Thermophilization of Afromontane forest stands demonstrated in an elevation gradient experiment

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Abstract. The response of tropical trees and tree communities to climate change is crucial for the carbon storage and biodiversity of the terrestrial biosphere. Trees in tropical montane rainforests (TMFs) are considered particularly vulnerable to climate change, but this hypothesis remains poorly evaluated due to data scarcity. To reduce the knowledge gap on the response of TMFs trees to warming, we established a field experiment along a 1300 - 2400 m elevation gradient as a proxy for warming in Rwanda. Seedling size trees of twenty species native to montane forests in East and Central Africa were planted in multispecies plots at three sites along the gradient. They have overlapping distributions but primarily occur in either transitional rainforest (~1600 - 2000 m a.s.l.) or mid elevation TMF (~2000 - 3000 m a.s.l.), with both early- (ES) and late-successional (LS) species represented in each elevation origin group. Tree growth (diameter and height) and survival were monitored regularly over two years. We found that ES species, especially from lower elevations, grew faster at warmer sites while several of the LS species, especially from higher elevations, did not respond or grew slower. Moreover, a warmer climate increased tree mortality in LS species, but not much in ES species. ES species with transitional rainforest origin strongly increased in proportion of stand basal area at warmer sites, while TMF species declined, suggesting that lower-elevation ES

1

species will have an advantage over higher-elevation species in a warming climate. The risk of higher-elevation and LS species to become outcompeted by lower-elevation and ES species due to a thermophilization response in a warmer climate has important implications for biodiversity and carbon storage of Afromontane forests.

1. Introduction

The global average temperature has already increased by 1.09 °C from the period 1850-1900 to 2020 and is projected to further increase by the end of this century to between 1.4 and 4.4 °C, depending on CO_2 emission scenarios, SSP1-1,9 and SSP5-8.5, respectively (Arias et al., 2021). Although warming in the tropical region is predicted to be less than in the boreal region (Arias et al., 2021), the warming sensitivity of tropical trees may be larger since they are adapted to a thermally stable environment (Doughty & Goulden, 2008; Ghalambor et al., 2006; Janzen, 1967) and may have a lower capacity to acclimate to increased temperature compared to plants from more seasonal regions (Crous et al., 2022; Cunningham & Read, 2002; Way & Oren, 2010).

Forest monitoring data have shown that increasingly warm and dry conditions during recent decades have caused a decline of the Amazon carbon sink (Brienen et al., 2015). More recently, there are indications of this occurring also in the Congo basin (Hubau et al., 2020). On top of these long-term trends, pronounced negative effects of warm and dry conditions during El Niño years caused negative effects on tree growth in Central America, Amazonia, West and Central Africa and South-West Asia as well as increased tree mortality in Amazonia (Clark et al., 2003; Lewis et al., 2011; Rifai et al., 2018). Both heat and drought contribute to these trends and patterns (Jung et al., 2017), and the two stress factors likely interact such that heat (and the associated increase in water vapor pressure deficit, VPD) increases the severity of drought stress and vice versa (Killi et al., 2017; Zhao et al., 2013; Baumann et al., 2021 & 2022; Humphrey et al, 2021). However, due in part to common co-variation of heat and drought, the direct effect of warming on tropical forests remains unclear (Docherty et al 2022; Piao et al., 2020; Wang et al., 2014; Zhou et al., 2013). While negative effects of decreasing precipitation have been demonstrated in stand-scale throughfall exclusion experiments (da Costa et al., 2010; Estiarte et al., 2016; Meir et al., 2014; Nepstad et al., 2007; Rowland et al., 2021), large-scale warming field experiments are lacking. This severely hampers our ability to predict the fate of the tropical carbon sink in a warming world.

Global meta-analyses of experimental data with trees indicate that warming usually has positive effects on leaf net photosynthesis and growth in cooler biomes but negative effects in the tropics (Crous et al., 2022; Lin et al., 2010; Way & Oren, 2010). While warming has an overall negative effect on tropical tree growth across studies (Way & Oren, 2010), it should be emphasized that this is not always the case. Large variability across studies and species has been observed from positive to negative effects (e.g. Slot & Winter, 2018; Dusenge et al., 2021; Wittemann et al., 2022). This may reflect large

2

65   variation in species origin temperature range and how this compares to experimentally applied temperature treatments, with positive effects being more likely if origin climate is rather cool and the warming treatment is modest.

Tropical montane rainforests (TMFs) are considered particularly vulnerable to changes in the environment but our knowledge on how they will respond to climate change is currently very limited (Boehmer, 2011; Salinas et al., 2021; Tovar et al., 2022).

70   TMFs occur at all continents within the tropical biome. The lower elevation limit varies widely between and within continents but using a general lower limit of 1000 m a.s.l., the cover has been estimated to 8% of the total tropical forest area (Spracklen & Righelato, 2014). They provide important ecosystem services, such as regulation of regional climate and hydrology (Alamgir et al., 2016; Martínez et al., 2009; Soh et al., 2019), storage of surprisingly large amounts of carbon, especially on the African continent (Cuni-Sanchez et al., 2021; Nyirambangutse et al., 2017; Okello et al., 2022), and hosting of high levels of

75   biodiversity and endemism (Kessler & Kluge, 2008). Warming may have smaller direct negative effects on higher-elevation species growing in cooler TMF environments (at their current distribution) than on lower-elevation species which may already grow near or at their thermal optimum (Feeley et al., 2020). On the other hand, a warmer climate can make lower-elevation species more competitive at higher elevations, over time shifting species distributions upwards at the expense of current higher-elevation species. Moreover, a warmer climate may shift the competitive balance between species with overlapping

80   distributions, to the disadvantage of those with ranges centred at higher, cooler elevations. Such shift has recently been observed in Andean montane forests (Duque et al., 2015; Fadrique et al., 2018). The tree community composition shift with warming observed in these studies was caused primarily by increased mortality in higher-elevation species, leading to increasing relative abundance of species with ranges centred at lower elevations, so called "thermophilization". These findings show that there is considerable variation in warming sensitivity among co-existing species, and that this is linked to species

85   distribution range and thermal niche. The underlying mechanisms behind the variation are not well understood, but a recent study on four species from contrasting elevation origins indicate that species differences in physiological temperature sensitivities play a role (Wittemann et al., 2022). Such species differences may be related to different growth strategies and the associated traits.

90   Tree species dominating in secondary and primary forests are examples of species groups with different growth strategies, i.e. early and late successional species, respectively. The early successional species are acquisitive and fast-growing with low wood density while late successional species are more conservative and slow-growing with higher wood density. Secondary forest has progressively become more common at the expense of primary forest due to land-use changes and now represent >50% of all tropical forests (Chazdon et al., 2009). However, it remains uncertain if the early successional species are winners

95   or loser in a warming climate and thus if climate change will amplify the expansion of secondary forests or not. There are experimental indications that photosynthesis and growth respond more negatively to warming inlate successional species (Carter et al., 2020; Cheesman & Winter, 2013a; Dusenge et al, 2021; Mujawamariya et al., 2023; Slot & Winter, 2018; Tarvianen et al., 2022; Vårhammar et al., 2015). However, these studies included only few species representing early and late

successional strategies, used artificial heating in chambers/infra-red heaters, or only looked at physiology. Field monitoring in a TMF in Kenya showed that the effects of high temperature on tree stem growth was more negative in late compared to early and mid-successional species (Gliniars et al., 2013). On the contrary early successional species have been found more susceptible to climate-induced mortality compared to late successional species (Aleixo et al., 2019; Baumann et a1., 2022; Elias et al., 2019; Feng et al., 2017; Herrera-Ramírez et al., 2021). A possible explanation to these discrepancies might be that early successional species are more drought sensitive (Elias et al., 2020), while late successional species are more heat sensitive.

Knowledge about climate and climate change responses of different tropical tree species is also crucial for tree plantation efforts. Historically, exotic species have been preferred in most tropical areas (Sands, 2005). However, many current plantation programs aim to increase the use of native tree species to diversify and enhance ecosystem services (Bremer & Farley, 2010; Galhena et al., 2013; Thomas et al., 2014), resilience to different stress factors (Aguirre-Gutiérrez et al., 2022; Brasier, 2008; Woodcock et al., 2017) and biodiversity (Brockerhoff et al., 2008; Stephens & Wagner, 2007). Moreover, multi-species native species plantations may be hydrologically preferable for nearby agriculture compared to monocultures with fast-growing exotic species (Sena et al., 2014). However, the current ambitions to promote the use of native tree species in tropical plantations is hampered by limited knowledge of their climate sensitivity, leading to large risks of failure if species are planted in the wrong place or without consideration of likely climate change during the coming decades (Aitken et al., 2008; Forrester et al., 2005; Thomas et al., 2014).

Elevation gradients offer the potential to study temperature responses of plants and ecosystems under ecologically realistic conditions (Körner, 2007; Malhi et al., 2010; Tito et al., 2020). However, most studies conducted along tropical elevation gradients have focused on characterizing differences in plant and ecosystem traits of existing natural vegetation, with different species or ecotypes being present at different elevations (Báez et al., 2015; Cuesta et al., 2017; Fadrique et al., 2018; Malizia et al., 2020; Mujawamariya et al., 2018). While such studies are relevant for exploring how climate shapes plant communities and ecosystems in the long term, they say little about the responses of trees under ongoing rapid climate change. Studies that integrate elevation gradient approaches with experimental manipulations have been suggested to bridge the gap between large-scale observational studies and smaller-scale controlled experiment with limited ecological realism (Sundqvist et al., 2013). A powerful but underused approach is to use multi-species plantations with genetically similar plant material established at different elevations. If tree species are planted in mixed stands, such studies also offer the possibility to explore climate change effects on tree stand composition. That is the approach taken in this study.

We investigated the growth and mortality responses of 20 tree species originating from two elevation ranges of African upland forests (montane and transitional rainforests having their mid-point of origin above and below 2000 m a.s.l., respectively). Seedling sized trees were planted in large and mixed multi-species plantations along an elevation gradient ranging from 2400

down to 1300 m a.s.l. elevation in Rwanda. The elevation gradient was used as a proxy for possible future warming and irrigation was applied to compensate for variation in rainfall along the gradient., The overall aim of the study was to determine the effect of a warmer climate on tree growth and mortality of tropical upland tree species with contrasting successional strategies and origin climate. Since this is a stand-level study, we could also assess warming impacts on tree stand composition within the experimental sites. Our specific aims were to test the following hypotheses:

H#1. Tree growth responses to a warmer climate are more positive (or less negative) in early than in late successional tree species.

H#2. 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 rainforests (< 2000 m a.s.l.).

H#3. Mortality increases in a warmer climate, and this is more pronounced in high-elevation and late successional compared to lower-elevation and early successional tree species.

H#4. Interspecific variation of growth and mortality responses leads to altered tree community composition in a warmer climate, favouring lower-elevation and early successional tree species.

2. Materials and methods

2.1 Experimental sites

Growth and mortality of tropical trees were studied within the TRopical Elevation Experiment in Rwanda (Rwanda TREE; see www.rwandatree.com) during two years after plantation (planting period was January 2018 to December 2019). Mixed plantations with 20 tropical tree species native to East & Central Africa were established at three sites along an elevation gradient from 2400 to 1300 m.a.s.l. (Table 1; Figure S1). From the highest to the lowest elevation, over a distance of c. 170 km, the mean annual temperature (MAT) increased by 5.4 °C while mean annual precipitation (MAP) decreased by approximately 50%. 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) in close proximity to the plantation buffer zone surrounding Nyungwe National Park (NNP), a TMF in the southwestern part of Rwanda. 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. The low-elevation site (LE; 1300 m a.s.l.) is located at Ibanda Makera in Kirehe district (2°6'31"S ;30°51'16" E), c. 126 km north-east of Rubona site, in the eastern part of Rwanda, near the border with Tanzania. 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 (Table 1; Figure S1). 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

5

165 montane and all species except one can be found at >2000 m elevation (Figure 1). Furthermore 18 out of 20 species used in this experiment naturally grow in the neighbouring NNP, ranging from 2950 down to 1600 m a.s.l. (Fisher and Killman, 2008; Nyirambangutse et al., 2017). With the HE site as control, the ME (Rubona) and LE (Makera) sites represent two different warming scenarios.

170 **Table 1.** Weather and soil characteristics of the sites along the elevation gradient. Weather data show mean ± standard deviation for two years, from 1st February 2018 to 31st January 2020. Soil T and SWC are measured at 10-20 cm depth on 6 plots and other soil data variables represents a mean of 0-30 cm depth of three blocks at each site. Wind, soil T and SWC were only measured during the 2019/20 period. HE, high elevation; ME, mid elevation; LE, Low elevation.

	Site:			P-values
	HE (Sigira)	ME (Rubona)	LE (Makera)	
Site characteristics				
Elevation (m a.s.l.)	2400	1600	1300	
Latitude	S 2° 30' 54''	S 2° 28' 30''	S 2° 6' 31''	
Longitude	E 29° 23' 44''	E 29° 46' 49''	E 30° 51' 16''	
Potential natural vegetation (PNV)	Tropical Montane Rain Forest	Lake Victoria Transitional rain forest	Evergreen & semi-evergreen bushland and thicket	
Climate				
MAP (mm yr^{-1})	2144 ± 61	1672 ± 136	1106 ± 33	
MAT (°C)	15.2 ± 0.1	20.0 ± 0.0	20.6 ± 0.1	
T air day mean (°C)	17.1 ± 0.2	22.4 ± 0.1	24.0 ± 0.3	
T air night mean (°C)	13.3 ± 0.1	17.5 ± 0.1	16.9 ± 0.03	
T air 180 cm 99%ile (°C)	23.1 ± 0.4	28.3 ± 0.3	31.3 ± 0.5	
T air 50 cm 99%ile (°C)	26.1 ± 0.8	30.0 ± 0.4	32.8 ± 1.1	
T air 180 cm 1%ile (°C)	10.9 ± 0.3	13.7 ± 0.3	11.3 ± 0.2	
T air 50 cm 1%ile (°C)	10.1 ± 0.2	13.5 ± 0.2	10.7 ± 0.4	
VPD day mean (kPa)	0.51 ± 0.03	1.03 ± 0.01	1.14 ± 0.03	
VPD 99%ile (kPa)	1.45 ± 0.004	2.47 ± 0.11	2.98 ± 0.16	
PPFD day mean (μmol m^{-2} s^{-1})	611 ± 66	764 ± 62	740 ± 31	
PPFD 99%ile (μmol m^{-2} s^{-1})	1683 ± 134	1884 ± 135	1841 ± 104	
Wind speed (m s^{-1})	0.6	0.7	0.3	
Wind speed gusts (m s^{-1})	1.2	1.2	0.7	
Wind speed gusts 99%ile (m s^{-1})	3.5	4.0	3.0	
Soil properties				
Soil T mean (°C)	16.4 ± 0.6a	22.0 ± 1.5b	22.0 ± 1.0b	**<0.001**
Soil T 99%ile (°C)	19.3 ± 1.2a	27.1 ± 2.5b	27.5 ± 2.5b	**<0.001**
Soil T 1%ile (°C)	14.6 ± 0.4a	18.9 ± 0.8b	18.8 ± 0.9b	**<0.001**
SWC (m^3 m^{-3})	0.26 ± 0.07a	0.19 ± 0.03b	0.20 ± 0.02ab	**0.024**
SWC 99%ile (m^3 m^{-3})	0.36 ± 0.04a	0.27 ± 0.05b	0.33 ± 0.03a	**0.005**
SWC 1%ile (m^3 m^{-3})	0.18 ± 0.05	0.14 ± 0.03	0.13 ± 0.02	0.068
SBD (g cm^{-3})	1.0 ± 0.03a	1.6 ± 0.1b	1.4 ± 0.1c	**<0.001**

6

Sand (%)	36.4 ± 2.0a	56.4 ± 1.4b	41.4 ± 1.6c	**<0.001**
Silt (%)	19.5 ± 1.7a	6.5 ± 0.5b	26.1 ± 0.6c	**<0.001**
Clay (%)	44.1 ± 3.4a	37.1 ± 1.1b	32.6 ± 1.1b	**0.002**
pH (Water)	4.2 ± 0.2a	5.0 ± 0.1b	6.1 ± 0.1c	**<0.001**
pH (KCl)	3.4 ± 0.1a	3.9 ± 0.04b	5.3 ± 0.2c	**<0.001**
Al^{3+} (meq/100g)	4.7 ± 0.4a	1.4 ± 0.4b	0.0 ± 0.0c	**<0.001**
CEC (meq/100g)	15.6 ± 2.1a	8.0 ± 1.0b	13.9 ± 1.1a	**0.002**
Available P ($\mu g\ g^{-1}$)	12.1 ± 3.9	14.1 ± 0.7	8.2 ± 2.5	0.095
$N\text{-}NH_4^+$ ($\mu g\ g^{-1}$)	11.3 ± 2.9	10.1 ± 2.3	7.1 ± 1.0	0.133
$N\text{-}NO_3^-$ ($\mu g\ g^{-1}$)	28.3 ± 1.9a	7.2 ± 3.0b	24.1 ± 4.6a	**0.001**
Tot N ($mg\ g^{-1}$)	2.73 ± 0.3 a	2.00 ± 0.4ab	1.26 ± 0.0b	**0.003**
Tot P ($mg\ g^{-1}$)	0.65 ± 0.02a	0.14 ± 0.04b	0.27 ± 0.02c	**<0.001**
Org C ($mg\ g^{-1}$)	38.6 ± 1.1a	27.1 ± 3.1b	27.3 ± 2.4b	**0.001**

175

PNV, defined by Kindt et al. (2014); MAP, mean annual precipitation; MAT, mean annual temperature; T air day, day temperature (PFFD >2 µmol m-2 s-1); T night, night temperature (PFFD <2 µmol m-2 s-1); VPD, Vapor Pressure Deficit; PPFD, Photosynthetic photon flux density. T soil, soil temperature at 10-20 cm depth; SWC, soil water content at 10-20 cm depth; SBD, soil bulk density; CEC, cation exchange capacity; Tot N and P, total nitrogen and phosphorus concertation; Org C, organic carbon concentration.

180 **2.2 Experimental design and plot preparation**

Before establishment of plantations, all vegetation consisting of bushes and trees was cleared and large roots were removed. At each site, 18 plots of 15 m x 15 m, spaced by 2.5 m paths, were established on a 50 x 102.5 m planimetric area. Within each plot, 20 different species with a replication of 5 (i.e. 100 trees per plot) were planted with 1.5 x 1.5 m spacing and randomized positioning of each tree individual. The total number of trees was 1800 (i.e. 18 plots x 100 trees) at each site. The 18 plots

185 allowed for a full factorial experimental design, with three water levels and two fertility levels and a replication of three plots for each of the six treatment combinations. Before mid-July 2019, all trees at all sites received water when needed, irrespective of the subsequent planned water treatment. During the first dry period in July-August 2018 all trees were manually irrigated, while all plants were exposed to the dry period from mid-July to end of August 2019. The water and nutrient treatments started in September and November 2019, respectively. No significant (P > 0.05) effect on diameter and height growth of the

190 treatments was observed during this period likely because September to December is within the rainy season. We therefore use averages of all plots in this study. Site maps with experimental design are presented in Figures S2-S4.
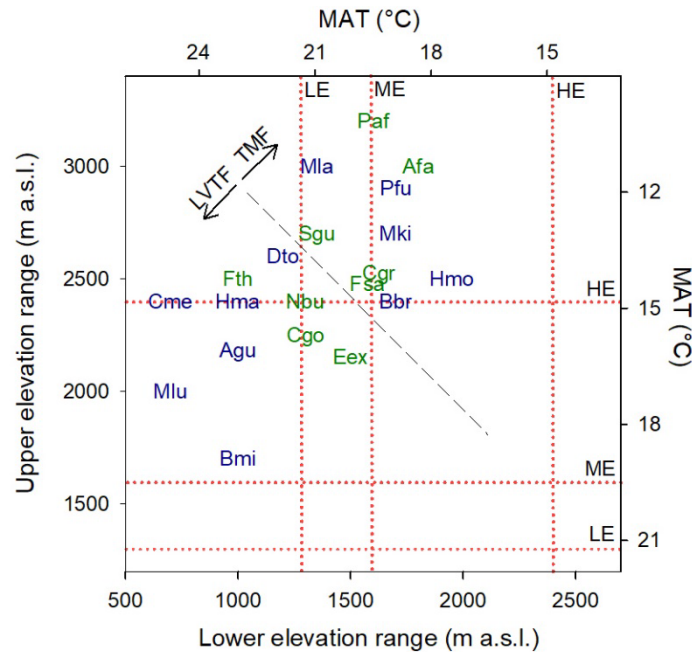
Figure 1. Commonly observed natural elevation ranges for the species used in the experiment (Blosch et al., 2009; Fischer & Killman, 2008; Kindt et al., 2014; Nyirambangutse et al., 2017). The mean annual temperature (MAT) scale was developed from a linear regression ($R^2 = 0.95$) of MAT versus elevation, using data from eight locations in Rwanda. The black dashed diagonal 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 red dotted lines. Species codes in blue and green are early and late successional species, respectively. For full species names, see Table 2.

2.3 Plant material

The tree species included in the experiment were selected to represent important and common species in two East and Central African forest types: montane forest (TMF > 2000 m a.s.l.) and transitional forest (LVTF ~1600-2000 m a.s.l.), see Figure 1 for species elevation ranges. From each forest type, species representing both early (ES) and late (LS) succession strategies were selected with the following number of species per combination: 5 ES/TMF, 5 LS/TMF, 6 ES/LVTF and 4 LS/LVTF (Table 2). Note that from literature, the classification *Ficus thonninghii* and *Markhamia lutea* into distinct successional groups is ambiguous (Table 2, S4), but according to our assessment they belong mostly to late and early successional groups respectively, and will here be treated as such. The species represent a mix of mostly evergreen and semi-deciduous trees, but also two deciduous species were included (Table 2).

8

The trees were propagated from seeds, cuttings or naturally generated seedlings, depending on species specific difficulties of propagation, in poly-pots in a nursery at Rubona research station (near ME-site) during 2017. The germplasms were collected from Nyungwe and Ndiza montane forests (high-elevation) or Rubona research station and Ruhande arboretum located in the transitional forest vegetation zone (mid-elevation) depending on forest type of origin. After six to twelve months in the nursery and having reached a height of ~5-75 cm, depending on species, each plant was randomly assigned to site, plot and plot position (as constrained by the experimental design) and transplanted to the experimental plots within a period of approximately one month at the turn of the year from 2017 to 2018. Details of the propagation and initial sizes of the trees are given in Tables S1-S3.

2.4 Environmental conditions

Weather stations were installed in an open space next to the plantations at all Rwanda TREE sites, equipped with sensors for measurements of temperature, relative humidity, solar radiation, precipitation and wind direction and speed (VP-3/VP4, QSO-S PAR and ECRN-100, Davis cup anemometer, respectively, from Meter group Inc, Pullman, WA, USA) connected to data a logger (Em50G, Meter group Inc). In addition, soil temperature and soil water content sensors (Teros 12, Meter group Inc) were installed in the centre of six plots connected to a data logger (Em60G, Meter group Inc). The recording of most parameters started late January 2018, while wind and soil measurements started late August 2018 (Table 1). All parameters were recorded every 30 min. The MAT measured from 1 February 2018 to 31 January 2020 at the HE-site (Sigira), ME-site (Rubona) and LE-site (Makera) were 15.2, 20.0 and 20.6 °C, respectively. The daytime and extreme temperatures (expressed as 99%ile) were 17.1/23.1 °C at HE-site, 22.4/28.4 °C at ME-site, and 24.0/31.2 °C at LE-site. The larger difference in the daytime and extreme temperatures compared to MAT between the ME and LE sites was mainly due to a larger diurnal range and lower night-time temperatures at the LE site. Also, MAP differed between sites, decreasing progressively from Sigira (2144 mm) to Rubona (1672 mm) and Makera (1106 mm; Table 1). However, the relative seasonal distribution of precipitation was similar at all sites, with highest rainfall in March–May and a dry period in June–August. Solar radiation was similar at ME and LE sites while the HE-site received on average less radiation, probably due to higher cloudiness as only small differences in monthly maximum radiation was observed between the sites (not shown). Differences in high light climate may influence species with early and late successional strategies differently (Ntawuhiganayo et al 2020), but we believe that the on average

Table 2. Taxonomy of species, their functional type and ecological and geographical distribution. TMF, tropical montane forest (~ > 2000 m a. s. l.); LVTF, Lake Victoria Transitional Forest (~ 1600 - 2000 m a. s. l.), ES, early successional; LS, late successional; The distribution is classified into W, west; C, central; E, east and S, south Africa.

Code	Scientific name and Author[1]	Family name[1]	Forest type[2]	Successional group[3]	Plant functional type[5]	Distribution[6]
Afa	*Afrocarpus falcatus* (Thunb.) C.N.Page	Podocarpaceae	TMF	LS	Evergreen	E
Agu	*Albizia gummifera (J.F.Gmel.)* C.A.Sm.	Fabaceae	LVTF	ES	Deciduous	C & E
Bbr	*Bridelia brideliifolia* (Pax) Fedde	Phyllanthaceae, (Euphorbiaceae)	TMF	ES	Semi-deciduous	C
Bmi	*Bridelia micrantha* (Hochst.) Baill	Phyllanthaceae, (Euphorbiaceae)	LVTF	ES	Semi-deciduous	W & E
Cgo	*Chrysophyllum gorungosanum* Engl.	Sapotaceae	LVTF	LS	Evergreen	E
Cgr	*Carapa grandiflora* Sprague	Meliaceae	TMF	LS	Evergreen	E
Cme	*Croton megalocarpus* Hutch.	Euphorbiaceae	LVTF	ES	Semi-deciduous	C & E
Dto	*Dombeya torrida* (J.F.Gmeel.) Bamps	Malvaceae, (Sterculiaceae)	LVTF	ES	Semi-deciduous	W, C & E
Eex	*Entandrophragma excelsum* Sprague	Meliaceae	LVTF	LS	Evergreen	C & E
Fsa	*Faurea saligna* Harv.	Proteaceae	TMF	LS	Evergreen	E & S
Fth	*Ficus thonningii* Blume	Moraceae	LVTF	LS [4]	Deciduous	W, C & E
Hma	*Harungana madagascariensis* Lam.ex.Poir	Clusiaceae	LVTF	ES	Semi-deciduous	W, E & S
Hmo	*Harungana montana* Spirlet	Hypericaceae	TMF	ES	Semi-deciduous	C
Mki	*Macaranga kilimandscharica* Pax	Euphorbiaceae	TMF	ES	Semi-deciduous	C & E
Mla	*Maesa lanceolata* Forssk.	Primulaceae	TMF	ES	Semi-deciduous	E
Mlu	*Markhamia lutea* K.Schum.	Bignoniaceae	LVTF	ES [4]	Evergreen	E
Nbu	*Newtonia buchananii* (Baker f.) G.C.C.Gilbert & Boutique	Fabaceae	LVTF	LS	Evergreen	W, C & E
Paf	*Prunus africana* (Hook.f.) Kalkman	Rosaceae	TMF	LS	Evergreen	E
Pfu	*Polyscias fulva* (Hiern) Harms	Araliaceae	TMF	ES	Semi-deciduous	E
Sgu	*Syzygium guineense* DC.	Myrtaceae	TMF	LS	Evergreen	E

[1]Taxonomy information from The World Flora Online (http://www.worldfloraonline.org). Family names are given according to Angiosperm Phylogeny Group (APG III) system and when applicable earlier family names is given in brackets; [2]Forest types follows the Potential Natural Vegetation's by Kindt et al. (2014); [3]Sources of successional group classification are given in the Table S4; [4]The classification of Fth and Mlu into distinct successional groups is ambiguous, but according to our assessment they belong mostly to the LS and ES groups, respectively (see table S4), and will be treated as such; [5]Semi-deciduous species drop variable amount of leaf mainly depending drought period severity, but are rarely completely defoliated; [6]According to our definition, central and east Africa distribution areas overlaps in Rwanda, thus trees with both C and E distributions will be found there, but only the main distribution areas are given.

8.5% lower high radiation at HE site compared to LE site likely has very limited effects. Soil temperatures were closely related to the site MAT, although it was probably also affected by radiation and canopy cover. Soil water content (SWC) was similar at LE and ME sites in spite of differences in MAP and soil texture (Table 1). The mean SWC at HE was substantially higher compared to the two other sites, probably because of both higher MAP, higher water-holding capacity due to higher soil clay content (Table 1), and lower evapotranspiration due to lower air temperature.

10

2.5 Soil characteristics

Before planting the trees, in November 2017 soil samples were collected at 0-10 cm and 20-30 cm in the center of each plot using soil sample rings (Ø 53 mm, Ejkelkamp soil & water, Giesbeek, the Netherlands). Soil bulk density (SBD), NH_4^+, NO_3^- and available P were analysed from composite samples of two adjacent plots, while the remaining soil parameters were analysed from composite samples of six plots. All values are presented as averages of 0-30 cm depth and as mean and standard deviation of three samples per site (each combining six plots), representing three blocks per site (Table 1). Oven dried (70 °C) soil samples of known volume was used to determine SBD. Samples for analysis of total N and P were pre-grinded using a mortar and pestle and further grinded to a fine powder with a ball mill (model MM 301, Retsch, Haan, Germany). N and P concentrations were determined by dry combustion using an elemental analyser (EA 1108, Fison Instruments, Rodano, Italy) and inductively coupled plasma mass spectrometry (AQ250; ACME Analytical Laboratories, Vancouver, BC, Canada), respectively. For all other parameters, fresh soil samples were sent for analysis to the Soil & Plant Analytical Laboratory at Rwanda Agriculture and Animal Resource Development Board (RAB) at Rubona research station, Rwanda.

The main soil texture differences between sites were a larger proportion of sand and less silt at Rubona (53-62% and 5-9%, respectively) compared to the soil at Sigira and Makera sites (35-45% and 15-27%, respectively) while the clay content was relatively high at all sites (30-50%). The soil pH (water) was 4.2 at the HE-site and increased with approximately one unit for each step down the elevation gradient, which explain the decline in Al_3+ with decreasing elevation but did not affect the cation exchange capacity (CEC). Soil fertility expressed as total N and P content tended to decline with decreasing elevation, partly explained by higher organic content at the HE site compared to the other sites. However, the available N (NH_4^+, NO_3^-) and P were not significantly affected by elevation, but NO_3^- was lower at the ME site.

2.6 Growth and mortality monitoring

The stem height (h) and diameter (D) of each tree were measured trimonthly during the first two years, starting at planting (December 2017/January 2018) and resulting in 8 censuses. The measurement of D was taken using callipers while h was measured with a measuring stick or, for larger trees, a telescopic measuring pole. For species having several stems, only the main stem (tallest) was measured regularly and presented in this study, but we also report the average number of living stems for each species observed at the 7th census (late September to early October 2019). At each census, dead trees or trees with reduced vitality were recorded. The D measurements of trees with a h below and above 250 cm diameter were done at stem base (~5 cm above ground, D_{base}) and at breast height diameter (D_{bh}), respectively. To compare the diameter of all trees irrespective of h, parallel measurements of D_{bh} and D_{base} were made at two consecutive censuses after the trees had reached a h of 250 cm as well as after three years. These data were used to develop species-specific functions to estimate the D_{base} for all trees on which D_{base} was not measured and at all census occasions using the following equation:

$$D_{base} = \frac{D_{bh}}{k \cdot h + a} \qquad (1)$$

where k and a are species-specific constants determined from change in D_{bh}/D_{base} ratio with h. Note that when roots were causing stem irregularities (swelling etc.) the D_{base} was measured above 5 cm from ground. As a quality assurance, all D and h data were plotted against time to identify outliers and missing values which were replaced by interpolated values. The interpolated values corresponded to <1.5% of the D_{base} and < 0.5% of the h values, out of 43 200 recordings for each variable.

$$RGR = \frac{lnX_2 - lnX_1}{t_2 - t_1} \quad (2)$$

2.7 Relative growth rate of D_{base} and h

The relative growth rate (RGR) of both D_{base} and h of the trees were calculated using the standard RGR equation: where X_1 and X_2, corresponds to D_{base} or h of the beginning and end, respectively, of each trimonthly census time interval (t1 and t2, respectively). Since RGR varies with tree size (Figure S5) the values were size standardized to be able to make size independent RGR comparisons of different species and sites. This was done for one small and one large tree size category, by averaging the RGR for D_{base} within ranges of 10-25 mm and 50-75 mm (D-RGR$_{D10-25}$ and D-RGR$_{D50-75}$) and for h within ranges of 75-100 cm and 250-300 cm (H-RGR$_{H75-100}$ and H-RGR$_{H250-300}$), respectively.

2.8 Tree stand composition

The site effect on tree stand composition was analysed by comparing the basal area (BA) of the four species groups, ES/TMF, ES/LVTF, LS/TMF and LS/LVTF. The BA is a stand level measure defined as the sum of cross-sectional stem area (A_c, calculated from D_{base} values) of living individuals expressed per ground area. The BA of each species group was calculated as follows:

$$BA = \frac{\sum_{i=1}^{n} A_{ci}}{A_p \frac{n+d}{100}} \quad (3)$$

where A_p is the plot area (225 m^2); n and d are the numbers of living and dead individuals per plot, respectively, within each species group. The term $n+d/100$ is to normalize for initial difference in number of individuals (i.e. number of species x 5 replicates per plot) between species groups (Table 2) but also to include both living and dead trees in the effect on BA. Absolute (cm^2 m^{-2}) and fractional (% of plot area) BA for each species group are presented as BA$_{abs}$ and BA$_{frac}$, respectively. The influence of mortality on BA for the four species groups was analysed by comparing the result from Eq. 3 with and without the term d. Although, this will not consider the dynamic effect of neighbouring trees exploring the space of the dead trees and thus potentially having larger D_{base} growth, it will give a reasonable estimate of the importance of mortality for BA of different species groups. Note that the BA$_{abs}$ and BA$_{frac}$ of the four species groups represented approximately 25% each, at the beginning of the experiment.

2.9 Statistics

315 The site and species effect on D_{base}, h (8th census), number of stems per individual (7th census), D-RGR$_{D10-25}$, D-RGR$_{D10-25}$, H-RGR$_{H75-100}$, H-RGR$_{H250-300}$ were analysed using a two-way ANOVA with site and species as fixed factors. The site and species group effect on BA$_{abs}$ and BA$_{frac}$ were analysed using a two-way split-plot (split between the four species groups within each plot) ANOVA with species groups as within and site as between subject factors. In case of significant site x species/species group interactions, the site effect was analysed separately for each species/species group, using a one-way ANOVA followed

320 by Tukey's post-hoc test. This latter type of analysis was made also for soil variables. All effects were analysed by using plot level means (n=18 or less when applicable per site). Test of normality (Shapiro-Wilk) was performed to test the distribution of data, and Levene's tested for homogeneity of variance. Normality was mostly obtained for analysis of individual species and sites. Homogeneity of variance were mostly obtained for analysis of individual species and species groups (for BA) while not when all species or species groups were analysed together. Effects were considered statistically significant at $P < 0.05$ if

325 homogeneity of variance was obtained and at $P < 0.01$ when homogeneity was not obtained. Furthermore, to reduce the potential bias caused by non-homogeneity, species with an unequal replication of RGR data on plot level (>1.5 ratio of highest and lowest number of plot replicates between sites) were not included in the statistical analysis. This reduced the number of species included in the standardized RGR analysis and was denoted 'not applicable' (na) in the presentation of statistical results. Greenhouse-Geisser correction was used to adjust degrees of freedom (df) for within subject factors violating the

330 sphericity assumption according to Mauchly's test. A GLM regression with Poisson distribution was used to analyse the site and species effect on tree mortality using records from individual trees. As the site x species interaction was significant, the site effect for each species was analysed by paired comparison of site using the same method. To reduce the effects of multiple analysis of site effects (3) the significant P-values was reduced to < 0.01. All statistical tests were made by using the SPSS 28.0 software package (SPSS, Inc., Chicago, IL, USA).

3. Results

335 **3.1 Overall effects of high temperature on growth and mortality**

Both site and species identity affected tree growth, expressed as absolute and relative stem D and h increment (Table 3; Figures 2a, b and 3). Tree mortality also differed between sites and species (Figure 2d). However, the responses to a warmer climate (i.e. site) was species specific, as shown by the highly significant (P<0.001) interactions between species and sites for all

340 analysed growth-related variables (Table 3). In the following, we will address how these species differences relate to contrasting successional strategy (early versus late successional) and climate of species origin (montane versus transitional forest).

Table 3. Results from two-way ANOVA for site and species (Sp.) effects on stem diameter at base (D_{base}); stem height; number

345 of stems per individual (stems#), absolute basal area (BA) of species categories and standardised relative growth rates (RGR) of

13

Variable	Sp#	Statistics	Source: Site	Sp.	Site * Sp.	Error	Total
Two years after plantation:							
D_{base}	20	df	2	19	38	1017	1077
		F-ratio	160.4	221.9	31.4		
		P-value	<0.001	<0.001	<0.001		
Height	20	df	2	19	38	1017	1077
		F-ratio	274.2	214.0	25.9		
		P-value	<0.001	<0.001	<0.001		
Stems#	20	df	2	19	38	1017	1077
		F-ratio	23.0	64.4	5.4		
		P-value	<0.001	<0.001	<0.001		
Mortality	17	df	2	16	20	1020	1080
		Wald Chi-Square	26.8	209.4	45.4		
		P-value	<0.001	<0.001	<0.001		
Standardised RGR:							
D-RGR$_{D10-25}$	19	df	2	18	36	956	1013
		F-ratio	215.2	150.4	26.6		
		P-value	<0.001	<0.001	<0.001		
D-RGR$_{D75-100}$	15	df	2	12	24	631	670
		F-ratio	4.2	5.5	5.8		
		P-value	0.016	<0.001	<0.001		
H-RGR$_{H75-100}$	16	df	2	16	32	821	872
		F-ratio	113.3	36.8	8.1		
		P-value	<0.001	<0.001	<0.001		
H-RGR$_{H250-300}$	12	df	2	12	24	653	692
		F-ratio	43.2	8.1	3.4		
		P-value	<0.001	<0.001	<0.001		

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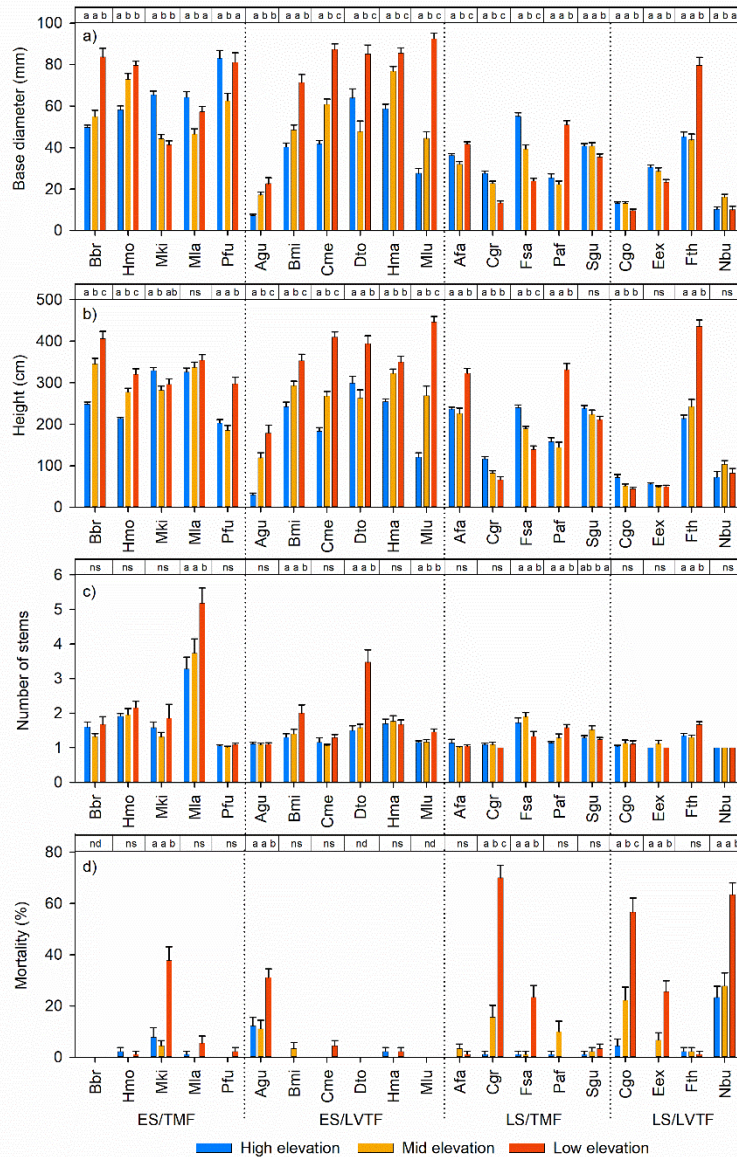
Figure 2 a-d. (a) Stem height, (b) stem diameter at base, (c) number of stems from ground per individual and (d) mortality in percent of planted individuals, two years after plantation (except number of stems that was recorded 21 months after plantation) of each species and site (High, Mid and Low elevation). Each bar shows plot level mean with standard error. For tree individuals having several stems, only the tallest stem was measured for diameter and height on each individual tree (panel a and b). Full species names are given in Table 2. Species are grouped into combinations of: ES, early successional; LS, late successional; TMF, tropical montane rainforest; LVTF, Lake Victoria transitional rainforest. The significances of the site effects for each species are reported at the top of each panel. Tukey´s post-hoc test was used for diameter, height and number of stems, while paired Poisson regressions was used for mortality. Different letters indicate significant differences (P < 0.05 except for mortality where P <0.01 was used); ns, not significant; nd, no dead individuals (panel d) and thus no variance analysis could be conducted. For statistical details, see Table S4.

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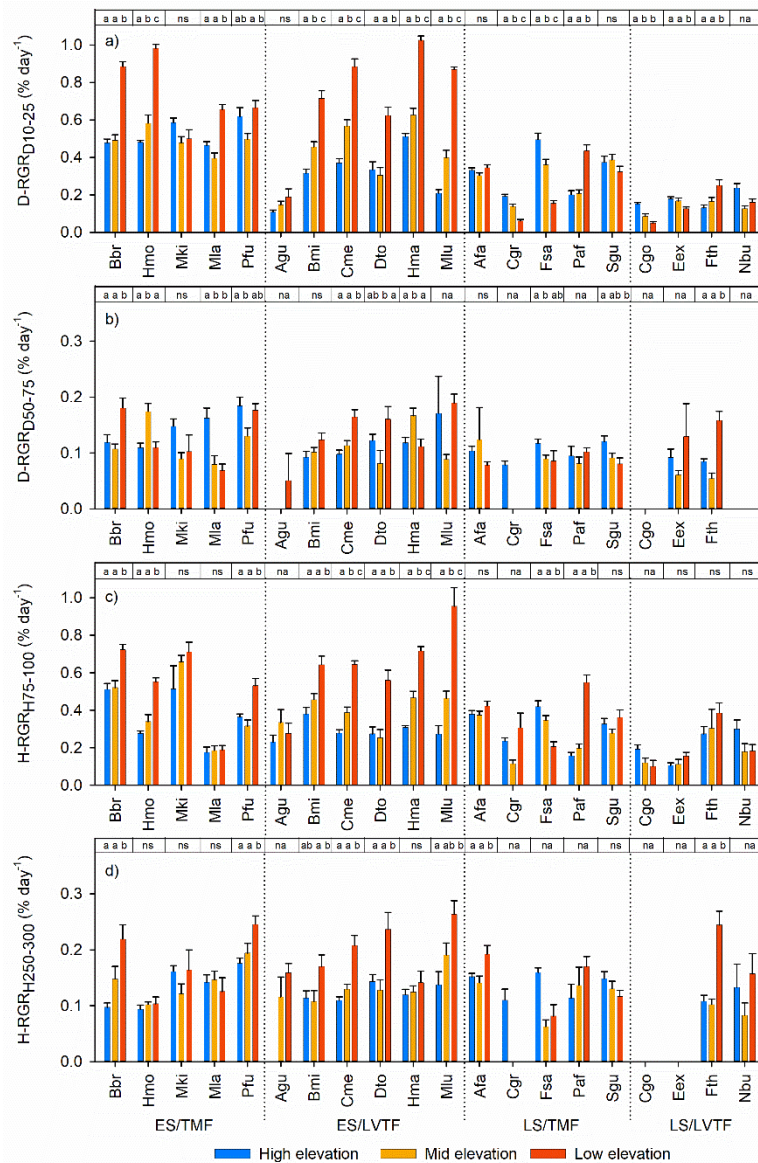
Figure 3 a-d. Standardised relative growth rates (RGR) of stem diameter at base (D_{base}) at a D_{base} of (a) 10-25 mm (D-RGR$_{D10-25}$) and (b) 50-75 mm (D-RGR$_{D10-25}$) and of height at a height of (c) 75-100 cm (H-RGR$_{H75-100}$) and (d) 250-300 cm (H-RGR$_{H250-300}$) of each species and site (High, Mid and Low elevation). Each bar shows plot level mean with standard error. Full species names are given in Table 2. Species are grouped into combinations of: ES, early successional; LS, late successional; TMF, tropical montane rainforest; LVTF, Lake Victoria transitional rainforest. The results of post-hoc test (Tukey's) for site effects for each species are reported at the top of each panel. Different letters indicate significant differences (P<0.05); ns, not significant; na, not applicable for the statistical analysis, due to too few replicates within the standardised diameter or height intervals. For statistical details, see Table S4 and for standardised RGR details, see Figure S2.

16

3.2 Growth of stem base diameter and height

The most typical growth curve patterns are illustrated for stem h in Figure 4, starting with a lag phase after plantation, followed by faster growth rates that decline with increasing size. As a result of species and site interactions the following growth trajectories were identified: i) increasing growth with warming in both ME and LE sites or only at the LE site, compared to the HE site (Figures 4a, b), ii) decreasing growth with warming (Figure 4c) and iii) no effect on growth by warming (Figure 4d). For a comprehensive view of growth trajectories of both D_{base} and h of all species, see Figures S6 and S7. For early successional species, warmer growth temperature significantly increased D_{base} and h growth in 8 out of 11 (8/11) and 9/11 species, respectively, but the response differed between elevation origin groups (Figures 2a, b; Table S5). A warmer climate significantly increased stem D and h in all early successional species (6/6) species of transitional forest origin, while early successional species of montane forest origin exhibited increased, decreased, or unchanged stem D and h with warming. In late successional species, stem D and h increased at warmer sites only in 3 out of 9 species, while others significantly decreased or were unaffected. In general, the late successional species grew slower compared to the early successional species at all sites and the responses to warming in late successional species did not depend on elevation origin. The effects of warm climate on stem D and h were strongly linked, except for *Albizia gummifera* which deviated substantially from the 1:1 line (Figure 5). On average, D_{base} and h after two years for early successional species increased by12% and 43% at the ME and LE sites, respectively, compared to the HE site, while corresponding values were -8% and +11% for late successional species, -7% and +10% for TMF species and +23% and +59% for transitional forest species.

3.3 Number of stems

For translation into stem volume production, also the multistem behaviour is important. The individuals of most tree species had one or two stems (Figure 2c). Eight species (5 late and 3 early successional species) have, on average, approximately one stem per tree at all sites. In 6/20 species, trees at warmer sites had significantly higher average number of stems than at the coolest site (Figure 2c). These six species belong to all four groups of successional and elevation origin combinations, but the increase at warm sites was particularly large in the two early successional species, *Maesa lanceolata* and *Dombeya torrida*. Noteworthy is that D_{base} and h of M. lanceolate did not respond to warming, instead warming increased wood volume through a significant increase in the number of stems, meaning that standing stock of 10 out of 11 early successional species responded positively to warming. Only the *Faurea saligna* (late successional and montane forest origin species) had a lower average number of stems at the warmest site.

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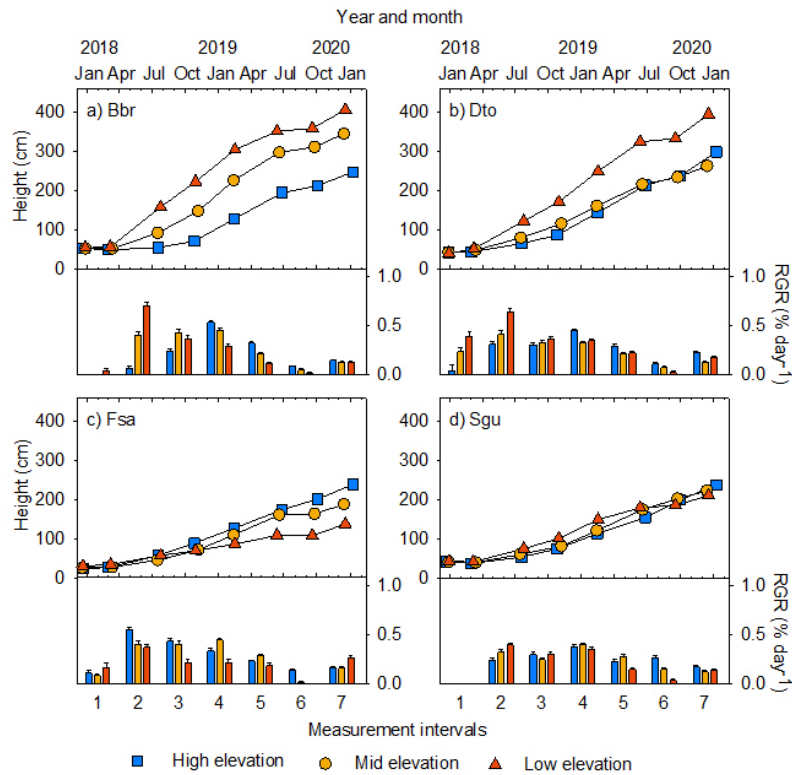
Figure 4. Examples of changes in stem height and relative growth rate (RGR) over 2 years, shown for four species at three sites of different elevation: (a) *Bridelia brideliifolia* (Bbr); (b) *Dombeya torrida* (Dto); (c) *Faurea saligna* (Fsa); (d) *Syzygium guineense* (Sgu). See Figures S6 and S7 for growth trajectories of all species.
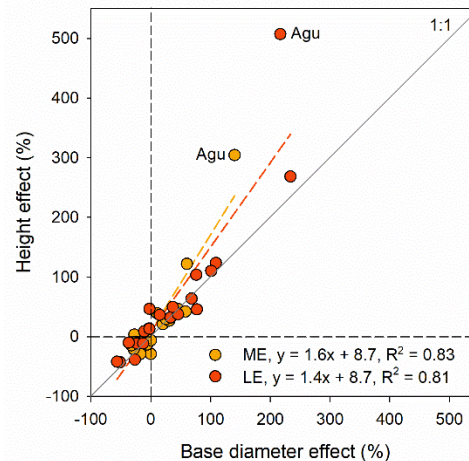
Figure 5. The stem height *versus* base diameter at mid (ME) or low elevation (LE) sites compared to the high elevation site, two years after plantation. Each marker is a species mean ($n = 20$). The two values that deviate most from the 1:1 line both belongs to *Albizia gummifera* (Agu).

18

3.4 Standardised RGR of stem diameter and height

Warmer growth temperature significantly stimulated the standardised RGR for smaller trees (10-25 mm D_{base} and 75-100 cm h) of both stem D_{base} (9/11) and h (8/11) in early successional species, respectively, which is similar to the effect on D_{base} and h after two years (c.f. Figures 2a, b and Figures 3a, c). As expected, the standardised RGR was generally lower for the late successional species and very few of these species grew faster at warmer sites. Instead, most of them grew slower or were not significantly affected. However, note that 1 and 2 out of 9 late successional species did not qualify for statistical analysis of D-RGR and H-RGR, respectively, due to low replication as a result of small sizes and high mortality (Table S5). Taken together, the similarities between warming effects on standing stock after two years and RGR indicate that the different initial sizes of the trees at planting (Tables S2, S3) do not appear to have had a systematic effect on the warming responses.

For larger trees, fewer individuals reached the size ranges (50-75 mm D_{base} and 250-300 cm h) which resulted in fewer plot replicates and fewer species that could be included in the analysis than for the smaller trees (Figures 3b, d, Table S5). However, the main picture is that both D-RGR and H-RGR for larger trees were lower than for smaller trees and that fewer large early successional trees were significantly stimulated by warming. This resulted in smaller differences between early and late successional species for larger trees compared to smaller trees, both regarding overall RGR and the warming responses. This may partly be influenced by an effect of the seasonal drought period in 2019, when no irrigation was applied in line with the design, causing a particularly negative effect on the larger trees (usually early successional) at the warmer sites with higher VPD and lower soil water content (Table 1), combined with possible higher hydraulic vulnerability among early successional trees.

3.5 Tree mortality

Warmer growth temperature increased tree mortality, especially at the warmest site (Figure 2d). Mortality >10% over the two years period were found in 7 species: 5/9 late and 2/11 early successional species. High mortality was equally common in species of both montane (3/10) and transitional (4/10) forest origin. The highest mortality was observed in the three late successional species *Carapa grandiflora*, *Chrysophyllum gorungosanum*, *Newtonia buchananii* (70%, 62% and 58%, respectively, at the warmest site). Moreover, Late-S species having high mortality (>20%) usually (4/5) had lower D_{base} and D-RGR at warmer sites (c.f. Figures 2a, 2d and 3a). The largest part of the mortality at the warmest site (76%) was recorded between July 2018 and June 2019 (Table S6). High mortality may partly be linked to small initial plant size, especially for the two early successional species *A. gummifera* and *Macaranga kilimandscharica* which were substantially smaller at planting compared to other species (Tables S2, S3). However, within species, it was predominantly not the small trees that died (data not shown). Furthermore, one of the late successional species with the highest warming-induced mortality (C. grandiflora) did not have smaller initial plant size than most other species in the experiment, so size is likely not the main explanation here. Another potential cause to the high mortality at the LE site is species-specific difficulties for plant establishment in high

19

temperatures. However, it should be noted that only six trees were recorded dead after the first three critical months. Five of these were replaced by new individuals from the nursery and was not included in the mortality data (Table S6). The fact that species with high mortality also responded negatively to warming in terms of growth rather suggest that species heat sensitivity was the main cause of warming-induced mortality.

3.6 Tree stand composition

Tree stand composition, expressed both as BA_{abs} and BA_{frac} of the four species groups (ES/TMF; ES/LVTF; LS/TMF; LS/LVTF) and resulting from changes in both D_{base} growth and mortality, was significantly affected by site (Tables 4, 5; Figure 6). The D_{base} growth contributed most to the site mean BA, while mortality affected BA by only 3.4% and 4.5% at HE and ME sites, respectively, but by 17% at the LE site (data not shown). BA_{abs} of transitional forest species was significantly stimulated at the LE compared to the HE site, while TMF species were unaffected or showed decreased values (Figure 6a). The BA_{abs} of the different species groups at the ME site were similar to either the LE (LS/TMF) or the HE sites (the other three groups). For BA_{frac}, values increased at warmer sites in both early and late successional species of transitional forest origin while it decreased for both early and late successional species of montane forest origin. All sites were significantly different from each other within each species groups, except for HE and ME sites in the late successional/transitional forest group (Figure 6b). With these contrasting responses of different species groups, there was a marked difference in tree stand composition between the sites (Figure 7). Compared to the coolest site, stands in a warmer climate had smaller BA fractions 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 fractions were almost doubled or halved, respectively.

20

460 **Table 4.** Two-way split plot ANOVA for site and species (Sp.) group effects on absolute (abs) and fractional (frac) basal area (BA) of four species groups (ES/TMF; ES/LVTF; LS/TMF; LS/LVTF). Greenhouse-Geisser correction was used to calculate the degrees of freedom (df) for within subjects as assumption of sphericity was violated. Note that, between subject analysis was not applicable for BA_{frac} as the sum value is 100% for each plot.

Variable	Source	df	F-value	P-value
BA_{abs}	*Between subject:*			
	Site	2	869.9	<0.001
	Error	51	27.7	<0.001
	Within subject:			
	Sp. group	1.9	372.1	<0.001
	Sp. group * site	3.8	43.7	<0.001
	Error	98		
BA_{frac}	*Within subject:*			
	Sp. group	2.2	764.5	<0.001
	Sp. group * site	4.4	58.0	<0.001
	Error	112		

465

Table 5. One-way ANOVA for site effects of absolute (abs) and fractional (frac) basal area (BA) of four species groups (ES/TMF; ES/LVTF; LS/TMF; LS/LVTF). Degrees of freedom are 2, 51 and 54 for site, error and total, respectively. See Figure 6 for post hoc tests.

Variable	Species group	Site effect: F-ratio	Site effect: P-value
BA_{abs}	ES/TMF	8.9	<0.001
	ES/LVTF	57.7	<0.001
	LS/TMF	11.5	<0.001
	LS/LVTF	29.3	<0.001
BA_{frac}	ES/TMF	46.5	<0.001
	ES/LVTF	89.6	<0.001
	LS/TMF	67.7	<0.001
	LS/LVTF	5.4	<0.001

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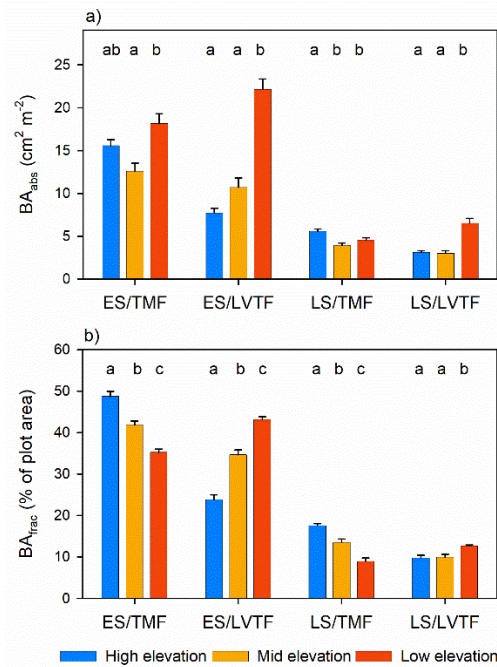
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Figure 6 a, b. (a) Absolut and (b) fractional basal area (BA_{abs} and BA_{frac}, respectivley) after two years per species category of early (ES) and late (LS) successional species from tropical montane rainforest (TMF) and Lake Victoria transitional rainforest (LVTF) from three sites at different elevations. Both BA_{abs} and BA_{frac} was standardised to compensating for the somewhat different initial number of individuals between the species groups (see eq. 3). Each bar show plot level mean (n=18) with standard error. Different letters above each species category indicate significant difference (P<0.05) between sites.
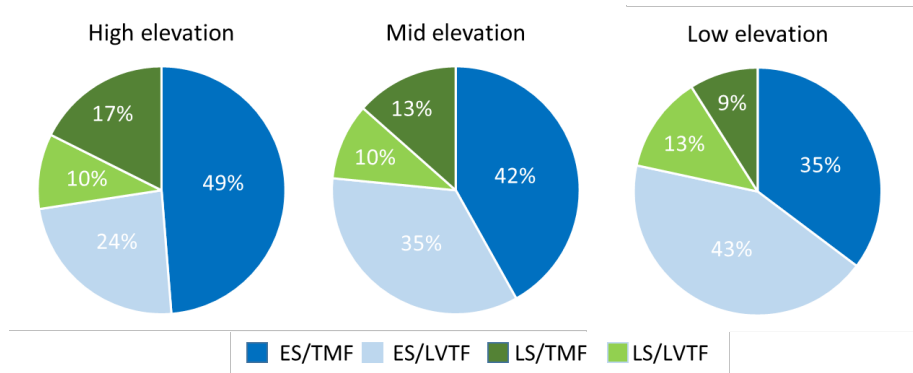
Figure 7. Fractions of basal area (BA_{frac}) two years after planting for four combinations of early (ES) and late (LS) successional species from tropical montane rainforest (TMF) and Lake Victoria transitional rainforest (LVTF) grown at three sites at different elevations. BA_{frac} was standardised to compensating for the somewhat different initial number of individuals between the species groups (see eq. 3).

22

4. Discussion

We used an experimental elevation gradient approach to explore the temperature responses of the growth and mortality of a broad range of tropical tree species with contrasting successional strategies and elevation ranges of origin in the Rwanda TREE project. Current knowledge on the temperature sensitivity of tropical tree growth is based primarily on either monitoring in intact forests (e.g. Bennett et al., 2021; Clark et al., 2003 & 2010; Damptey et al., 2021; Herrera-Ramírez et al., 2021; Hubau et al., 2020; McDowell et al., 2018; Slot et al., 2021; Sullivan et al., 2020) or controlled warming experiments on small plants grown in chambers (e.g. Cheesman & Winter, 2013a, Cheesman & Winter, 2013b; Slot & Winter, 2018; Wittemann et al. 2022). The semi-controlled experimental approach of Rwanda TREE bridges the gap between these two types of studies by using large plantations with the same species and genotypes grown at three sites spanning 5.4 °C in MAT, with irrigation to compensate for site differences in precipitation. Moreover, by using mixed multi-species tree communities, we could assess the implications of interspecific variation in temperature responses for tree stand composition in a warmer climate. This has, to our knowledge, never been explored in an experimental and tropical setting before.

4.1 Warming effects on early and late successional species

Warmer climate stimulated the standing stock of stem volume related variables (D_{base}, h and number of stems) after two years in 10 out of 11 early successional species while responses of late successional species were mixed, including increases, decreases and no significant changes (Figure 2). Similar patterns were observed for standardized RGR of both D_{base} and h (Figure 3, Table S5). These results support our first hypothesis (H#1), stating that the growth of early successional species respond more positively to warming than late successional tree species. They are in accordance with results from a study with potted seedlings grown in the same soil at the three Rwanda TREE sites, where warming strongly stimulated biomass growth in the early successional species *Harungana montana* but not in the late successional species *Syzygium guineense* (Dusenge et al., 2021). This supports that the site effects and successional group difference observed here were caused by climate responses rather than by site differences in soil conditions (Table 1). Moreover, other studies on photosynthesis of trees in Rwanda showed stronger negative effects of high temperature and warming in late successional compared to early successional tree species (Vårhammar et al., 2015; Tarvainen et al., 2022; Mujawamariya et al., 2023). The finding of contrasting warming responses of early and late successional species is also in line with results on photosynthesis and growth in warming experiments with tropical tree seedlings conducted in indoor climate-controlled chambers (Slot & Winter, 2018) as well as in field chambers (Cheesman & Winter 2013b). Finally, our results are consistent with field observations of negative effects of temperature on stem growth being stronger in late compared to early and mid-successional species in a TMF in Kenya (Gliniar et al., 2013). Several lines of evidence thus indicate a shift in competitive balance favouring early over late successional species in a warmer climate.

23

The loss of competitiveness of late compared to early successional species at warmer sites may in part be linked to the high sun exposure of plants in this study. When plants were small, especially during the first year of the experiment, they were growing in open conditions. This may have been stressful for late successional species due to their generally lower tolerance to high light intensities, as observed in previous studies (Poorter, 1999; Veenendaal et al., 1996). However, it is likely not high solar radiation per se that is harmful for many late successional species at the warmer sites in our experiment since peak and mean solar radiation was actually slightly lower at LE compared to the ME site, while growth of several species was significantly lower at the LE compared to the ME site. An indirect effect of heat is more likely, such that the lower inherent stomatal conductance of late compared to early successional species (especially at the LE site; Mujawamariya et al., 2023) leads to higher leaf temperatures and stronger physiological heat stress under warm conditions. This has indeed been observed in previous studies in Rwanda (Vårhammar et al., 2015; Ntawuhiganayo et al., 2020; Tarvainen et al., 2022; Mujawamariya et al., 2023). The negative effect of a warmer climate observed in some late successional species in this experiment may therefore be stronger than effects that would have occurred in understorey conditions. However, while late successional species as young trees often grow in the understorey, they also frequently occur in forest gaps in TMF forests (data from Nyirambangutse, et al. 2017). The lower competitiveness of sun exposed late successional seedlings in a warmer climate thus implies an amplified disadvantage at early stand developmental stages compared to early successional species. Since early stand development is a crucial phase for tree stand composition, this handicap of young late successional seedlings is likely to endure into later stages.

4.2 Warming effects on species of different elevation origins

The finding that tree growth of many species is stimulated by warmer climate is contrary to field observations that warm conditions decrease tropical tree growth (Clark et al., 2003, 2010 & 2013; Dong et al., 2012; Feeley et al., 2007; Way & Oren, 2010; Vlam et al., 2014; Hubau et al., 2020). However, this study is on montane and highland tree species that naturally grow in rather cool conditions, with prevailing mean annual temperatures at the middle of the species elevation ranges of approximately 15 to 21°C (Figure 1). It is therefore not surprising that tree growth in many species was stimulated at the warmer sites compared to the coolest site, provided that we irrigated during the first 1.5 years to avoid drought stress.

The stimulation of growth rate at warmer sites was especially high for the group of early successional species with a transitional forest origin (+39% and +140% at the ME and LE sites, respectively, compared to the HE site, Figure 3a). Thus, at least for early successional species, results supported the latter part of H#2, stating that warmer climate stimulates growth of species from lower elevation of origin. There was also a partial support for the first part of the H2, stating that warming decreased tree growth in species from higher elevation of origin (TMF) as warming had negative effects on tree growth in 5 out of 10 TMF species. Our results are in line with findings in a controlled chamber warming experiment with seedlings of four of the species used in this study, where the lowest-elevation species was better at physiologically acclimating and growing at high growth temperatures than the highest-elevation species (Wittemann et al., 2022). The differences in warming response of species with different elevation origins (transitional vs montane forests) also corroborates the observation of thermophilization in Andean tropical forests, where tree species with their distribution ranges centred at lower elevation had gained in relative abundance

as climate got warmer over time, at the expense of higher-elevation species (Duque et al. 2015; Fadrique et al. 2018). The present study and the chamber warming study on Rwandan tree species (Wittemann et al., 2022) suggest that warming-induced declines in abundance of higher-elevation species is underpinned by lower capacity of leaf physiology and tree growth
550 processes to handle, or benefit from, warming.

4.3 Warming effect on tree mortality

Warmer climate increased tree mortality in late successional species, but not often or much in early successional species (Figure 2d). However, there was no clear difference between montane and transitional forest species (Figure 2d) and, thus, H#3 was therefore only partly supported. The lack of expected difference between montane and transitional forest species
555 conflicts with the observations that thermophilization is driven by higher mortality of species with higher elevation ranges (Duque et al. 2015). It may be that the limited number of species in this study has masked possible influences of species origin, or that such will show up at later stages in the experiment.

The findings of highest mortality in especially the slow-growing late successional species (cf. Figure 2a, b & d) are in line
560 with Laurance et al. (2004a) who observed increased mortality among slow- compared to fast-growing tree species, in an analysis of growth measurements made in 18 one- hectare plots over up to three decades in the Amazon rainforest. However, opposite to these results, more recent long-term studies of mortality in 24 Australian plots and 189 Amazonian plots with tropical forest concluded that fast growing species were at highest risk under increasing drought and high VPD, respectively (Baumann et al 2022; Esquivel-Muelbert et al., 2020). Moreover, studies in Amazonia and Borneo rainforests observed
565 especially high mortality among early successional tree species during hot and dry conditions in El Niño years (Alexio et al., 2019; Slik, 2004). Interestingly, the Early-S species with high mortality in Slik (2004) belonged to the genus *Macaranga* (seven species) which was the same genus as one of the two early successional species with high mortality in our experiment (Figure 2d).

570 The contrasting results of our study and some of the previous observational studies may be a consequence of early successional species being more sensitive to drought while late successional species are more sensitive to high temperature and VPD, particularly at young ages. Indeed, most of the mortality in the observational studies, especially of genera affiliated to wetter climatic regimes, were attributed to drought/water stress (Esquivel-Muelbert et al., 2017). If considering only the effect of warming when there is no water limitation, as in our irrigated study, then early successional species might be protected against
575 heat stress by transpiratory cooling while late successional species (with lower transpiration) experience stronger physiological heat stress. This was indicated in a previous Rwandan common garden study with seedlings (Vårhammar et al., 2015) as well as in a recent Rwanda TREE study exploring upper heat tolerance in tropical tree species (Tarvainen et al., 2022). However, the reliance on transpiratory cooling to prevent overheating in early successional species may not be a feasible strategy during drought, possibly contributing to the above-mentioned reports of high mortality in early successional species.

25

580

The higher mortality in early successional species in monitoring studies may be likely linked to higher hydraulic vulnerability compared to late successional species (Apgaua et al., 2015; Eller et al., 2018), as well as to their demography with higher recruitment rate and shorter life span (Laurance et al., 2014b; Nyirambangutse et al., 2017). These effects may be mainly expressed by taller mature trees, which may contribute to explain the difference between our results and long-term observational studies (Baumann et al 2022; Esquivel-Muelbert et al., 2020). Thus, we cannot exclude that the mortality pattern among successional groups may change with increasing age and size of the trees. If late successional trees mainly respond negatively to warming in young ages, the recruitment rate may still be inhibited causing at least a transitional shift in species composition. Consequently, the succession from secondary to primary forest will be slower, with implication for both large-scale carbon storage (across stands at different successional stages) and how fast the final goals of forest restoration can be achieved. Recovery of species composition is already a slow successional process (>century), which may thus be even slower in a warmer climate (Poorter et al., 2021).

4.4 Tree stand composition

We showed that Early-S species with transitional rainforest origin strongly increased their total and fractional basal area at warmer sites, while montane forest species declined (Figure 7), supporting H#4. These results are in line with the thermophilization observations in Andean tropical forests along elevation gradients, where tree communities have experienced directional shifts in composition towards greater relative abundances of species with ranges centred at lower, warmer elevations during recent decades (Duque et al. 2015; Fadrique et al. 2018). This neotropical thermophilization was caused primarily by increased mortality of more cool-adapted and heat-sensitive species (with higher elevation ranges), while the tree stand composition shift at warmer sites observed in this study was mostly explained by positive growth responses of species with lower elevation ranges. Contributions by mortality were small since it was highest in species with small trees that do not contribute much to basal area. However, since late successional trees grow slower but in the long term grow taller (Laurance et al., 2014b; Nyirambangutse et al., 2017), similar species-specific mortality rates in a mature forest would have had a much larger influence on BA. At later stand development, it is likely that the increased competitiveness and growth of lower-elevation origin species in a warmer climate will lead to increased warming-induced mortality of higher-elevation species also in the Rwanda TREE plantations, when competition for resources increase (Lohbeck et al., 2013). 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., 2016; 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 disentangle the mortality mechanisms of different climate variables and how it interacts with different groups of species.

26

5. Conclusion and implications

Like in studies of leaf morphology (Mainshimwe et al., 2022) and photosynthesis (Dusenge et al. 2021; Tarvainen et al., 2022; Wittemann et al. 2022; Mujawamariya et al., 2023) in the Rwanda TREE project, the tree growth response to warming was highly species specific. This points out the importance of including several species representing different ecological niches when assessing warming responses of highly diverse tropical forests. We showed that a warmer climate increased tree growth in most early successional species while responses of late successional species were more variable. Growth stimulation in early successional species was stronger in species originating from transitional rainforest compared to higher-elevation montane forest. Several of the late successional species had both decreased growth and increased mortality at warmer sites. At the stand level, the contribution of transitional forest species to stand basal area increased at the expense of montane forest species at lower elevation and warmer climate, and thus demonstrated a thermophilization response. We conclude that many tropical highland and montane species show potential growth stimulation in a warmer climate, while other species are likely to be threatened by projected increases in temperature. In particular, higher-elevation and late successional species risk to become outcompeted by lower-elevation and early successional species. This may challenge local and regional biodiversity in African high-elevation forests where the level of endemism usually peaks above 2000 m a.s.l. (Platts et al., 2013; Kessler & Kluge, 2010; Richter, 2008). While lower-elevation species may move uphill under warming, montane species have limited options with shrinking thermally suitable areas at increasing elevation and nowhere to go when reaching the top of the mountain. If our results for young trees influence stand community composition at later successional stages, the increased mortality of late successional species in combination with increased growth of early successional species will likely result in faster carbon turnover but lower carbon storage of tropical forests (Nyirambangutse et al, 2017; Aleixo et al. 2019).

The successful establishment of mixed plantations in this experiment demonstrates that it is not necessary to wait to plant late successional species until early successional species have established and formed closed canopies. Simultaneous plantation of carefully selected climate and site adapted early and late successional species may thus speed up forest restoration considerably. Our results contribute to reduce the current uncertainty in native tree species restoration strategies (Aitken et al., 2008; Forrester et al., 2005; Thomas et al., 2014). They also help to improve the ability to model tree demography of Afromontane forest under climate change (Pugh et al., 2020) facilitating better predictions to support forest-based climate change mitigation and adaptation in this region.

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