolia*), or (ii) solely at the low elevation site (*Dombeya torrida*) compared to the higher elevation site, (iii) decreased growth with warming (*Faurea saligna*), and (iv) no observable effect of warming on growth (*Syzygium guineense*). For growth responses of both tree stem diameter and height in all species, see Paper I: Figures S6 and S7..

A warmer climate significantly increased stem diameter (D) and height (h) in all early-successional species from transitional forests, whereas early-successional species from montane forests showed varied responses (Figure 7a, b). Among late-successional species, only 3 out of 9 showed increases in stem D and h at warmer sites, with the others either decreasing or remaining unaffected. Late-successional species generally grew slower than early-successional species, and their responses to warming were not influenced by elevation origin. The relationship between stem D and h was strong, except for *Albizia gummifera* (Figure 8). On average, early-successional species increased D by 12% and h by 43% at medium and low

elevation sites compared to high elevation site, while corresponding were -8% and +11% in late-successional species, -7% and +10%, in montane forest species and +23% and +59% in transitional forest species.

Multi-stem structure and behaviour is important for conversion of stem d and H measurements into tree stem volume production if these parameters are not recorded for all stems. Six out of 20 tree species had a significantly higher average number of stems at warmer sites than at the coolest site (Figure 7c). These six species belong to all four groups of successional and elevation origin combinations, with particularly large increases in the early-successional species *Maesa lanceolata* and *Dombeya torrida* (Figure 7c). Notably, *M. lanceolata* did not show changes in stem diameter and height with warming, but increased wood volume through more stems. This suggests that 10 out of 11 early-successional species responded positively to warming.

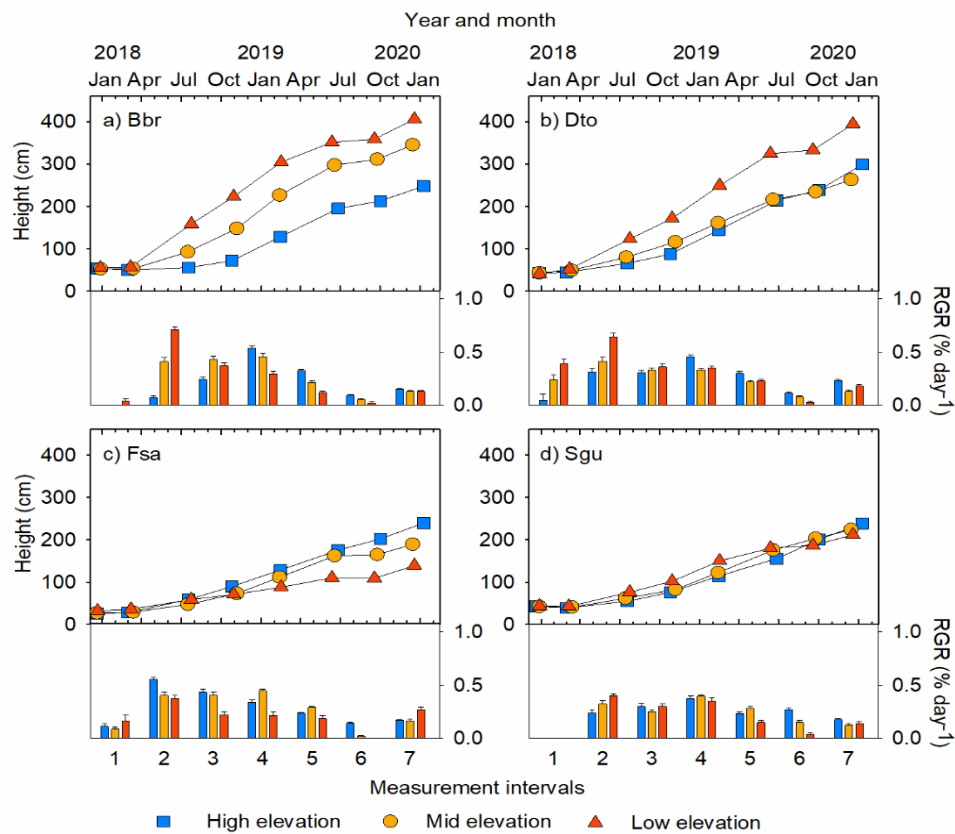


Figure 6. Examples of changes in stem height and relative growth rate (RGR) over 2 years, showing different warming responses for four species: (a) Increased growth with warming - *Bridelia brideliifolia* (Bbr), (b) Increase growth only at warmest site - *Dombeya torrida* (Dto), (c) Decreased growth with warming - *Faurea saligna* (Fsa), (d) No warming response of growth - *Syzygium guineense* (Sgu) (Paper I).

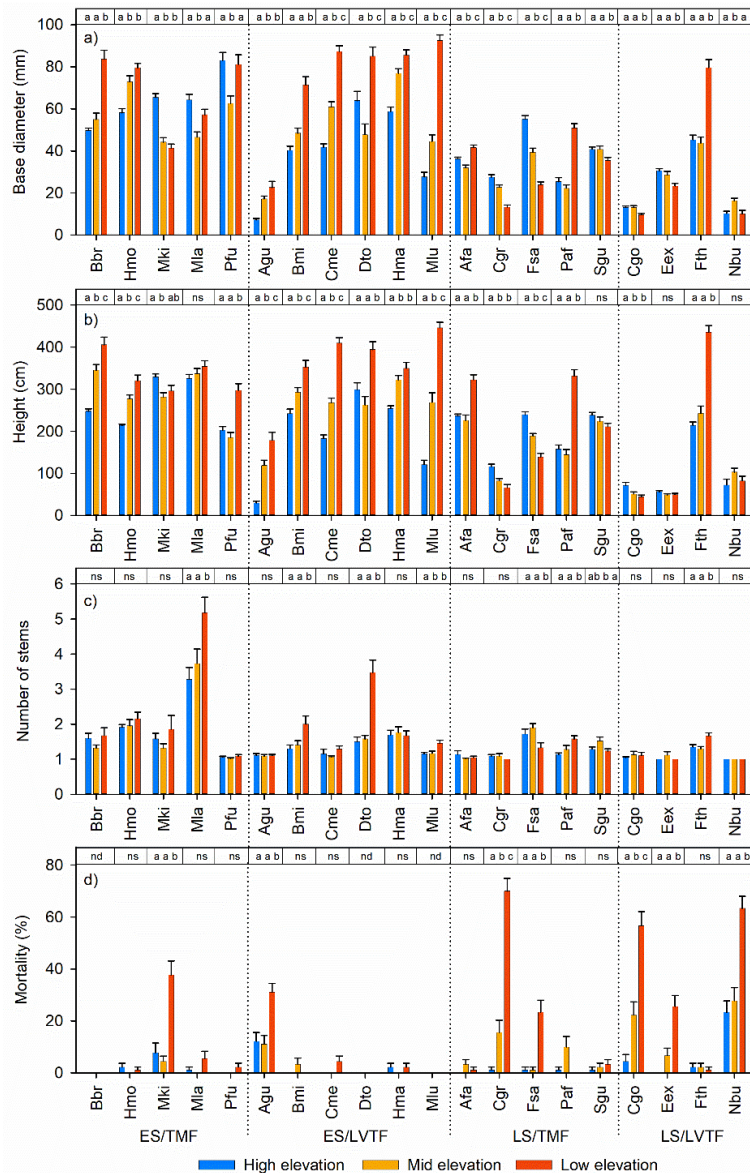


Figure 7. Base diameter (a), tree height (b), number of stems (c) and tree mortality (d) of species from different successional groups and forest type of origin, two years after planting. ES and LS, early- and late-successional species; TMF and LVTF, Tropical Montane Forest (>2000 m a.s.l.) and Lake Victoria Transitional Forest (1600-2000 m a.s.l.).

The RGR for smaller early-successional trees (with D_{base} of 10-25 mm and height of 75-100 cm) were mostly higher at warmer sites for both stem diameter (8/11 species) and height (8/11 species). Late-successional species generally had lower RGR, with most growing slower or being unaffected at warmer sites (Paper I: Figure 3a, c). For larger trees (with D_{base} of 50-75 mm and h of 250-300 cm), fewer early-successional tree species (stem diameter 3/11) and height (6/11 species) were significantly stimulated by warming (Paper I: Figure 3b, d). The 2019 seasonal drought, without irrigation, likely reduced the growth at warmer sites, especially in larger early-successional trees, due to higher vapor pressure deficit (VPD) and lower soil water content at these sites (Paper I: Table 1), combined with possible higher hydraulic vulnerability among early-successional trees.

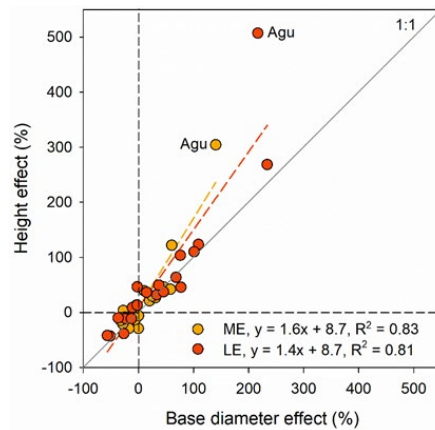


Figure 8. The effect on tree stem height at mid-elevation (ME) and low-elevation (LE) sites compared to the high-elevation site plotted against corresponding values for base diameter 2 years after plantation. Each marker is a species mean ($n = 20$). The two values that deviate most from the 1:1 line both belong to *Albizia gummifera* (Agu).

Warmer growth temperature increased tree mortality, especially at the warmest site (Figure 7d). Over two years, the mortality exceeded 10% in seven species: five late-successional species (5/9) and two early-successional species. High mortality was similarly common in species of montane (3/10) and transitional (4/10) forest origin. The highest mortality was observed in the three late-successional species *Carapa grandiflora*, *Chrysophyllum gorungosanum*, and *Newtonia buchananii* (70%, 62%, and 58%, respectively, at the warmest site). Late-successional species with high mortality at the low elevation site (>20%) generally had lower stem diameter and growth rates at this site compared to cooler higher elevation sites. Most mortality occurred between July 2018 and June 2019, i.e. before the first dry period without irrigation. High mortality may be linked to initial small plant size, but within species it was not predominantly the smaller trees that died. Species-specific difficulties in establishing at high temperatures likely contributed, with heat stress being a possible cause of higher mortality at lower elevation sites.

6.2 Warming responses of growth and biomass allocation of potted trees (Paper II)

In Paper II, an experiment was conducted to determine the warming responses of trees planted in pots with the same soil and grown at the three sites of the mixed tree plantation experiment. The study used two species with contrasting growth responses in the larger experiment: the early-successional *Harungana montana* and the late-successional *Syzygium guineense*. The growth results after one year showed that the total dry biomass was significantly higher at the warmer sites in *H. montana* while in *S. guineense*, it remained constant across all sites (Figure 9a, b).

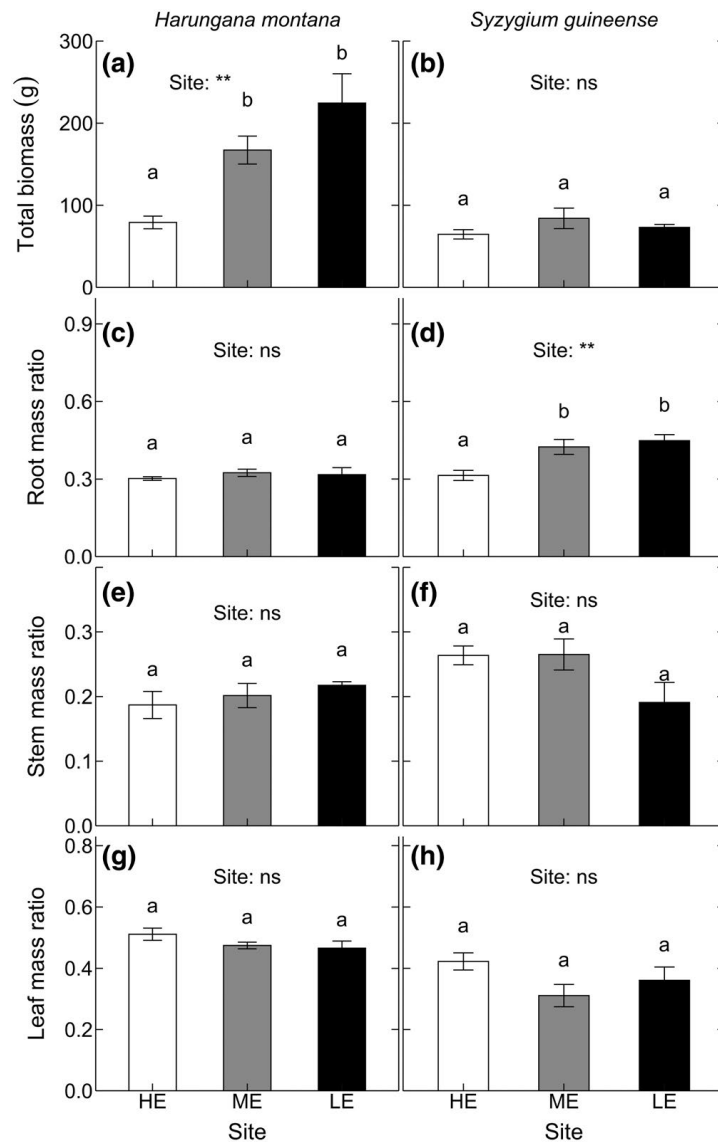


Figure 9. Total plant biomass and its allocation in *Harungana montana* (a, c, e, g) and *Syzygium guineense* (b, d, f, h). (a, b) Total seedling biomass; (c, d) the proportion of total plant biomass allocated to roots (Root mass ratio), (e, f) stems (Stem mass ratio) and (g, h) leaves (Leaf mass ratio). Colors represent different sites (high-elevation Sigira, HE = white; intermediate-elevation Rubona, ME = grey; low-elevation Makera, LE = black). Different letters on bars represent differences between sites (Tukey post-hoc test, $p < 0.05$). Means \pm SE. $n = 4-6$ (Paper 2).

For *H. montana*, dry biomass of leaves, stems, and roots increased at warmer sites but there was no change in biomass allocation (Figure 9c, e, g). For *S. guineense*, the root biomass fraction increased at warmer sites, while there were no significant changes in leaf and stem biomass fractions (Figure 9d, f, h). These biomass patterns are consistent with the observed effects on D_{base} and h of for both species in the mixed tree plantation - warming experiment (Figure 7a, b).

6.3 Responses of growth and biomass allocation to different degrees of shade (Paper III)

Total tree biomass and RGR were strongly influenced by radiation, with marked reductions observed under dense canopy conditions in the potted tree - shade experiment (Figure 10a, b).

Species showed significant differences in both biomass allocation and growth rate (Paper III – Table 2). Overall biomass and RGR were relatively similar between shade-tolerant and shade-intolerant species representing late- and early-successional groups, respectively. However, shade-tolerant species grew better under low radiation regimes, but unexpectedly, the two groups performed equally well under high radiation (Figure 10a, b). Although radiation levels significantly influenced total tree biomass and RGR across all species, the reduction in RGR under dense canopy conditions varied among species, being least pronounced in the shade-tolerant species *Entandrophragma excelsum* and most severe in the shade-intolerant species *Croton megalocarpus*. In the other four species, the RGR reductions were intermediate but somewhat larger in the shade-intolerant species species *Polyscias fulva* (59%) and *Dombeya torrida* (52%; denoted *Dombeya goetzenii* in paper III) than in the shade-tolerant species *Syzygium guineense* (49%) and *Carapa grandiflora* (46%).

The shade-tolerant species *C. grandiflora* and *E. excelsum* responded to shading by increasing the fractions of leaves, branches, and petioles compared with the shade-intolerant species (*C. megalocarpus*, *D. torrida* and *P. fulva*) had high fractional investments in stems and larger growth reductions when shaded (Figure 10c). The shade-intolerant species plus *S. guineense* instead responded to shading by increasing their stem biomass fractions. Both shade-tolerant and shade-intolerant species had similar fractional investments into roots and all except *E. excelsum* and *P. fulva* responded to shading by decreasing this fraction.

6.4 Tree stand composition (Paper I)

Tree stand composition, expressed as both absolute (BA_{abs}) and fractional (BA_{frac}) basal area of the four species groups: (i) early-successional tropical montane forest, (ii) early-successional transitional forest, (iii) late-successional tropical montane forest, and (iv) late-successional transitional forest was significantly affected by site (Paper I: Figure 6a, b; Table 5). Changes in BA reflected both D_{base} growth and mortality patterns. The BA_{abs} of transitional forest species of both successional groups was significantly stimulated at the LE compared to the HE site, while montane forest species were unaffected or showed decreased values. At the ME site, the BA_{abs} values resembles those of either the LE site (for late-successional montane forest species) or the HE sites (for the other three groups).

The initial BA_{frac} of each species group was expected to be 25%, but due to interspecific size differences among nursery plants, it varied between 19% and 32%, but with no significant differences between sites (Figure 11). After two years, clear shifts had occurred: compared to the coolest site, stands in a warmer climate had smaller BA_{frac} of montane forest species and larger fractions of transitional forest species. The differences were particularly large for the early-successional/transitional forest and the late-successional/montane forest groups, where the BA_{frac} were nearly doubled or halved, respectively. compared with the coolest site, stands in warmer climates had smaller BA_{frac} of montane forest species and larger fractions of transitional forest species. These contrasts were most pronounced for the early-successional transitional forest and late-successional montane forest groups, where BA_{frac} nearly doubled and halved, respectively.

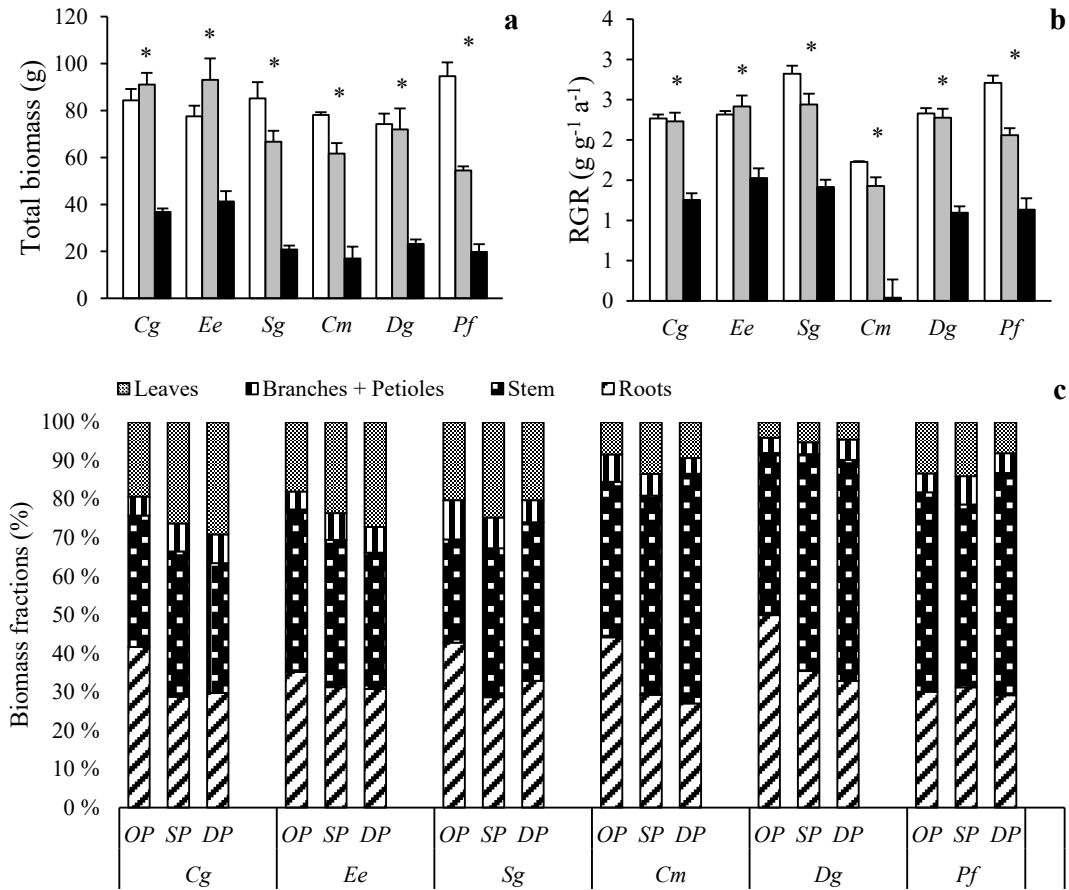


Figure 10. (a) Total biomass, (b) relative growth rate (RGR) and (c) biomass allocation (%) of *Carapa grandiflora* (Cg), *Entandrophragma excelsum* (Ee), *Syzygium guineense* (Sg), *Croton megalocarpus* (Cm), *Dombeya goetzenii** (Dg) and *Polyscias fulva* (Pf) planted in open (white in a, b; OP in c), sparse canopy (gray in a, b; SP in c) and dense canopy (black in a, b; DP in c) plots. Species to the left (Cg, Ee, Sg) are shade-tolerant and species to the right (Cm, Dg, Pf) shade-intolerant. Leaf biomass data represent leaves attached at the time of harvest. The error bars represent standard errors ($n = 3$). The symbol * in (a) and (b) indicates significant variation among radiation regimes within a species. Overall statistics results are provided in Paper III: Table 2. **D goetzenii* used in Paper III is a synonym to *Dombeya torrida* in Paper I,

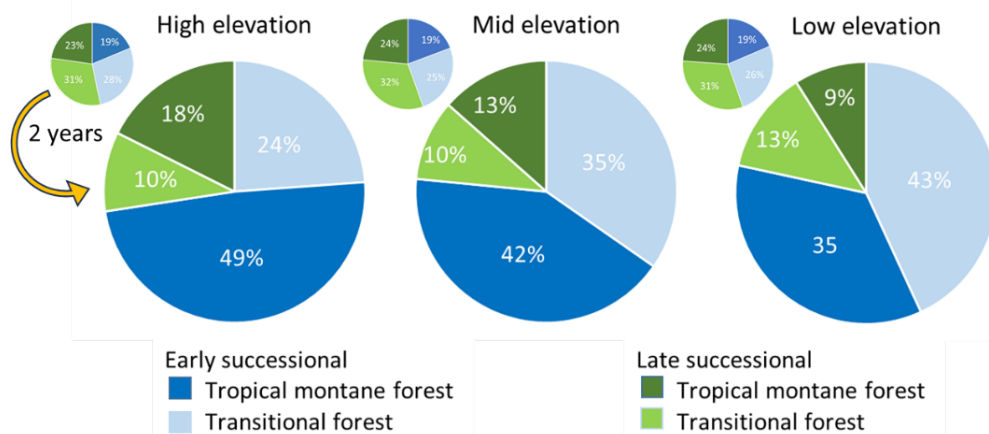


Figure 11. Fractions of basal area at planting (small pie-charts) and after 2 years (large pie-charts) for four combinations of early-successional and late-successional species from tropical montane rain forest (TMF) and Lake Victoria transitional rain forest (LVTF) origin grown at three sites at different elevations (Modified from Paper I).

6.5 Photosynthesis, respiration, and stomatal conductance (Paper II and III)

In the potted tree - warming experiment, the responses of net photosynthesis (A_n) to short-term leaf temperature variation were similar for the two species, *Harungana montana* and *Syzygium guineense* across at ME and LE sites (Figure 12a, b). However, at the HE sites, *H. montana* showed significantly higher A_n at moderate temperatures compared to *S. guineense* (Figure 12a). For both species, A_n remained relatively constant between 18°C and 30°C across all sites, but declined sharply above this range, particularly for *H. montana* at the HE site where A_n decreased to levels comparable to those observed at the other sites and in *S. guineense*.

The decline in A_n above 30°C for both species was primarily due to stomatal closure associated with high vapor pressure deficit (VPD) in the leaf chamber at elevated temperatures (Figure 12c, d). Stomatal conductance decreased with increasing leaf temperature and was not significantly different between the three sites across the measuring temperature range of 18–40°C in either species (Figure 12c, d). However, when assessed at a standard leaf temperature of 25°C (g_{s25}), *S. guineense* exhibit 25% and 50% higher stomatal conductance at ME and LE sites, respectively, compared to those at HE site (Paper II: Figure 3).

No significant change was observed for the thermal optimum of A_n , carboxylation efficiency (V_{Cmax}), or maximum electron transport (J_{max}) in response to the warmer growth conditions at lower elevations for either species (Paper II: Tables 1 and 4). For *H. montana*, the non-significant shifts in the thermal optimum of A_n (T_{optA}) were 3.2°C and 1.9°C higher for seedlings at ME and LE, respectively, compared to HE. For *S. guineense*, the shifts were only 0.4°C and 1.4°C, respectively (Paper II: Tables 1 and 4). These shifts represent a non-significant average change of 0.34°C and 0.16°C per 1°C of warming for *H. montana* and *S. guineense*, respectively (Paper II: Figure S3).

Leaf dark respiration at a common leaf temperature of 25°C (R_{d25}) acclimated to warming in both species (Figure 13). In *H. montana*, R_{d25} was 37% and 53% lower in seedlings grown at the ME and LE sites, respectively, compared to seedlings grown at the HE site (Figure 13). In *S. guineense*, R_{d25} was on average 32% lower at the two lower-elevation sites compared to HE site (Figure 13). When data were pooled across sites within each species, R_{d25} showed a positive relationship with V_{Cmax25} and J_{max25} (Paper II: Figure 6), indicating some level of coordination between respiration and photosynthetic capacity.

However, this relationship did not reflect a strong thermal acclimation response, as key photosynthetic parameters such as T_{optA} , activation energy, and maximum rates of Rubisco carboxylation and electron transport remained largely unchanged in warm-grown trees of both species.

In the potted tree - shade experiment, shade-tolerant species *Carapa grandiflora* (Cgr) and *Entandrophragma excelsum* (Eex) showed largely consistent photosynthetic responses across the three radiation regimes (open, sparse, and dense canopies). These species had significantly lower values of V_{Cmax} and J_{max} than shade-intolerant species in open plots, but not under lower light conditions (Figure 14).

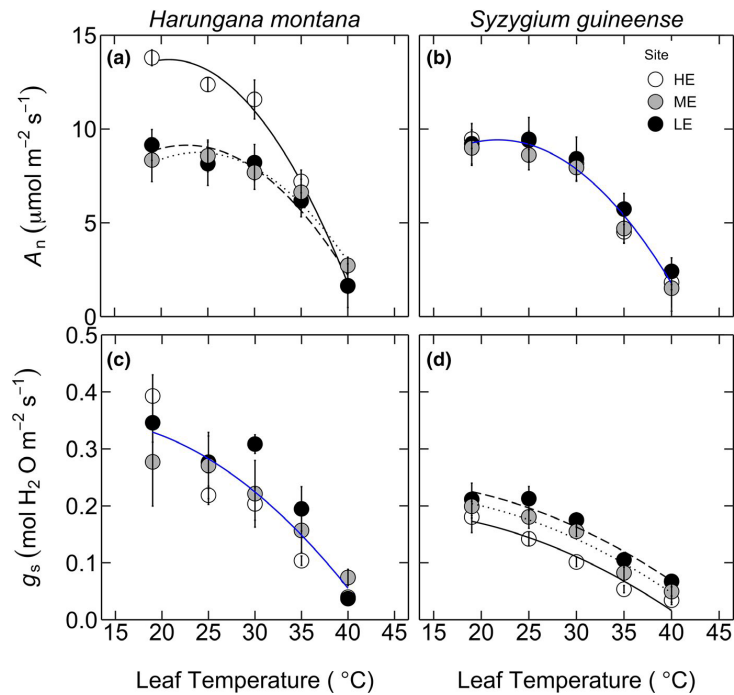


Figure 12. Gas exchange responses to temperature in *Harungana montana* (a, c) and *Syzygium guineense* (b, d) grown at different sites in Rwanda-TREE. (a, b) Net CO₂ assimilation rate (c, d) stomatal conductance (gs). Symbol colors represent different sites (high-elevation Sigira, HE = white circle; intermediate-elevation Rubona, ME = grey circle; low-elevation Makera, LE = black circle). Solid blue line (b, c) is the overall regression line fitted with Equation (4) when sites do not differ. Black lines (a, d) are linear regressions fitted for different sites (HE = solid line; ME = long dashed; LE = dotted). (a, b) are fitted with Equation (1) and (c, d) with a quadratic function. Means \pm SE. n = 4–6 (Paper II)

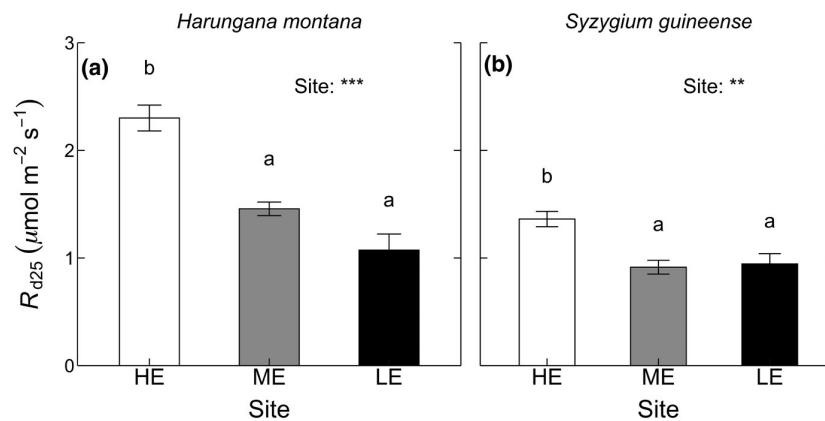


Figure 13. Leaf dark respiration measured at 25°C (R_{d25}) in *Harungana montana* (a) and *Syzygium guineense* (b) grown at different sites in Rwanda-TREE. Colors represent different sites (high-elevation Sigira, HE = white; intermediate-elevation Rubona, ME = grey; low-elevation Makera, LE = black). Different letters on bars represent differences across the three sites (Tukey post-hoc test, $p < 0.05$). Means \pm SE. n = 4–6 (Paper II).

In open canopy conditions, light-saturated net photosynthesis (A_n), V_{cmax} , and J_{max} were higher in the shade-intolerant species (*Croton megalocarpus*, *Dombeya torrida*, *Polyscias fulva*, and *Syzygium guineense*) compared to Cgr and Eex (Figure 14a–c). Under dense canopies, photosynthetic parameters were more similar across species.

Stomatal conductance followed a similar trend to A_n , with shade-intolerant species maintaining higher values than shade-tolerant species even under dense canopies (Figure 14e). Leaf dark respiration (R_d) and light compensation point (LCP) were lower under dense canopies but showed no significant differences among species or shade-tolerance groups (Paper III: Figure 4).

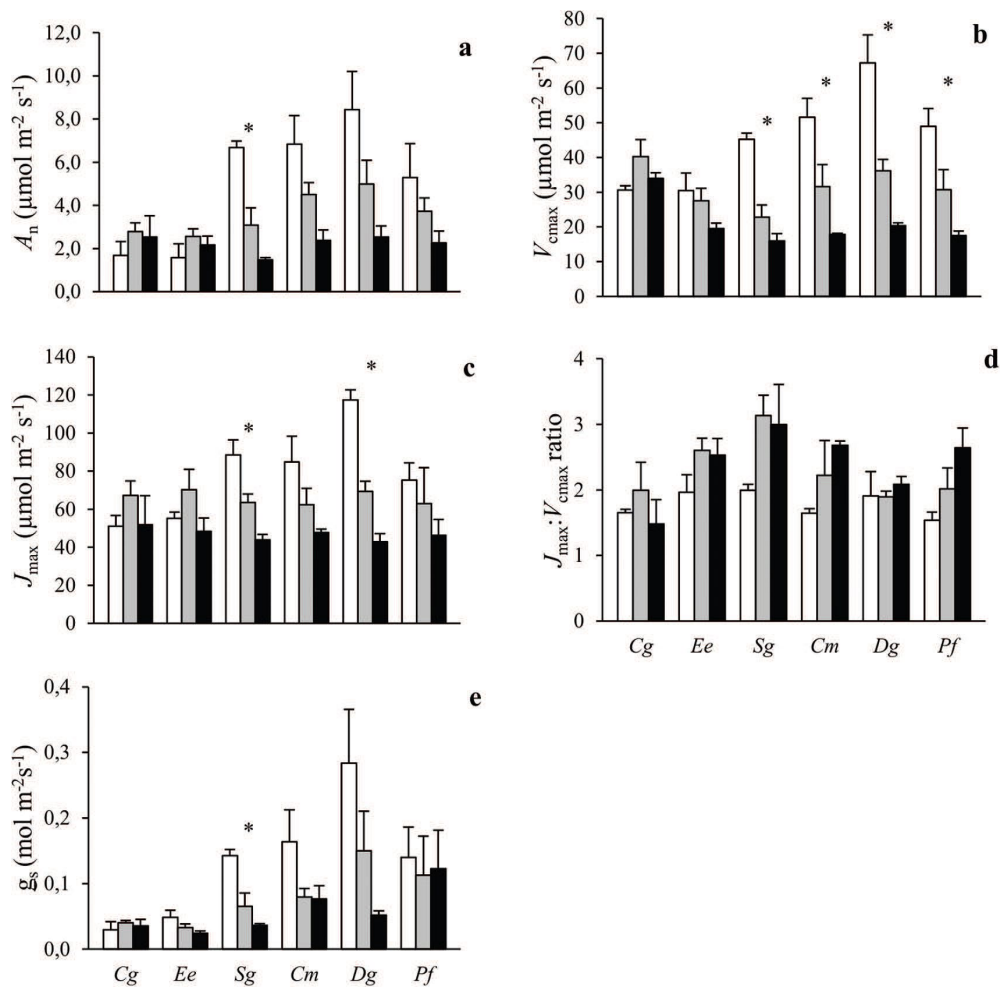


Figure 14. The (a) light-saturated net CO₂ assimilation (A_n), (b) maximum rates of photosynthetic carboxylation (V_{cmax}) and (c) electron transport (J_{max}), (d) $J_{max} : V_{cmax}$ ratio and (e) stomatal conductance (g_s) of six tropical tree species grown in open (white), sparse canopy (gray) and dense canopy (black) plots. Species to the left (Cg, Ee, Sg) are shade tolerant and species to the right (Cm, Dg, Pf) shade-intolerant. The error bars represent standard errors ($n = 3$). The symbol * indicates significant variation among radiation regimes within a species. Species: *Carapa grandi_ora* (Cg), *Entandrophragma excelsum* (Ee), *Syzygium guineense* (Sg), *Croton megalocarpus* (Cm), *Dombeya goetzenii* (Dg) and *Polyscias fulva* (Pf).

6.6 Selection of native tree species suitable in different regions of Rwanda with respect to climate change sensitivity – literature review (Paper IV)

In the literature study of suitable tree species, 81 native tree species known for their ecological and socio-economic value in Rwanda were analyzed. These species were selected to represent different vegetation types across the country's topo-climatic gradients. The selection was based on classifications from the VECEA project (Kindt et al., 2014), which identified Potential Natural Vegetation (PNV) in East Africa, providing a useful framework for understanding species climatic adaptation. Further methodological details are provided in the Methods section. The selected species were classified according to Agro-ecological regions, actual flora vegetation types, and the PNV where the geographical distribution of these species corresponded to specific regions within Rwanda, such as Afromontane rainforest, Lake Victoria transitional forest, and bushland areas. The study assessed species suitability for planting based on environmental requirements, plant traits, and ecosystem services including provision, supporting, regulating, and cultural services.

6.6.1 Vegetation types of vs topography, environment, and traits

The results show clear relationships between elevation, climate and traits of species from different PNVs. The species upper elevation limits increased significantly with increasing precipitation ($p = 0.037$) while lower elevation and low precipitation range did not correlate significantly. Wood density increased significantly with decreasing minimum precipitation (Figure 15a, $p < 0.001$). Maximum tree height increased significantly with elevation, peaking around 2700 m a.s.l., before declining at higher elevations (Figure 15b, $p = 0.006$), suggesting that while the tallest species may grow up to this elevation, actual tree height likely starts to decline slightly earlier. Both tree size and wood density have implications for wood quality, carbon storage capacity and hydraulic functions, but they have opposite relationship to elevation and precipitation, as precipitation is increasing with elevation. The fruit size decreased with increasing elevation (Figure 15c, $p = 0.061$), and increasing maximum tree height (Figure 15d, $p = 0.013$), although only nearly significant for elevation. Most trees at high elevation therefore have smaller fruits, although there are exceptions.

The frequency of species tolerating low precipitation is significantly higher at high elevation compared to low elevation ($p = 0.001$). Furthermore, the frequency of montane species according to Blosch et al. (2009) has a higher minimum precipitation tolerance ($p = 0.027$) compared to species from other vegetation types (Paper IV: Table 4). There is a higher frequency of tree species that can grow tall among montane species compared to species from other vegetation types according to both the classification by Kindt et al. (2014), ($p = 0.002$) and Blosch et al. (2009), ($p < 0.001$). This is also supported by the higher frequency of tall trees (> 20 m) at higher elevations ($p = 0.001$). There is a higher frequency of species with large fruits (> 20 mm) in lower vegetation types according to Kindt et al. (2014), ($p = 0.036$).

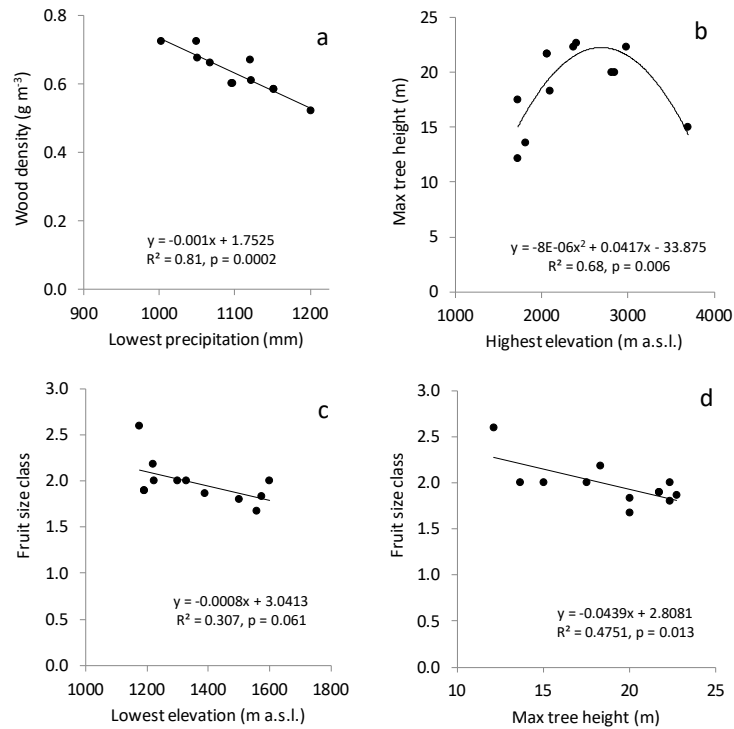


Figure 15. Relationship between average tree traits and environments of species from 11 different potential vegetation types in Rwanda. a) Average wood density vs lowest precipitation where the vegetation type occurs; b) maximum average tree height vs highest elevation of the vegetation type; c) maximum average fruit size class vs lowest elevation where the vegetation type occurs; d) maximum average fruit size class vs maximum average tree height within the vegetation types.

6.6.2 Ecosystem services

Among the selected species, the most commonly reported use was for medicinal purpose (83%), followed by construction (79%), fuel (68%) and food (58%). Cultural and supporting ecosystem services were associated with 56% and 53% of the species, respectively, while regulating services were documented for only 31% (Paper IV: Table S2). Tree species providing food and fodder were significantly more frequent at elevations below 2000 compared to at or above 2000 m a.s.l. ($p = 0.054$ and 0.024 , respectively), whereas those supplying packing material and handicrafts were more frequent at higher elevations (Paper IV: Table 7). Species used for charcoal had denser wood ($\geq 0.6 \text{ g cm}^{-3}$), while those for clothing had lighter wood ($< 0.6 \text{ g cm}^{-3}$). Taller species ($> 20 \text{ m}$) were typically used for construction, furniture, and tools, and slow-growing species were often preferred for building materials (Paper IV: Table 8).

Aggregated analyses showed edible species were more prevalent in low-elevation and non-montane forests. Shade-providing species (e.g., for tea/coffee) were also more frequent outside montane forests, likely due to broader crowns. Fiber-producing trees were tall but had low wood density. Early-successional species commonly supported agroforestry, while species aiding soil formation had low-density wood. Trees supporting honey production tended to bear larger fruits.

6.6.3 Tree multifunctionality

Out of the 81 studied species, 17 provided ecosystem services across all four main categories (provisioning, supporting, regulating, and cultural), and 18 contributed to at least five of six provisioning subcategories (Paper IV: Table 9 and 10, respectively). Only seven species met both criteria— *Senegalia polyacantha* (earlier, *Acacia polyacantha*), *Vachellia seyal* (earlier, *Acacia seyal*), *Afrocarpus falcatus*, *Albizia adianthifolia*, *Ficus thonningii*, *Lannea schimperi*, and *Trema orientalis*—representing diverse ecological zones and successional stages.

7 Discussion

7.1 Growth responses to warming (Paper I, II)

Mixed multi-species tree plantations established along an elevation gradient were used to assess how Afromontane species respond to temperature and how interspecific variation influence future tree community composition under warming. Growth responses to warming varied between successional groups and among species from different elevation of origin. A complementary study using two species from both successional groups, grown in 11-litre pots filled with soil from the high elevation site at all three sites to eliminate soil as a possible confounding factor, showed similar results as in the mixed tree plantation.

7.1.1 Successional strategies

The findings from the first two years of growth in the mixed plantation indicate that a warmer climate stimulates growth of stem volume-related variables (D_{base} , h , and stem count) in most early-successional species (Figure 7). The responses of late-successional species were more diverse, showing increases and decreases, as well as no significant changes. These results support my first hypothesis **H1 - Paper I**, stating that tree growth responses to a warmer climate are more positive (or less negative) in early- than in late-successional tree species. The results are in concordance with the observations on potted trees in Paper II, growing in the same soil at all sites, where warming strongly stimulated biomass growth in the early-successional species *H. montana* but not in the late-successional species *S. guineense* (Figure 9 a, b). These findings therefore provide additional support for **H1s - Paper I and II**. This indicates that the site effects and successional group difference observed in the plantations were at least partly caused by climate responses rather than by site differences in soil conditions.

The result agrees with observations of tropical late-successional species being more negatively affected by warming compared with early-successional species in controlled-environment chamber experiments (Cheesman & Winter, 2013; Slot & Winter, 2018), field experiments (Carter et al., 2020; Li et al., 2020) and field observations (Gliniars et al., 2013). Several lines of evidence thus indicate that warmer climate empowers early-successional species to be more competitive than late-successional species. The lower competitiveness of late- compared to early-successional species at warmer sites could in part be the fact that they were exposed to high sun when they were small, especially during the first year of the experiment when they were growing under open conditions. This formed the basis for **H4 - Paper III**, as high light

exposure can be stressful for late-successional species which generally have lower tolerance to intense radiation (Poorter, 1999; Veenendaal et al., 1996), and perhaps particularly so under warmer conditions. However, results from Paper III did not support this hypothesis. Growth comparison under different light intensities showed that three late-successional species grew at similar rates as three early successional species under open sky at a mid-elevation site (Figure 10a, b), suggesting that high light exposure was not the cause of their comparatively lower growth rates at warmer climate in the mixed tree plantations (Paper I).

The positive warming responses of many species in this study contrasts with other findings on tropical trees showing reduced growth under warm conditions (Clark et al., 2003; 2010; 2013; Dong et al., 2012; Feeley et al., 2007; Hubau et al., 2020; Vlam et al., 2014; Way & Oren, 2010). The likely reason is that the present study used montane and highland species, which naturally grow in comparatively cool conditions (mean annual temperatures around 15 to 21°C).

7.1.2 Elevation of origin

My findings showed that warmer climate stimulated tree growth of many species, especially early-successional species with a transitional forest origin for which growth increased by +39% and +140% at the mid elevation (ME) and low elevation (LE) sites, respectively, compared to the high elevation (HE) coolest site). This supports *H2 - Paper I*, at least for early-successional species. The results were in line with findings in a controlled chamber warming experiment with seedlings of four Rwanda TREE species where those originating from lower elevation was better at physiologically acclimating and growing at high growth temperatures than the species originating from high elevation (Wittemann et al., 2022). Potential warming responses on species with different elevation origins (transitional vs. montane forests) have also been demonstrated in Andean tropical forests, where tree species that were centered at lower elevation had gained in relative abundance as climate got warmer over time, at the expense of higher-elevation species; so-called thermophilisation (Duque et al., 2015; Fadrique et al., 2018). My study and the chamber warming study on Rwandan tree species (Wittemann et al., 2022) suggest that warming-induced declines in abundance of higher-elevation tree species are caused by lower capacity of leaf physiology and tree growth processes to handle, or benefit from, warming.

7.1.3 Biomass allocation

In the study with seedlings potted in the same soil and grown at different elevations, total dry biomass significantly increased at the warmer sites for *H. montana* (early-successional and fast-growing species), while it remained constant for *S. guineense* (late-successional and slow-growing species). Also, biomass allocation responses differed between the two species. In *H. montana*, biomass allocation among plant parts did not change with warming. In contrast, *S. guineense* allocated relatively more biomass to roots at warmer sites, accompanied by a non-significant decline in allocation to leaf and stem (Figure 9 c-f). If similar allocation pattern occurs in other late-successional species, it could help explain their reduced above-ground growth under warmer conditions observed in the mixed tree plantation experiment (Paper I). Warming increased growth in early-successional species can be attributed to two linked

processes. First, the greatly increased leaf biomass (Figure 9) and increased total canopy leaf N (Paper II: Figure S8) in a warmer climate may have enhanced crown-level carbon fixation despite observation of lower leaf level maximum net photosynthetic rates (Figure 12a). Second, if a similarly strong downregulation of respiration occurred in plant parts other than upper-canopy leaves (Figure 13), lower respiration rates at ambient night temperatures (Mujawamariya et al., 2021)— may have contributed to increased carbon availability for tree growth under warming conditions.

7.2 Response to shade (Paper III)

The potted tree - shade experiment showed that late-successional species invest relatively more into plant organs maximizing light interception (i.e., leaves and branches, Figure 10c) than early-successional species. This difference was strongest under low radiation, showing that it is the result of both species adaptations and acclimation responses supporting both carbon gain hypothesis and **H1 - Paper III** which states that shade-tolerant species have a whole-plant biomass allocation strategy that maximizes light interception when grown in the understory through greater relative investment in branches and leaves. Early-successional species grown under dense canopies had high fractional investments in stem biomass and exhibited low RGR (Figure 10). This represents a strategy to try to escape from the shade of neighbouring trees by rapid vertical growth, but without succeeding (Grubb, 2016; Montgomery, 2004; Lourens Poorter et al., 2018). The allocation strategy of late-successional and shade-tolerant species was successful with respect to total growth under deep shade conditions, as judged by the smaller growth declines under low radiation in late-successional shade-tolerant species compared with early-successional shade-intolerant species (Figure 10 a, b).

While biomass allocation patterns supported the carbon gain hypothesis, leaf morphology did not, since the late-successional shade-tolerant species had higher LMA than early-successional shade-intolerant species under shade conditions (Paper III: Figure 2a). This is in line with several previous studies on tropical tree species (Coste et al., 2005; Kitajima, 1994; Manishimwe et al., 2022; Mao et al., 2014). Although leaf dark respiration (R_d) and light compensation point (LCP) were lower beneath dense canopies, as expected, these traits did not differ significantly among species, indicating they are poor predictors of shade tolerance in tropical montane forests species. Thus, neither leaf morphology nor leaf physiology supports the carbon gain hypothesis or **H2 - paper III**. A successful late-successional and shade-tolerant species thus seems to need both a whole-plant architecture that is favourable for light interception (in agreement with the carbon gain hypothesis) and leaves that are strong enough to endure biotic and abiotic stress in the understory (in agreement with the stress tolerance hypothesis suggested to explain shade tolerance; Valladares and Niinemets, 2008; Valladares et al., 2016). Even though high LMA does not maximize short term light interception and carbon gain, it might increase the carbon gain over the entire leaf lifespan thanks to better physical protection against herbivores and mechanical stresses of longer-lived leaves (Kitajima & Poorter, 2010; Mao et al., 2014); Coste et al., 2011; Gommers et al., 2013; Reich, 2014).

Under sunny conditions in open plots, the late-successional and shade-tolerant species *C. grandiflora* and *E. excelsum* exhibited the highest leaf temperatures (36–38 °C), supporting **H3**

- **Paper III** (Paper III: Figure 6). Higher leaf temperatures in the low-transpiring late-successional species *E. excelsum* at the lower-elevation sites was also reported in another study in the mixed tree plantations (Tarvainen et al., 2022). These temperatures exceed the optimal range for photosynthesis (25–30 °C; Vårhammar et al., 2015), indicating heat stress. Correspondingly, both species showed reduced photosynthetic capacity — lower V_{cmax} and J_{max} (Figure 14b, c) — in open plots, but not under lower light, suggesting thermal inhibition of photosynthetic enzymes (Sage & Kubien, 2007). This physiological sensitivity may partly explain the observed warming-induced mortality and growth reductions in some late-successional species in the mixed tree plantation experiment (Figure 7). In another study with 12 Rwanda TREE species in the mixed tree plantation experiment, Manzi et al. (2024) reported on high and stressful leaf temperatures, but no significant differences between early-successional and late-successional species, nor between species originating from different elevation ranges.

7.3 Mortality responses to warming (Paper I)

Warmer climate increased tree mortality, particularly in late-successional species. However, there was no clear difference between montane and transitional forest species. My findings therefore only partly supported **H3 in Paper I**. It is possible that the relatively low number of species in each successional and elevation origin group (4-6) has concealed possible influences of species origin or that these will show up at later stages in the experiment.

The results of higher mortality in late-successional species are supported by Laurance et al. (2004), who observed stronger increases in tree mortality among late- compared to early-successional species when analysing growth measurements made in eighteen 1 ha plots over up to 3 decades in the Amazon rain forest. However, opposite results were found in long-term monitoring studies of mortality in 24 Australian (Bauman et al., 2022) and 189 Amazonian (Esquivel-Muelbert et al., 2020) tropical forest plots which found higher mortality risk in early-successional species under increasing VPD and drought, respectively. The reason of higher mortality in early-successional compared to late-successional species found in these monitoring studies may be likely linked to higher hydraulic vulnerability (Apgaua et al., 2015; Eller et al., 2018) and the risk of increased height in mature trees (Bauman et al., 2022; Esquivel-Muelbert et al., 2020). The difference between our results and long-term observational studies (Bauman et al., 2022; Esquivel-Muelbert et al., 2020; Slik, 2004; Aleixo et al., 2019; Miyamoto et al., 2021) may be explained by the fact that they have been conducted in taller mature trees while our study was done on small trees in young stands with high sun exposure. These differences in tree size and light environment likely influenced both hydraulic stress and mortality dynamics. Another difference is that most mortality in field studies is likely linked to drought (or the combination of heat and drought) while I studied irrigated young plants and, thus, primarily warming responses. However, it cannot be excluded that the mortality difference between successional groups may change with increasing age and size of the trees, or when trees are exposed to seasonal drought stress. Notably, mortality in both *Harungana* species increased sharply after approximately four years, whereas other early-

successional species continued to perform well at the warmer, low-elevation site (unpublished data).

Many observational mortality studies, especially of genera associated with wetter climatic regimes, attributed effects to drought stress (Esquivel-Muelbert et al., 2017). But if considering only the effect of warming when there is no water limitation, early-successional species might be less sensitive than late-successional species. This is because late-successional species with lower transpiration rates would experience higher leaf temperatures and stronger physiological heat stress than early-successional species which are to some degree protected against heat stress by transpiratory cooling. This was showed in a previous Rwandan common garden study with seedlings (Vårhammar et al., 2015) as well as in one study on three species in the mixed tree plantations (Tarvainen et al., 2022). The reason why there was no successional group difference in leaf temperature in another Rwanda TREE study might have been that most leaf temperature measurements were made in the dry period, when transpiration rates were generally low in all species (Manzi et al., 2024).

7.4 Tree stands composition (Paper I)

My findings showed that early-successional species with transitional rain forest origin significantly increased their total and fractional basal area at warmer sites, while montane species declined (Figure 11). This supports *H4 in Paper I*, which suggests that interspecific variation in growth and mortality responses drives shifts in tree community composition under warming, favouring lower-elevation and early-successional species. These results align with thermophilisation trends in Andean and Afromontane forests, where communities have shifted towards greater dominance of species from lower, warmer elevations in recent decades (Cuni-Sanchez et al., 2024; Duque et al., 2015; Fadrique et al., 2018). However, in contrast to the observations by Duque et al. (2015), thermophilisation in the mixed tree plantation experiment was driven by differences in growth responses rather than by higher mortality of species with higher elevation ranges.

It is also possible that the observed growth reduction in higher-elevation late-successional species at warmer sites is an indication of coming mortality (Cailleret et al., 2017; Esquivel-Muelbert et al., 2020). However, there are several climate-related pathways towards mortality (Gora & Esquivel-Muelbert, 2021; Zuleta et al., 2022), and future research should try to ascertain the mortality mechanisms of different climate variables and how they interconnect with different groups of species.

If the negative effect of warming on late-successional trees is high at young ages, this will likely cause at least a transient shift in species composition in more mature stands. The succession from secondary to primary forest will likely be slower in a warmer climate, with implications for both large-scale carbon storage goals of forest restoration efforts and carbon storage of natural forests under high disturbance regimes (Poorter et al., 2021).

7.5 Multifunctionality of tree species (Paper IV)

The literature study in Paper IV highlights the multifunctionality of native tree species in Rwanda, with over 75% of the 81 selected species providing services across multiple

ecosystem categories—provisioning, supporting, regulating, and cultural – which is in line with another study of ecosystem services in Africa (Wanagi et al., 2016). Similar to the studies by Bigirimana et al., (2016) and Mawula (2009), provisioning services such as medicine, construction material, fuel and food were most commonly reported. Trait variation (e.g., height, wood density, fruit size) was linked to elevation, climate, and vegetation zones, influencing species suitability for ecosystem service provision (Bunker et al., 2005; Chave et al., 2005; Masozera, 2008; Ramage et al., 2017).

High-elevation Afromontane species often supported income-generating services by providing timber for construction and shade, while lower-elevation species favoured food and fodder provision. However, many multifunctional species were not strong fruit providers, underscoring the need to integrate traits and ecosystem service complementarity in species selection (Benz et al., 2020). Seventeen of the 81 species showed broad service potential, supporting multifunctional landscapes and food security (Galhena et al., 2013; Mbow et al., 2013; Vinceti et al., 2013). Emphasis on native species aligns with Rwanda’s national reforestation goals (Ministry of Lands and Forestry, 2017) and broader calls for native species to enhance ecosystem resilience and biodiversity (Kehlenbeck et al., 2013; Thomas et al., 2014).

Despite their value, native trees remain underused due to limited knowledge on their growth and service potential (Ndayambaje et al., 2013; Seburanga, 2013). This review advocates for species-specific guidance based on traits and site suitability to inform agroforestry planning, climate adaptation, and sustainable livelihoods through value chain development and landscape restoration.

7.6 Study limitations

The elevation gradient study with young, mixed tree species planted across three sites (Papers I and II) faced limitations, both methodological and contextual. One major constraint was the variation in environmental variables between sites, especially precipitation. To mitigate this during the initial study period (July–August 2018), all trees were manually irrigated. However, from mid-July to the end of August 2019, plants were exposed to a natural dry season. Water and nutrient treatments were introduced only later, in September and November 2019, respectively. My study focused on the first two years of data and did not include the effects of these water and nutrient treatments. Future studies under different water and nutrient regimes will offer deeper insights into how soil moisture and nutrient availability shape species performance and resilience to climate change. A key limitation is the short duration, capturing only the first two years following seedling establishment. Short-term experiments are less likely to capture long-term processes such as tree maturation, successional dynamics, or ecosystem-level feedbacks. Many species may exhibit delayed responses to environmental stressors, making it difficult to draw conclusions about long-term survival or productivity.

High mortality rates observed in some species may be linked to the initial use of small individuals with poorly developed root systems, which likely limited their ability to access sufficient water and nutrients—particularly under dry conditions. Future studies using more

robust planting stock with established rooting systems could help determine whether size at planting or inherent species traits drive this pattern of mortality.

Moreover, the study simplified complex ecological interactions. For instance, understory vegetation was removed, which may have altered natural competition dynamics for light, water, and nutrients. Such interactions, including species–species facilitation or competition, are important drivers of growth and survival in natural forest systems and should be incorporated into future designs. The potted experiments in Papers II and III benefited from using uniform soil across sites but were limited by restricted soil volume, which may have constrained the growth of larger species compared to smaller ones.

A limitation of the potted tree – shade experiment (Paper III) was the structural setup of the experiment. Early-successional species planted under mature tree canopies were not awarded by prioritizing vertical growth since overstorey trees were several meters tall. This setup may not reflect natural regeneration conditions in canopy gaps. Future research should consider using seedlings of the same age, grown under uniform light conditions to better replicate natural regeneration scenarios.

The literature review (Paper IV) was inherently constrained by the availability, scope, and quality of published data. There may be overrepresentation of certain ecosystem services (e.g. provisions) and underrepresentation of others (e.g. cultural or supporting services), potentially biasing the results and conclusions.

In summary, while this thesis provides valuable insights into early responses of tropical tree species to warming under relatively ecologically realistic conditions compared to many growth chamber and green-house experiments, certain limitations highlight the need for long-term, multisite experiments with more comprehensive designs to fully understand forest dynamics under climate change. Future Rwanda TREE studies, including the water and nutrient treatments, will help address some of these limitations.

8 Implication and recommendations

8.1 Forest Restoration and Climate Adaptation

My findings show that successful establishment of mixed tree plantations indicates it is unnecessary to delay planting late-successional species until early-successional canopies have formed. Simultaneous planting of climate- and site-adapted early- and late-successional species can therefore accelerate forest restoration. These results help reduce uncertainty in native species restoration strategies (Aitken et al., 2008; Forrester et al., 2005; Thomas et al., 2014) and improve modeling of Afromontane forest dynamics under climate change (Pugh et al., 2020).

A trait-based approach may further enhance Rwanda’s plantation programs by guiding species selection suited to local conditions, reducing mortality, and improving plantation success. Promoting native species supports biodiversity, ecosystem services, and climate resilience, contributing to multifunctional landscapes and food security.

8.2 Technical Recommendations

Promote mixed tree plantations combining early- and late-successional native trees to accelerate canopy closure and enhance resilience. Species selection should be site-specific, guided by elevation, climatic sensitivity, and key functional traits. In exposed or degraded areas, temporary shading or nurse species can aid establishment, while diversification across planting zones can reduce risks from climate extremes and monoculture failures.

8.3 Scientific Recommendations

Extend long-term monitoring to assess growth, survival, and ecosystem functions beyond establishment. Investigate interactions between heat and drought stress, particularly in shade-tolerant species, and examine below-ground responses such as root and mycorrhizal dynamics. Integrate landscape-scale and modelling approaches to link species-level responses with broader outcomes, including carbon storage, biodiversity, and water regulation.

8.4 Policy Recommendations

Use these findings to inform Rwanda’s 30/20 reforestation strategy by integrating resilient native species across elevation zones. Incorporate species-specific climate sensitivity data into national restoration policies and decision tools, and strengthen incentives for native species use in community-based projects. Enhanced collaboration among researchers, managers, and policymakers is essential to translate science into effective, climate-smart restoration practices.

8.5 Recommendation of species

Several early-successional species showed strong growth and positive warming responses, particularly *Bridelia bridelifolia*, *Bridelia micrantha*, *Croton megalocarpus*, *Polyscias fulva*, *Dombeya torrida*, and *Markhamia lutea*, making them highly suitable for climate-smart restoration in Rwanda. Late-successional species such as *Afrocarpus latifolius*, *Prunus africana*, and *Ficus thonningii* also demonstrated resilience to warming, suggesting potential for mixed-species reforestation. Integrating findings from Paper IV, light-response analyses revealed contrasting shade-adaptation strategies: late-successional species optimized light interception, while early-successional species invested in stem growth to escape shade. Together, these results indicate that early-successional and transitional-forest species are best adapted to future warmer conditions, whereas some montane specialists may be at risk. However, drought sensitivity remains untested, underscoring the need for further research under hotter and drier future climates

9 Conclusions

This study revealed substantial interspecific variation in the temperature responses of Afromontane tree species, with important implications for forest composition and plantation planning under a warming climate. Consistent with previous Rwanda TREE project studies on leaf morphology and photosynthesis (Manishimwe et al., 2022; Mujawamariya et al., 2023; Tarvainen et al., 2022; Wittemann et al., 2022), the responses were highly species-specific. Warming generally enhanced growth in early-successional species, whereas late-successional species showed more variable responses, including reduced growth and higher mortality at warmer sites.

Growth stimulation was strongest in species originating from transitional rainforests compared to high-elevation montane forests, indicating that warmer conditions may favour lower-elevation, thermophilic species. Consequently, transitional forest species increasingly dominated stand basal area at lower, warmer elevations—evidence of thermophilisation. These results suggest that projected temperature increases could threaten late-successional and high-elevation species through competitive displacement, potentially reducing biodiversity and carbon storage in tropical montane forests.

Additional experiments on light regimes showed contrasting shade-adaptation strategies: late-successional species allocated more biomass to leaves and branches to maximize light interception, while early-successional species invested in stem growth to escape shade. This whole-plant perspective highlights that shade tolerance in tropical trees depends more on biomass allocation strategies than on leaf-level physiological traits alone, providing refined support for the carbon gain hypothesis.

The literature review shows that many native Rwandan tree species are highly multifunctional, supporting diverse ecosystem services and resilient landscapes. Trait–environment relationships underscore the need to match species to local conditions to maximize ecological and livelihood benefits. Yet native species remain underused, highlighting the need for trait-based, site-specific guidance for restoration, agroforestry, and climate adaptation in Rwanda.

Finally, my findings help reduce current uncertainties in native tree species selection for forest restoration, particularly under changing climatic conditions (Aitken et al., 2008; Forrester et al., 2005; Thomas et al., 2014). Based on both experimental and literature data, I identified several promising native species that demonstrated resilience to increased temperatures and are therefore suitable for planting in warmer part of Rwanda, considering future climate warming.

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