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Temperature increase explains loss of productivity in Borneo rainforest with largest impact on suppressed trees and logged stands

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Utrecht, October 6th 2021

Final report submitted following a major research project
Master's programme in Environmental Biology
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ACKNOWLEDGEMENT

My highest gratitude belongs to my daily supervisor and mentor René Verburg. Through his curious mind and optimistic attitude, I always found a way forward where there seemed to be a blocked path. When in doubt, he supported me with invaluable knowledge and experience. This project would have been impossible without him- and also a lot less fun!

Special thanks goes to Gijs Steur, who spent hours of his time on explaining and advising me on statistical matters and modelling and helped me to understand what possibilities my data offered me and which not.

I also want to thank my friends Lucia Troeger and Carlos Moretti for proofreading my manuscript and Donatas for sticking with me during moments of low motivation. Thank you!

ABSTRACT

Tropical forest ecosystems are affected by the impacts of climate change. Rising temperatures and increased occurrences of extreme weather events, such as heatwaves, fires, and drought alter forest ecology and carbon dynamics. Most studies to date focused on the impact of climate change on tree carbon dynamics in mature tropical forests, but only very little information is available for logged forests. This said, human-altered forest is now more abundant than old-growth forest. These disturbed stands may further not return to their initial state for decades which can lead to a greater vulnerability towards other stressors. This implies that most of the tropics are currently under the double threat of logging impact and climate change and that the interaction between these two remains insufficiently studied.

Using a dataset of permanent plots in Borneo, I investigated the effects of warming temperatures on carbon sequestration in selectively logged tropical forest compared to old-growth forest. I used stepwise multiple regression analysis to relate the carbon sequestration rates of individual trees to local temperatures while correcting for environmental and stand-level data. Logging by itself increased tree-level carbon gains (for an average tree +4.5 kg year⁻¹), but showed a negative interaction with warmer temperatures, suggesting that logged plots may be less resilient to warming than undisturbed plots. Another aspect that was studied was the effect of temperature on different strata of the forest, using crown illumination data. The analysis revealed that shaded trees were affected more severely by warmer temperatures with a loss in carbon sequestration rates of 28 % compared to only 8% in dominant trees with good crown illumination. This result is highly unexpected, as the canopy is thought to be shielding understory trees from increased temperatures. To my knowledge, this relationship has not yet been reported in the scientific literature and should be of interest for future research on tropical forest ecology.

Key words: climate change; warming; carbon sequestration; tropical forest; selective logging; growth suppression; forest strata

LAYMAN'S SUMMARY

Global warming has been shown to impact tree growth, which is a problem because trees have an important role to play in mitigating climate change. As trees grow, they absorb carbon dioxide from the atmosphere and turn it into wood, roots and leaves. Around half of a tree's biomass is made out of carbon, meaning that they are great carbon storage containers. But tree growth can be slow under some conditions, for example in extreme temperatures or when there is a lack of water. Research was able to answer many important questions about how severely the climate affects plant growth, but this knowledge stems mostly from studies on primary forest. That is, forests that have not been altered by humans, for example through selective logging. It is unfortunately true that today more than half of the remaining tropical forest area is affected by human activity of some form. This means that the analyses and predictions of how the tropics will react to climate change are only half true. The other half, regarding logged and disturbed forests, remains largely uncertain.

In my research project I attended the question how logged forests react to climate change - in particular global warming. I used a dataset in which tree growth rates of tropical forest plots in Borneo had been recorded over several years and then related these growth rates to the rise in temperatures in that time period. Since some of the forest plots had been logged in the past and some had been left to grow in peace, I could compare the impact of warming on untouched forest with that on disturbed forest. The result of my statistical analysis showed that trees in logged forest are slightly - but significantly - more affected by warming temperatures than trees in old-growth forest. So, the warmer the temperatures, the less the trees grew; and if a tree was located in an area disturbed by logging, it's growth was slowed down more severely by the warming. This is an important finding as it may change the way we will calculate tropical forest carbon storage in the future.

A second, somewhat surprising finding was made in the understory. These are the deeper parts of the forest, which are almost entirely shaded by the crowns of taller trees. Here too I found a strong negative reaction to warmer temperatures, even in areas that had not been affected by logging. This result came as a surprise, because trees in the understory are roofed and shielded by the canopy cover - not only from sunlight, but also from heat. So it would have been expected that the most severe impact of rising temperatures would occur in the canopy trees and not in the understory trees. My data suggested however, that growth slowed down more than three times as much in the understory than in the canopy layer when temperatures increased. This effect has not been described before in scientific literature and might turn out to be really important for our understanding of how climate change affects forests in the tropics.

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I. INTRODUCTION

1.1 BACKGROUND

The Intergovernmental Panel on Climate Change (IPCC) recently released an alarming report regarding the pace of climate change (IPCC 2021). The report outlines the consequences of faster global warming: intensified flooding events, heatwaves, wildfires, thawing of ice sheets and rising sea levels in the coming decades. All of this will affect, or has already begun to affect human livelihoods. It also highlights the indisputable role of humans in causing climate change through global emissions of the greenhouse gas carbon dioxide (CO₂) and our urgent responsibility to reduce these emissions swiftly and effectively.

While reducing CO₂ emissions is the main active step in halting climate change, removal of carbon will also play an essential role in the climate solution. Efforts are being made to develop processes and tools that are capable of the large scale removal and storage of carbon, but none has yet achieved the inherent efficiency of one of earth's most natural processes: photosynthesis. Around 17% of anthropogenic CO₂ emissions are yearly sequestered by the world's forests (Harris et al. 2021). This is why tropical rainforests are a crucial contributor to carbon offsetting by acting as a so-called carbon 'sink' (Brienen et al. 2015, Poorter et al. 2016, Harris et al. 2021). About 25% of all terrestrial carbon is currently stored in the tropics with a carbon residence time of decades or even centuries (Bonan 2008, Galbraith et al. 2013) and additional CO₂ is continuously being absorbed from the atmosphere to be stored in soils and biomass. This occurs at different speeds in different regions. And while carbon sequestration rates differ between trees due to individual and local growing conditions, analyses of old-growth tropical forests have estimated a yearly overall pantropical carbon sink of ca. 0.5 Mg C ha⁻¹ (Baker et al. 2004, Phillips et al. 2008, Lewis et al. 2009a). These estimates are now being revised however, because more recent research points out the continuous weakening of tropical carbon sinks over time (Mitchard 2018, Hubau et al. 2020). New data show that the Amazon's capacity to take up carbon has been so severely decreased that it is now on the brink of turning into a net carbon source (Gatti et al. 2020). Hubau et al. (2020) suggest further that African and Asian rainforests - which have not yet reached this tipping point - are following the same trajectory and are likely to become carbon sources in the near future as well. So what is causing rainforests to shift from carbon sink to carbon source? The main culprits are large-scale deforestation and forest degradation. Large amounts of stored carbon are released during decomposition of harvested biomass, as well as during fires which are lit by farmers in order to clear space for other crops.

Selective logging, the commercial harvesting of mature timber trees from a given area is the most common form of human disturbance in rainforests (Bousfield et al. 2020). As the remaining forest is left to regenerate, changes in forest composition, age structure and microclimate heavily affect the functioning of the ecosystem (Malhi et al. 2014, Song et al. 2020). Tree mortality remains as high as twice the baseline in the years after logging (Okuda et al. 2003, Figueira et al. 2008) and the forest community is altered by fast growing, light-demanding pioneer species which colonize the freed up space (Sist & Nguyen-The, 2002). The canopy gaps which are left by logged and dying trees impact how the lower strata of the forest are affected by climatic factors such as radiation, temperature and humidity (Hardwick et al. 2015). The thermal buffer which is usually provided by the canopy layer is dramatically lowered in logged forest compared to old growth forest, leading to more extreme

microclimates and heterogeneity (Blonder et al. 2018). The gaps created by logging take years to close, and a full recovery of the disturbance may take several decades or longer, as the original species composition is restored very slowly (Chambers et al. 2004, Asner et al. 2004b).

This said, also positive impacts can be observed after selective logging activity. Under the closed canopy cover of a mature forest, growth of smaller trees is suppressed, as not enough light reaches their leaves. But in logged forests, the additional amount of radiation through canopy gaps can be sufficient to measurably promote growth of suppressed trees after logging (Asner et al. 2004, Herault et al. 2010). As we have seen, there is a plethora of impacts that logging causes in forest ecology. But despite the fact that partially logged forest is now more frequent than primary forest (IUCN 2021), most research on rainforest carbon dynamics focuses on old-growth forest, with very little attention being paid to logged forest (Riutta et al. 2018). The research at hand aims to add to the literature on logged forest carbon dynamics.

Not only logging activity, but also climate change is suspected of playing a role in the conversion of forest carbon sinks to carbon sources. Tropical forests are subjected to much narrower fluctuations in temperature than forests in higher latitudes and are therefore physiologically less well adapted to climatic changes (Cunningham & Read 2002). In accordance with this, some experimental evidence has suggested that higher temperatures impair CO₂ assimilation in tropical tree species (Clark et al. 2003, Doughty & Goulden 2008, Way and Oren 2010) and that global warming might thus lead to declining tree growth rates and a weakened carbon sink. This vulnerability of tropical forests to higher temperatures raises some concerns over the possibility of a positive feedback loop, with carbon sequestration abilities of forests ever decreasing in a changing climate and in turn CO₂ concentrations driving temperatures higher.

One aspect to consider is that higher concentrations of carbon in the atmosphere can also stimulate higher CO₂ sequestration rates. This effect is called CO₂ fertilization and has demonstrably led to a greening of the Earth (Zhu et al. 2016). However, Van der Sleen et al. (2014) examined physiological responses to increased atmospheric CO₂ and did not report stimulated biomass growth as was expected. They argue that other factors may have counteracted the effect, such as limiting resources, energy investment into leaves instead of stem growth, or climate-related stressors, such as increased temperature and drought. It could be the case that CO₂ fertilization alone is not enough to offset the negative effects of climate change on forest carbon sequestration and that rising temperatures and increased mortality due to droughts are outpacing the CO₂ fertilization effect (Malhi 2008). Empirical research has also supported this concern, showing that rising temperatures have indeed led to decreased primary productivity in rainforests (e.g. Feeley et al. 2007, Sullivan et al. 2020). It is now widely assumed that primary productivity - in particular woody biomass production - is slowed down by the closure of plant stomata in high temperatures, leading to lower carbon sequestration rates (e.g. Doughty et al. 2009, Wu et al. 2018). However, yet again these results have been studied mainly in primary forest, disregarding the altered conditions that may prevail in logged forests and the possibility of an interaction between these two stressors.

1.2 RESEARCH AIM

Predicting the responses of logged tropical forest to future climate conditions is essential, as they impact the global carbon balance. Tropical forests are one of the largest carbon sinks, and the processes that affect the growth rates or vitality of these ecosystems need to be understood in order to reach a basis for the most appropriate policy decisions.

The aim of this study is to develop a statistical model to describe how logged and old growth tropical forests are affected by temperature. Growth models can be used to quantify to what extent forests are able to mitigate climate change through capturing CO₂. Single-tree growth models are the standard for predicting growth and yield in many regions because of their precision and resolution. These distance-independent models use a list of attributes, e.g. tree species, diameter at breast height (DBH), and wood density (WD) for each individual tree on a plot based on which the aboveground biomass can be estimated (Weiskittel et al. 2011). When designing such growth models, several environmental parameters must be accounted for, because tree growth depends on multiple internal and external factors. Intrinsic factors comprise tree size, age and species (King et al. 2006, Ramanantoandro et al. 2016); extrinsic factors include climate, soil type, human disturbance and competition with neighbouring trees for light and water (e.g. Kozłowski 1991, Toledo et al. 2010, Scholten et al. 2017, Rozendaal et al. 2020) to name a few.

From 1976 to 1993, growth and environmental parameters of over 7000 rainforest trees in Eastern Kalimantan, Borneo were monitored. In this study I make use of this long-term tree growth dataset, including a plethora of environmental conditions gathered in old growth as well as logged tropical forest. The comparison between logged and unlogged plots will allow me to investigate the effects of human disturbance on rainforest resilience to climate change. The research question is as follows: “How does warming affect carbon sequestration in logged tropical rainforests compared to old growth rainforests, when correcting for environmental factors and tree properties?”.

In contrast to previous large-scale studies, the presented analysis will be conducted on a very fine scale, including site characteristics as well as individual tree condition and growth rates that were recorded over 16 years on 10x10m subplots. Individual factors, such as species specific wood gravity, tree height, light availability, and health conditions are valuable data when trying to predict carbon sequestration rates.

Since multiple confounding variables may affect tree growth, the model takes such factors into account. The research was driven by two main hypotheses: First, increases in temperature affect forest carbon sequestration negatively, and second, logged rainforest is more sensitive to temperature changes than old growth rainforest, thus leading to a stronger decline in carbon assimilation rates in logged stands. During further exploration, it became evident that warming affects different forest strata in different ways, with the most negative effects occurring in the shaded understory. While this was not the initial focus of this study, the results appear to not have been reported in previous scientific literature. One aim was thus, to investigate and report on this unexpected sensitivity of the understory to global warming. Time series data on crown illumination are further not frequently available and thus the results are worth reporting.

II. METHODS

2.1 RESEARCH SITE

The ITCI concession from which the data was obtained was located in the province of East Kalimantan on the Indonesian part of the island of Borneo. The landscape is characterised by clayey soils and tropical lowland rainforest dominated by Dipterocarps. Borneo's rainforests hold approximately 60% (457.1 Mg ha⁻¹) more aboveground biomass per hectare than the Amazon rainforest (288.6 Mg ha⁻¹), which is partly explained through its species composition (Slik et al 2010). Dipterocarps include several large, emergent species that rely on wind dispersal and thus often reach heights of 70 m. Also wood densities of canopy-layer and emergent trees were found to be much higher in Borneo than in the Neotropics (Paoli et al. 2008).

The climate is isothermal with rainfall maxima during April and December and rainfall minima from June through October. There is no dry season as rain levels usually stay above 100 mm. The mean annual rainfall in the ITCI area ranges between approximately 2000 mm in the north, and 2500 mm in the south (Voss 1982). Temperatures range from 19°C to 35°C with an average of 27°C in all months. The northern parts of the concession area experience slightly higher temperatures.

A total of 13 plots comprising an area of 11.55 ha were studied, of which 4.35 ha had been subjected to logging in the past. The stand density was higher in old growth forest with around 430 trees per hectare compared to 380 trees per hectare in logged forest.

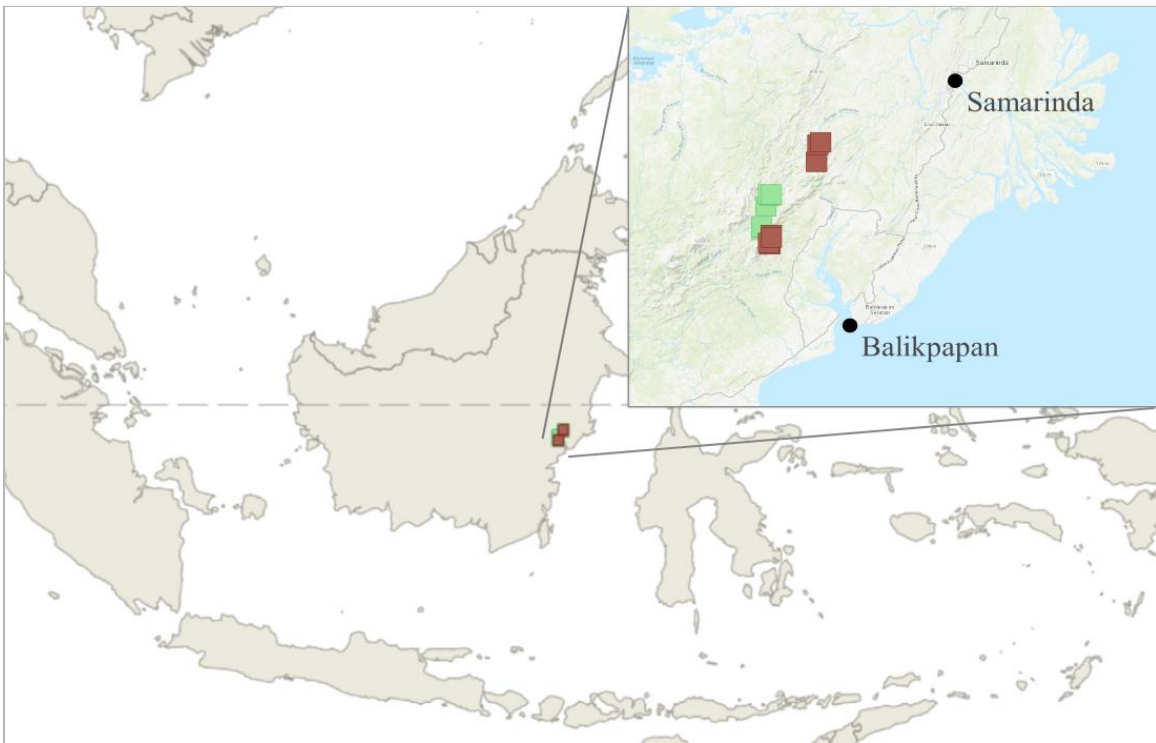


Fig. 1 The location of the 13 study plots. Logged over plots are marked in dark red, old growth plots in light green. The two adjacent weather stations are shown in black.

2.2 AVAILABLE DATA

Forest inventory data of the ITCI concession area between 1976 and 1993 had been stored and procured since the 1970s and were readily available. However, some relevant parameters had to be added to the dataset. These are climatic variables on the plot level as well as species specific wood density values. Duration of drought has been found to be an important indicator for water deficit and drought impact (Van Loon et al. 2014), thus, length of consecutive dry months was calculated to create a variable called ‘drought length’.

2.2.1 ITCI and Tropenbos Surveys

From 1976 to 1993 several surveys were conducted on the study area by various researchers (Eijk-Bos 1996, Verburg & van Eijk-Bos 2003). The survey measurements included bole height at the beginning of the surveying period, tree diameter at breast height (DBH), a status classification of tree damage (with 0 = flawless and 1 = damaged), and percent crown illumination (PCI). The latter was recorded on a scale from 0% (no direct sunlight) to 100% (full overhead light) for each tree. Tree bole height was measured only once in 1977.

After 1988 Tropenbos took over the surveying and in addition to the previously mentioned tree features measured a range of soil characteristics. The soils in the study area have been characterized as Ultisols according to the USDA Soil Taxonomy (Tropenbos, 1990). The loamy soils are strongly weathered, well drained and poor in nutrients. The Tropenbos soil survey reported low phosphorus concentrations across sites. Tropical forests are typically considered phosphorus-limited (Vitousek et al. 2010, Baribault et al. 2012, Santiago & Goldstein 2016). High levels of aluminum possibly even reaching toxicity were also reported, however, no adverse effect of aluminum on tree growth was found in this analysis. Topsoils differed spatially in chemical composition, specifically regarding potassium, magnesium and phosphorus concentrations. Permanent plots under logged-over forest exhibit slightly more fertile A-horizons than under primary forests.

2.2.2 Environmental Variables

Topography and soil conditions have been recorded on a subplot level with plot sizes of 10x10 meters. Data on such small scales isn’t frequently available. Thus a model could be developed in which local conditions are accounted for at very high resolution, revealing effects which in other studies may have been overlooked due to environmental noise.

Although measures of temperature and precipitation were taken at the two nearby weather stations in Balikpapan and Samarinda, both were located near the sea while the permanent plots lay more than 40 km inland and at slightly higher elevations. Therefore the climate data from these stations may not be very representative, nor are they suitable to assign separate temperature values on the plot level. Thus, in order to achieve a higher resolution of weather data, the ‘Worldclim 2’ dataset was used. This freely accessible database provides extrapolated weather data with a resolution of 21 km². The extrapolation considers elevation, distance to the coast and satellite derived variables atop of the available weather station data (Harris et al. 2014; Fick and Hijmans 2017) making it a more accurate estimate. For each plot, I extracted the parameters monthly sum of precipitation, mean monthly

temperature and maximum monthly temperature for the 16-year timespan using the R packages “raster” and “rgdal” . Some of the plots have identical climate values, as they overlap within a raster unit of 21 km².

Since DBH measurements were taken once a year, weather parameters were also transformed to a yearly level. The transformations conducted were: 1. Summarizing precipitation data as total amount rainfall between two measurements; 2. calculating drought length as the longest span of consecutive dry months in each timestep using a precipitation threshold of 100 mm; 3. averaging of yearly mean and maximum temperatures for each time interval. Temperature was further transformed in a separate step to allow for the comparison of temporal fluctuations within plots (See section 2.3.2).

2.2.3 Biotic Variables

Species specific wood gravity, also called ‘wood density’, depends partly on tree species and must be accounted for in forest carbon estimates, as it determines the amount of carbon stored in woody biomass (Phillips et al. 2019). A 25 cm tree of a softwood species may for example store 1.3 tons of carbon in its bole while a hardwood species of the same height and diameter could store up to 3.5 tons of carbon. Values for wood density (WD) for each tree were determined using the global database made available by the International Council for Research in Agroforestry, short ICRAF (Harja, Rahayu & Pambudi 2013). The ICRAF database is publicly available and consists of a collection of several databases containing plant functional traits. Where wood density could not be determined on the species level, I used the average WD on the genus or subplot level (Baker et al. 2004, Rozendaal et al 2020).

Other biotic variables were the yearly measures of tree diameter as well as an initial estimate of bole height in the first year. To complement this sparse available data, missing height measures were simulated as described in section 2.3.1.

2.3 PROCESSING OF FOREST INVENTORY DATA

In order to relate environmental variables directly to forest carbon gain instead of just tree diameter growth, the aboveground carbon gain was calculated using the allometric equation given below. Average carbon gain values on the tree level are presented in Table 1 in section 3.1. Temperature values of each plot were centered around the plot-mean to extract temporal variation.

2.3.1 Estimating AGB and Bole Height

To prepare the dataset, individuals with anomalous data were excluded: trees that -

- 1.) were smaller than 14 cm in diameter (the surveying threshold before 1980);
- 2.) grew more than 7.5 cm diameter in a single year, and
- 3.) shrank more than 25% of their initial DBH - were excluded. Trees with missing information or only a single measurement were also removed from the dataset. A total of 4328 trees were ultimately included in the calculations and the statistical analyses.

Aboveground biomass (AGB) of trees larger than 14 cm DBH was estimated using a pantropical allometric equation adapted for the region of Borneo. Both tree diameter and tree height are

considered in the allometric equation, as Feldpausch et al. (2012) found that tree height significantly improves forest biomass estimations and should be included to reduce uncertainty. The allometric equation used is shown below:

$$(1) \quad AGB = 0.673(\rho D^2 H)^{0.976}$$

Where ρ = wood specific gravity, D = diameter and H = bole height (Chave et al. 2014).

Biomass increments as well as carbon sequestration in tree stems were then calculated on an annual basis for each tree. The tree height was not available for the full dataset, since bole height had only been measured in the first year of recordings. Therefore, missing height values had to be simulated using the general D:H relationship. This was done by fitting an asymptotic regression on the available height data and simulating the missing height values on the basis of each tree's diameter.

$$(2) \quad H = a + (a - b) * e^{-exp(cD)}$$

In equation 2, the variables b and c are constants estimated by the regression model, variable a represents the horizontal asymptote for the tree diameter : tree height curve. Initial measurements of tree bole heights were made once in 1977 and were used to fit the asymptotic regression model. To increase the fit for the trees with already existing height data, an additional factor was added describing the difference between expected and measured height for each individual (See Appendix). Aboveground carbon stocks were calculated by multiplying aboveground biomass by 0.5 which is the approximate C concentration of woody biomass (Brown & Lugo 1982, Malhi et al. 2004). Carbon gains per hectare are shown in Figure 3 in section 3.1.

2.3.2 Group Mean Centering of Temperature Measures

The plots which lay between -0.6°S and -0.75°S exhibited higher overall temperatures according to the Worldclim extrapolations. This led to a confounding factor in the dataset: all of the warmer plots had been subjected to logging, causing temperature to be positively correlated with logging activity. To deal with this, the mean plot temperature was subtracted from each plot, centering the data around a baseline value. This way the relative increase in temperature over a time period can be analysed for its impact on tree growth. Group mean centering is a mathematical approach of making hierarchical data comparable on one hierarchy level, while excluding the other. In this case it means that relative changes in temperature over time are extracted and used for further analysis, while variation between different sites is excluded. The advantage of this method is that temperatures are compared to their baseline instead of between different locations. The main drawback is the underlying assumption that a temperature increase in an already hot plot (e.g. 77-3) has the same consequences as a temperature increase in a relatively cool plot (e.g. 71-1L).

There are two centering approaches in multilevel regression: overall mean centering (OMC) and group mean centering (GMC). In OMC the mean of the full sample is subtracted from all values, while for the GMC each individual's group mean is subtracted. GMC is a useful tool to obtain the independent micro and macro level contributions of a certain predictor. (Enders & Tofghi, 2007).

When comparing a model with absolute temperatures to a model with group mean centered temperatures, the R^2 value increases by 2%, suggesting a better model fit. Further, this transformation allowed the inclusion of logging as a variable, because the multicollinearity between these two variables was resolved.

2.4 STATISTICAL ANALYSIS

Statistical analyses were run in RStudio on R version 4.0.2. Stepwise backward regression was conducted using the ‘MASS’ package. The ‘corrplot’ package was used to assess multicollinearity. OLS multiple regression analysis was used to test for explanatory effects of crown illumination, trunk damage, temperature, precipitation, drought length and soil nutrients on biomass growth rates.

2.4.1 Variable Selection and Multicollinearity

In regression analysis, the inclusion of explanatory variables can be seen as the formulation of hypotheses, while the step-by-step selection serves as a falsification process. In the case of this dataset, with a wide range of environmental parameters available, careful selection of independent variables was especially important because multicollinearity is likely to occur and mask relevant effects as well as it may decrease the power of the analysis. Variable selection was aided by theoretical and mechanistic understanding of the subject matter.

A machine learning model with a large quantity of variables is not only more difficult to use in a different context due to its high demand for the measurement of environmental variables, it is also more likely to be overfitting the data: to describe the error instead of the trend. The number of parameters should be reduced based on preexisting theoretical knowledge and the ultimately resulting model should be verified using some form of validation set in order to avoid overfitting.

Based on initial data exploration, I included tree specific measurements such as wood density and percent crown illumination (PCI), climatic variables (temperature deviation, sum of precipitation and drought length) as well as the site parameters clay content, P (extractable phosphorus) and soil organic carbon in the modelling process.

If predictor variables correlate between each other, multicollinearity is introduced in the model, thus correlated variables need to be excluded. If not, this leads to unreliable p-values and false conclusions as effects are ascribed to variables arbitrarily. Spearman correlation was used in order to investigate multi-collinearity between parameters and to detect correlations of more than 30%. For each correlating pair of variables it was then decided which entity of the pair should be kept. For example, drought duration was removed from the pool of explanatory variables as it had a correlation of 71% with annual temperature deviation (See Table 3 in section 3.2.1). This correlation is likely coincidental and not meaningful, however it would interfere with the model stability so drought duration was removed from the analysis. Most site parameters describing different aspects of soil chemistry and physiology were removed as well after they were found to be a) strongly correlated between each other or b) not significant for the model outcome. Soil leaching may be the common driver of collinearity between some of these variables, as it deprives the soil of all nutrients alike. I therefore chose magnesium (MG) as a proxy for soil nutrients, as it positively correlated with potassium, calcium and phosphorus concentrations.

2.4.2 Linear Regression

A backward stepwise regression analysis was conducted to explain variations in yearly biomass gains with the variables chosen in the previous selection steps. The model parameters are reported in table 4 in section 3.2.

Ordinary Least Squares (OLS) regression depends on several statistical assumptions in order to produce reliable estimates. These assumptions have been tested as described in the following. Normality and homoscedasticity of residuals were investigated using QQ-plots, as well as a residuals versus fitted values plot. Non-normality of residuals was observed at first, however this was due to the strong skewness of the variable biomass growth. A log transformation was applied to meet the assumption of normality of the dependent variable. Subsequently, normality of residuals and homoscedasticity was observed.

OLS further assumes that observations are independent in order to avoid autocorrelated residuals. However, the yearly recurring measures of a tree are dependent on each other and thus are autocorrelated. This can cause an increased type 1 error (Liang & Zeger 1995).

In such cases, Linear Mixed Effect Modelling (LMM) is often used to account for the similarity within groups and in doing so deal with the autocorrelation. Such grouping factors can be, for example, location, species, or repeated measures of the same individual. Whether a grouping factor is appropriate and would significantly improve the regression can be tested by calculating the Intraclass Correlation Coefficient (ICC). This statistic describes whether the variation between groups is larger than the variation within each group.

ICC values were calculated on the levels of individual trees, species, plots and subplots as random effects. In all cases ICC values were below 0.5 which is considered a low correlation score (Koo and Li 2016), suggesting that none of the possible grouping factors explain enough variation to justify the use of random effects in modelling. Based on this analysis, LMMs were no longer pursued and measurements were treated as independent.

2.4.4 Model Validation

In order to avoid overfitting, a model should be validated using a so-called validation set. This is a randomly selected subset of data that has been withheld from the training of the model and that is later used to verify the accuracy of predictions. In this study, the validation technique used was k-fold cross validation, a method in which the dataset is split up into a number of validation sets (k), each of which is then compared to the model that is calculated from the rest of the data. The sampling factor k was chosen to be 10-fold according to the original size of the dataset.

III. RESULTS

3.1 ASSESSMENT OF DATA

To provide an overview of the dataset, basic statistics describing the local conditions of the 13 study plots were calculated and are presented in Table 1. Magnesium (Mg) was used as a proxy variable to indicate soil fertility, since it was positively correlated with other important nutrients (CaO, P₂O₅, K₂O) and negatively with Aluminum which is a toxic agent. Correlations between variables will be described in more detail below (See section 3.2.1).

Table 1. The summary statistics of the 13 study sites are ordered ascendingly by growth rates (average trunk biomass gain per year). Magnesium (MgO) is used as a proxy for overall soil fertility.

Plot	Size (ha)	Logged	Samples	DBH (cm)	WD (g/cm ³)	T (°C)	MgO (mg/100g soil)	Growth (kg)
76-5	0.25	no	477	35.37	0.70	30.13	0.51	15.33
77-2	0.35	yes	352	23.97	0.53	31.50	0.95	16.39
76-6	0.25	no	663	30.89	0.72	30.12	0.41	16.53
76-3A	0.50	no	1087	33.43	0.74	30.10	0.37	17.75
76-3B	0.75	no	1624	31.43	0.73	30.10	0.41	19.61
76-4	1.65	no	2403	32.49	0.73	30.16	0.74	21.38
72-8	2.00	no	2929	30.07	0.72	30.13	0.70	23.31
77-3	0.84	yes	888	30.17	0.75	31.49	1.63	24.33
71-1V	1.14	no	1936	30.96	0.71	30.07	1.06	25.08
76-1	1.32	yes	1646	29.46	0.73	30.76	0.92	26.16
72-2	0.35	yes	855	26.17	0.57	30.76	2.78	27.97
77-1	0.84	yes	749	28.88	0.68	31.49	0.47	28.04
72-1	0.50	yes	966	27.48	0.65	30.75	0.92	28.16
71-1L	0.66	yes	833	32.51	0.77	30.05	1.11	31.39

With 31.5°C on average, the temperatures are highest in plots 77-2 and 77-3 which have the most northern location. The lowest average tree diameter was measured in plot 77-2. This is also the plot that experienced the most damage due to logging and skid roads (64% of basal area was lost). Wood densities are lowest in the logged plots 77-2, 72-2 and 72-1 and highest in the logged plot 71-1L. The average wood density is significantly lower ($t(8703) = 15.39$, $p < .001$) in logged ($M = 0.68$, $SD = 0.21$) than in old growth plots ($M = 0.73$, $SD = 0.16$). The highest Mg concentration was measured in plot 72-2, which is an outlier. To test for a significant difference between the Mg concentration of logged and unlogged subplots, Wilcoxon rank-sum test was used, since the data were not normally distributed. The result showed that Mg concentrations were significantly higher ($p < .001$) in logged ($Med = 0.87$, $n = 490$) compared to old growth subplots ($Med = 0.64$, $n = 650$). Even when omitting the outlier plot from the data, the significant result remained stable.

Trees that were located on logged plots exhibited higher growth rates, except for plot 77-2 which had been severely damaged in the past. To assess the effect of logging on trees in different strata and stages of development, a more detailed investigation of the logging effect was conducted with special attention on the size classes (diameter at breast height) shown in the Figure below.

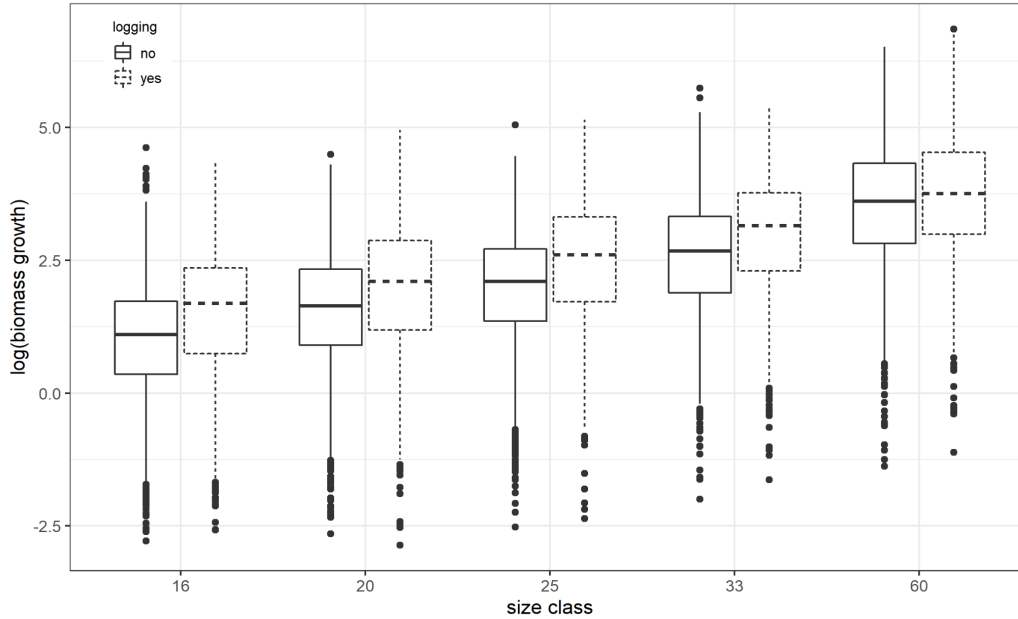


Fig. 2. Yearly logarithmic biomass growth rate of old growth (solid line) and logged (dashed line) forest plots. The dataset was subdivided into five size classes. The name of each tree class equals its mean DBH.

The DBH classes were named after the mean of each class range. The size ranges are: 14 - 18cm, 18.1 - 22cm, 22.1 - 28cm, 28.1 - 40cm and > 40cm. For better comprehension and visualization, biomass growth rates were log-transformed in the above shown figure. However, as the actual growth rates may be of more interest, the following statistics are also reported as absolute and relative values in Table 2.

Table 2: The mean yearly gain of biomass in old growth versus logged forest plots across different tree size classes. Absolute values in kilograms are shown, as well as relative differences as a percentage of virginal growth rate. The relative growth difference between logged and old growth forest in each size class was tested for significance using a Welch t-test with *** indicating $p < .001$

Size class	Old growth (kg)	Logged (kg)	Absolute difference (kg)	Relative difference	t	p
16 cm	4.63	8.14	3.51 (± 0.25)	76 (± 5) %	13.88	< .001 ***
20 cm	7.73	13.15	5.43 (± 0.48)	70 (± 6) %	11.37	< .001 ***
25 cm	11.53	19.72	8.19 (± 0.66)	71 (± 6) %	12.48	< .001 ***
33 cm	22.26	31.95	9.70 (± 1.06)	44 (± 4) %	9.15	< .001 ***
60 cm	59.59	74.94	15.35 (± 3.54)	26 (± 5) %	4.33	< .001 ***

Significantly higher growth rates were observed throughout all diameter size classes in the logged forest plots. The largest absolute increase in productivity was found in the biggest tree size class ($M = 15.35$, $SD = 3.54$); however, growth efficiency is typically known to decline with tree size (Stephenson et al. 2014). When put into proportion, it becomes evident that the largest growth efficiency relative to tree size was in fact present in the lowest size class ($M = 0.76$, $SD = 0.05$). The relationship is shown in Table 2.

To assess the carbon dynamics of the investigated plots, mean yearly carbon gains per hectare were determined and are shown in Figure 3. The carbon sequestration values were calculated using the allometric equation discussed in section 2.3.1 and are based on bole height only - meaning that the here presented values only include the carbon sequestration rates of the stems, not tree branches, leaves, or roots.

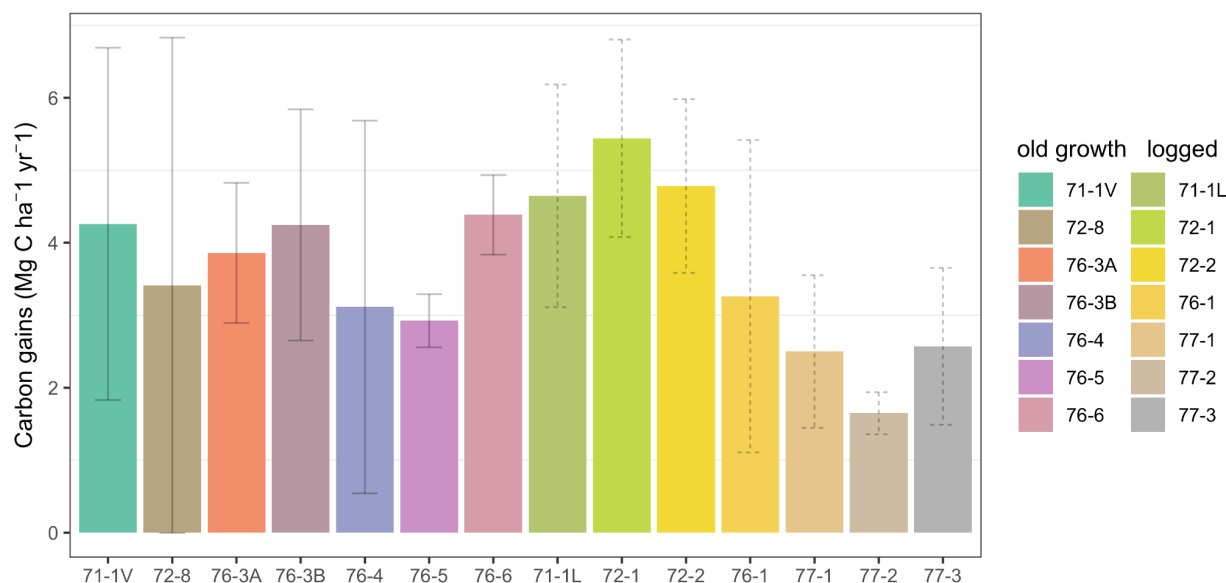


Fig. 3. Plotwise yearly carbon sequestration per hectare. Dashed error bars are used for logged plots, solid error bars for old growth forest plots.

The highest carbon gains were measured on the logged plots 71-1L, 72-1 and 72-2. Despite this however, the overall carbon sequestration rate was slightly higher in old growth forest with $3.74 \text{ Mg ha}^{-1}\text{year}^{-1}$ compared to only $3.55 \text{ Mg ha}^{-1}\text{year}^{-1}$ in logged forest. The difference was not significant however ($t(8) = 0.33$, $p = 0.748$).

Logged forest plots evidently have a lower mean tree circumference ($M = 28.31$, $SD = 16.28$) than old growth plots ($M = 31.66$, $SD = 19.73$) as larger trees had been removed during harvest. This is relevant as it explains why the carbon sequestration rate is higher in logged plots on the tree level (See Table 1), but not on the stand level.

3.2 MULTIPLE REGRESSION ANALYSIS

In this section the outcome of the variable selection process is described as well as the resulting multiple regression equation. Further, the outcome of cross validation is reported in section 3.2.3.

3.2.1 Variable Selection

In order to exclude possible confounding relationships between the independent variables, correlations between them were investigated. Correlations above a threshold of 0.3 were sought out and resolved by removing the less relevant member of the pair (these decisions were made on grounds of theoretical backgrounds) until no highly correlated variables remained. Table 3 summarizes these pairs sorted by the corresponding spearman correlation coefficients.

Table 3. Pairs of correlated predictor variables above a cutoff value of 0.3. Parameters shown in bold were used further in multiple regression analysis, those not bolded were excluded in order to avoid multicollinearity.

Variable A	Variable B	Spearman correlation
Logging	Max. Temperature	0.867 ***
Magnesium	Phosphorus	0.739 ***
Temperature deviation	Drought duration	0.708 ***
Logging	Phosphorus	0.739 ***
Percent crown illumination	Basal area of larger neighbors	0.665 ***
Magnesium	Potassium	0.519 ***
Max. Temperature	Phosphorus	0.453 ***
Drought duration	Max. Temperature	0.408 ***
Potassium	Phosphorus	0.387 ***
Magnesium	Max. Temperature	-0.367 ***
Temperature deviation	Precipitation	0.310 ***

The competition index ‘basal area of larger neighbors’ (BAL) had been considered as a descriptor of the competition impact on individual growth rates. However, it was highly correlated with percent crown illumination (67%), which was a direct measure and a better predictor for tree dominance than BAL. Drought length had to be excluded from further analysis due to its strong correlation with local temperature deviation (71%). Sum of precipitation was also excluded, as it had a strong positive correlation with temperature. The high correlation between logging and maximum temperature (87%) was due to the northern location of logged plots, thus maximum temperature was excluded from further analysis and instead temperature deviation was used (See section 2.3.2).

3.2.2 Regression Model

Following the above described selection process, 12 explanatory variables remained for further regression analysis. Using a backward stepwise approach, the model was further reduced until it contained only significant variables on an alpha-level of .05. Four variables were ultimately selected.

Table 4. Statistics for the biomass-gain model developed in stepwise multiple linear regression. Exact t and p-values are given (***) indicates p-value <.001). Interactions are reported with a colon between variables.

Coefficient	Estimate	Std. Error	t value	p value	
(Intercept)	1.26	0.02	72.30	< 2e-16	***
PCI	0.02	0.00	90.87	< 2e-16	***
Stem damage (1)	-0.27	0.02	-14.78	< 2e-16	***
Logging (1)	0.14	0.02	7.39	1.52e-13	***
Temperature	- 3.36	0.21	-16.03	< 2e-16	***
Temperature : Logging	-1.67	0.25	-6.75	9.75e-11	***
Temperature : PCI	0.03	0.00	10.43	< 2e-16	***

A significant regression equation was found with an adjusted R² value of 0.401, or 40.1% of variance explained ($p < 0.00$, $F_{5, 17546} = 1959$). The model estimates with accompanying p-values are presented in Table 4 above. The categorical variables logging and stem damage were coded as dummy-variables with 0 = old growth, 1 = logged, and with 0 = flawless, 1 = damaged.

During further analysis, polynomial equations were used to explore the non-linear relationship between temperature and growth; however, no significant improvement of the model was observed. Interactions between all variables were systematically tested, however apart from those listed above, no other significant interactions were found.

To test whether the significant interactions between logging, temperature and PCI improved the prediction, ANOVA was used. The result of ANOVA showed that including the interaction term between temperature and logging improved the model significantly ($F_{1, 17547} = 37.42$, $p = 0.00$). The same could be observed for the interaction term between temperature and percent crown illumination ($F_{1, 17547} = 100.64$, $p = 0.00$). Other predictor variables did not lose significance when interaction terms were included in the model. The factors temperature, logging and PCI did not change dramatically when the interactions were added, nor did their signs change.

The interactions are illustrated in Figure 4 below. For simplicity and better visualization, PCI was reduced to 5 categorical light levels ranging from 0 to 100 percent crown illumination. In regression analysis, PCI was treated as a continuous variable. As previously, biomass growth rates are shown with log transformation in the figures to improve visualization, but absolute values in kilograms are reported in the description below.

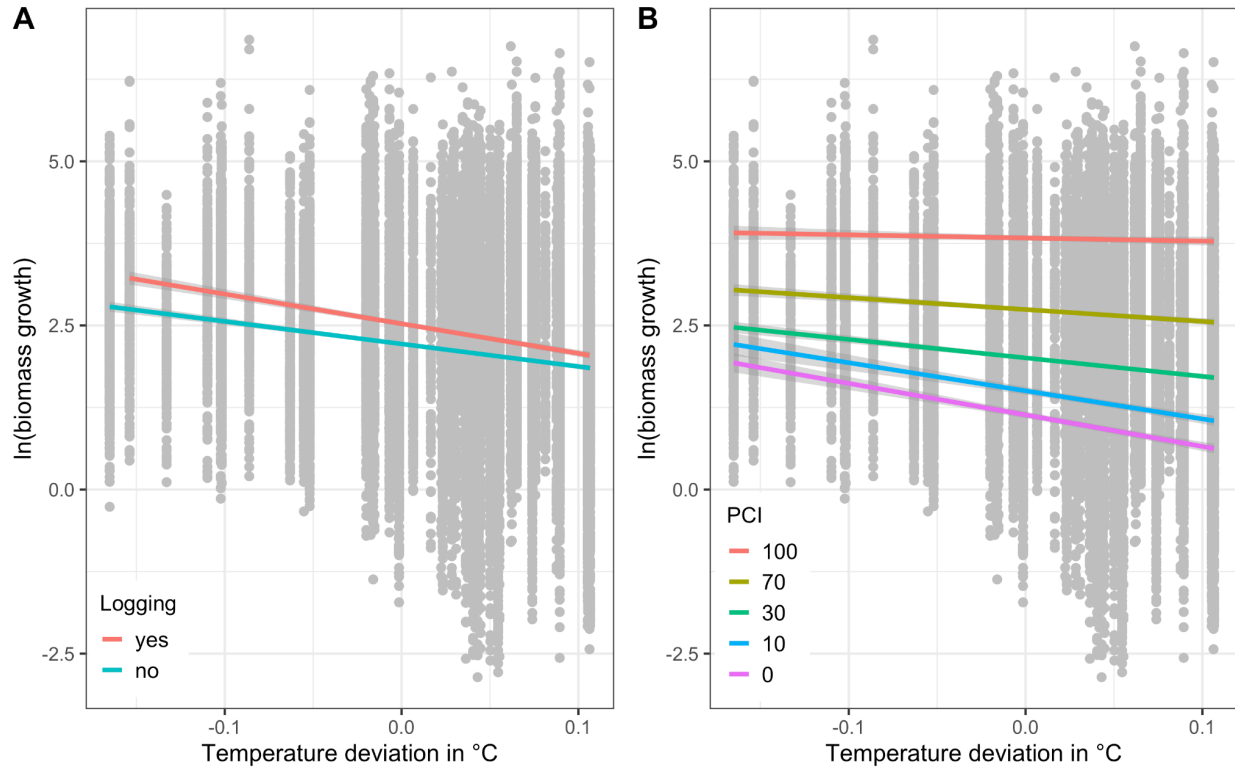


Fig. 4. Biomass growth as a function of local temperature deviation. Figure A shows the effect of logging (red line) compared to no logging (blue line). In Figure B, lines signify percent crown illumination with red line indicating 100% illumination of crown and purple line marking complete shading of crown.

Two patterns can be observed in the above figure. The function describing the impact of logging and temperature on growth (Fig. 4A) shows a higher overall growth rate in logged plots (26 kg year^{-1}) compared to old growth plots (22 kg year^{-1}) as well as a steeper decline of growth rates under high temperatures when the plot was previously logged. This matches the results of the multiple regression model, which predicted a higher intercept in samples from logged plots compared to old growth plots and a significant negative interaction between logging activity and temperature (See Table 4).

Secondly, Figure 4B shows that a low crown illumination percentage coincides with low overall biomass growth rates (5 kg year^{-1}) compared to trees with well illuminated crowns (75 kg year^{-1}). The graph also shows a steeper decline in growth rates across a temperature gradient for trees with a low PCI. The trees that were most exposed to sunlight exhibited a drop in yearly biomass productivity of - 8% between the coldest and the warmest years. Trees that received no direct sunlight experienced absolute losses in biomass productivity of - 28%. The analysis yielded the same results when repeated on data from only old growth forest in order to exclude the effect of logging and its consequences for forest demographics.

In order to control for species variability between the understory and the canopy layer and to assess the possible interaction of functional groups on temperature resilience, the investigation was also repeated within different wood density classes. The analysis was conducted for trees below 0.5 g/cm^3

and again for trees between 0.5 g/cm³ and 0.8 g/cm³ and finally for only trees above 0.8 g/cm³. Results indicated no significant differences between wood density classes.

2.2.3 Model Assumptions and Cross Validation

To test the model assumptions, QQ-plots and Residual versus Fitted plots were produced and are shown in Figure 5. The plots below show clearly that residuals of log-transformed growth values are normally distributed, unbiased and homoscedastic.

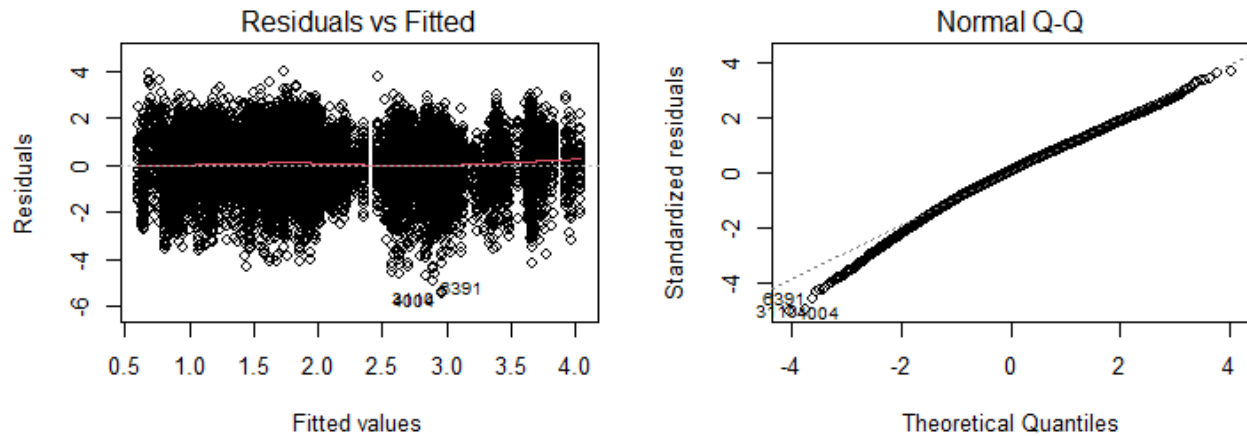


Fig. 5 Results of Normal QQ plot and Residual versus Fitted plot to verify model assumptions

An observed versus predicted plot was generated to visualize the ability of the developed growth model to predict biomass growth. In the below Figure 6 it is visible that the predictions are close to the perfect fit line, indicating that the model is valid and capable of predicting growth rates based on the selected explanatory variables. The predictions are generally underestimating high growth values and overestimating low growth values. This phenomenon is called regression towards the mean, which is a common effect observed in linear regression analysis (Barnett 2004).

Because the model had been trained on data that was then used to produce the observed versus predicted plot, there was still the possibility of overfitting the data. To avoid this issue, the reliability of the model results was tested using cross validation. The final R² resampling result of 10-fold cross validation was 40.14%, which was very similar to the R² value initially found during regression analysis (R² = 40.1%). This indicates that the regression coefficients do not result from an overfit model and can be applied to new data.

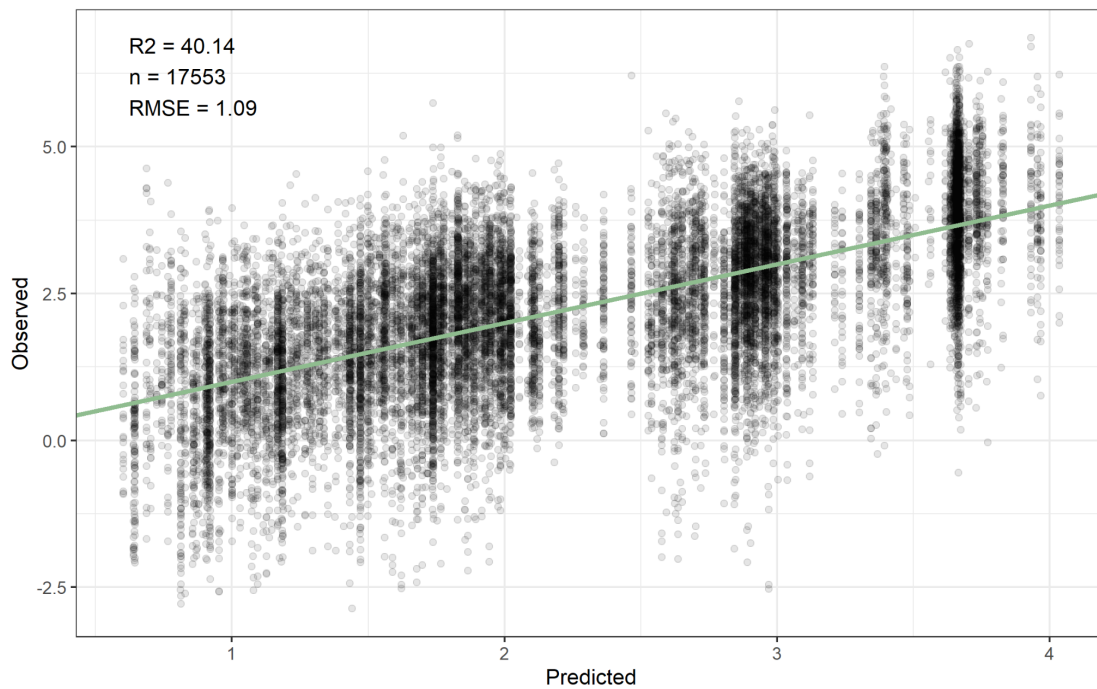


Fig. 6 Scatter plot of observed values for $\ln(\text{biomass growth})$ versus model prediction. Green line indicates the perfect fit line where predictions are identical to observed values. R^2 and RMSE results of 10-fold cross validation are shown.

IV. DISCUSSION

Using a 16-year repeated measures dataset, I was able to investigate how different environmental stressors affected tree growth in both old growth and logged forest plots. Some of these effects also interact with each other, adding to the level of complexity. The results suggest that increased temperature has a negative influence on biomass growth rates, with trees in logged plots and those limited by light being affected most severely. The implications of these findings on tropical forest dynamics will be discussed in some detail.

4.1 EFFECT OF LOGGING AMONG SIZE CLASSES

Due to the thick canopy cover of tropical rainforests, light is the largest limiting factor in this ecosystem (Rüger et al., 2009). Perhaps not surprisingly then, growth rates of small trees were positively influenced by logging activity in the study area, as logging opens up the canopy and allows previously suppressed trees to thrive (Weiskittel et al. 2011, Vatrax et al. 2018). Growth rates increased as much as 76% of the virginal value in the smallest size class (See Table 2). To check whether this effect may have been caused by a shift in species composition, the analysis was repeated under exclusion of typical pioneer species from the genera *Mallotus*, *Macaranga*, *Anthocephalus*, and *Fagraea*. The recruitment of such fast growing, low wood-density species may cause diameter growth rates to increase in a disturbed forest, representing an indirect effect of logging. To investigate the direct effect of logging on tree growth as caused by altered environmental conditions, I excluded this option. However, the repeated analysis revealed no impact of the pioneer species on biomass growth rates (See Appendix Figure A1).

The data also suggest increased growth rates of larger trees (> 60cm) that were not limited by light. This points at the presence of a different limiting resource apart from light availability, which became available after competitive release through logging. A possible candidate could be phosphorus, which is a macronutrient commonly limited in the heavily depleted soils of the tropics (e.g. Vitousek 1984, Dalling et al. 2016). Phosphorus was measured in the soil survey data, but due to the strong positive correlation with logging activity ($r_s = 59.5\%$) could not be included into the dataset. This could mean that phosphorus availability was higher at logged sites, however, it could also be a manifestation of the local variability in soils. The virginal plots are grouped together in the same geographical location which could explain their similar soil composition better. Furthermore, past studies have shown that phosphorus limitation is usually exaggerated by logging activity, not improved (e.g. Frizano et al. 2003, Lawrence et al. 2017). Phosphorus is therefore likely not the cause for increased biomass gain in this dataset.

Another possible explanation is the increased rainwater runoff in partly logged forests with canopy gaps. As precipitation decreased continuously with time in the present dataset, water may have become a more and more limiting factor. Logged forest plots could have allowed more rain water to reach the soil compared to the amount of water that evaporates from the closed canopy layer, leading to a water limitation only in old growth plots. This hypothesis was not further pursued in the study at hand as precipitation was correlated with temperature values. It remains unclear what was the cause for increased growth in dominant trees. A study design which includes measurements before and after logging would be more suitable to investigate this issue.

The tempting question arises, whether logging may increase the tropical carbon sequestration capacity due to its growth stimulating effect. While logging slightly increased biomass growth within individual trees in the present dataset, on the plot level, logged plots showed lower carbon sequestration rates than old growth forest. This results mainly from the demographic shifts present in logged plots and the overall decreased number of trees. Mortality was an aspect that could not be included in the present analysis, but has been shown to be high in the years after logging, further deteriorating the carbon pool.

The negative impacts of logging on the ecosystem cannot be overemphasized. Tree mortality rates rise dramatically after logging due to logging paths, damage done to surrounding trees and the removal of undergrowth (Okuda et al. 2003, Figueira et al. 2008). Tree mortality could not be assessed in the present dataset, as it was not specifically recorded and large insecurities existed regarding the individual mortality events. But it is absolutely certain that increased mortality together with other negative consequences, such as depletion of the already nutrient poor soil, loss of biodiversity, and last but not least, the overall decreased productivity on the plot level due to long term demographic shifts render any positive effect that logging may have on individual biomass growth rates negligible. The loss of carbon to the atmosphere during and after logging outweighs the gain of stimulated biomass growth manifold.

4.2. IMPACT OF CLIMATIC VARIABLES ON GROWTH RATES

The main focus of this study was the impact of rising temperatures on individual tree growth in logged, compared to primary forest. Previous research has shown that forests affected by logging were more prone to drought-induced tree mortality (Qie et al. 2017). The reason for this may be that selectively logged forests become more vulnerable to extreme climate, as their climate shielding through the canopy layer decreases (Hardwick et al 2015, Blonder et al. 2018). The dense vegetation of the canopy can be up to several meters thick, forming an effective layer of protection by blocking out wind, rainfall, sunlight and heat. Smaller trees therefore enjoy a more stable climate, while dominant individuals are more strongly exposed to variations in temperature and radiation. In selectively logged forests however, gaps that are created in the canopy disturb the microclimate that usually shields understory trees. The literature is not unequivocal though: Senior et al. (2017) found contrary evidence suggesting that the thermal buffer in rainforests can stay intact even after intensive logging activity.

My results do suggest a linkage between logging activity and temperature resilience. The significant interaction term (Temperature : Logging = -1.67, $p < .001$) that was found in the regression analysis indicates that tree growth in logged forest plots was affected more negatively by elevated temperatures than in old growth forest. For undisturbed forest, the temperature variable had a significant negative coefficient of -3.36 ($p = < .001$), indicating that with every one degree change in temperature, the average biomass gain of a tree decreases by 3.36 kg. Logged plots on the other hand experience a yearly productivity loss of 5.03 kg per one degree temperature change. Trees on logged plots had a slightly higher growth rate at baseline temperatures, but this growth rate advantage diminished as temperatures rose, leading to ultimately lower productivity (Fig 4A). Global forest degradation through selective logging puts the majority of forests into this vulnerable situation. Therefore this relationship is of serious concern for estimates of the rainforests carbon storage

capacities. The next step should be collecting and analysing microclimate data in order to evaluate the impact of subcanopy temperatures on tree growth more precisely.

Another aspect of climatic influence on the studied area was the interaction effect between temperature deviation and PCI. Trees of lower strata which were more light-limited and in general also smaller, exhibited more extreme responses to unusually high temperatures than dominant individuals (See Figure 4B). This result comes as a surprise, because as mentioned before, the lower strata of a forest are thought to be shielded by the microclimate against high temperatures. It was expected that trees in the canopy would be more severely affected by warming, since it has been shown that canopy leaves reach temperatures of up to 4 °C hotter than leaves in other strata and thus exceed the photosynthetic thermal optimum (Miller et al. 2021). An explanation might thus be that canopy trees need to be especially well adapted to deal with high temperatures, making them resilient towards a slightly warmer climate. Such adaptations include reduction of photosynthetic activity, stomatal closure and heat shock proteins (Teskey et al. 2014). It is however not apparent why those mechanisms should not be present in understory trees as well.

Another explanation could be that the lower strata were more affected by warming temperatures because they consist of other tree species than the canopy layer. Hardwood species for example are often shade tolerant and can spend a long time in suppression until a gap in the canopy opens up for them. Softwood species on the other hand tend to escape from the low-light environment quickly and invest more energy into vertical growth instead of structural stability in the form of wood density. In order to assess the possible impact of different growth strategies and functional groups on temperature resilience, the analysis was repeated within different wood density classes. This way I could exclude the possibility that only trees of a specific wood type were affected by this understory heating effect. The results showed the same pattern as was seen in Figure 4B for all different wood density classes, indicating that biomass gain is affected by temperature across different functional groups (Also see Figure A2 in the appendix).

This relationship between light availability and sensitivity to temperature is a tentative result that has to my knowledge not yet been reported in scientific literature. It may have major implications for future carbon gain predictions, since the understory trees which are at risk according to the present analysis, are also the trees of the future. Forest management and timber trade may need to adapt, as growth rates of understory trees are slowed down by a warming climate. Logging cycles might be affected by prolonged development phases of shaded trees. This conclusion stands in contrast with the findings of Buentgen et al. (2019) who, in a study on temperate forests, observed more rapid turnover rates and increased growth speeds with rising temperatures. However, rainforest trees are likely already operating at their temperature maximum, explaining why temperature increases in this biome could lead to impaired growth rates (Daughy & Goulden 2008).

Since the permanent plots were discontinued in the 1990s, today's biomass growth on these plots is unknown. The developed model was used to generate predictions for temperature values that occur in Borneo today. With temperatures being slightly more than one degree hotter than during the last measurement in 1993, it was expected that carbon gains should be drastically lower. The model predictions resulted in unrealistic tree growth values, including some negative growth values for smaller trees. (See appendix Figure 3). This is probably due to the fact that a linear model can not capture the complex non-linear relationship between temperature and tree growth. Tree growth is

enhanced by warming temperatures up to the point at which the photosynthetic temperature optimum is exceeded. At even warmer temperatures plant growth is then inhibited through stomatal closure and lowered photosynthetic rates. The present study suggests that the decline in growth then saturates, closing in on zero, as temperatures rise even higher. However, at some point trees would be under such high heat stress that mortality occurs. Sullivan et al. (2020) mention that the long term responses of tropical forest may further be aided by adaptation to warmer temperatures. They argue that thermal resilience can locally be much higher thanks to individual acclimatisation and plasticity as well as demographic shifts and changes in species composition, than short term analyses might reveal. This study covers a relatively big timeframe, further, Verburg & van Eijk-Bos (2003) could not reveal any changes in species composition in the forest of the presented dataset.

Next to temperature deviation several other climatic variables (precipitation, drought duration, maximum temperature) were included in the analysis, but multicollinearity forced me to limit the selection of variables to temperature deviation only. However, drought especially may be of interest as it can dramatically alter forest structure through elevated tree mortality and edge effects (Phillips et al. 2010, Bennett et al. 2015, Qie et al. 2017) and is assumed to become even more stressful for trees under rising temperatures in a future climate (Corlett 2016). Gora & Esquivel-Muelbert (2021) report that extreme weather events, particularly drought, wind and lightning disproportionately affect mortality rates of large trees and thereby regulate tropical forest carbon dynamics. In combination with the slowing of growth in smaller trees that was shown in the study at hand, this would mean a dramatic decline in the ability of tropical forests to sequester and store carbon.

It is expected that in a future climate extreme weather events will increase in frequency and intensity (e.g. Seneviratne et al. 2012, Spinoni et al. 2018). Mortality could not be analysed, so no full picture could be given regarding the impact of these factors on the full carbon pool within the study area and the biomass residence time. Qie et al. (2017) revealed that the carbon sink of the entire island of Borneo was temporarily halted during the El Niño–Southern Oscillation event (ENSO) of 1997, as CO₂ sequestration was equaled by carbon losses from logged forest areas. Edge effects and forest fragmentation are to blame for the high loss of carbon because forest edges don't have the same protective microclimate as the deeper forest areas. It is not quite clear whether these effects contain themselves to tree mortality or if tree growth rates are also affected. What is clear is that as land conversion, forest degradation and habitat fragmentation continue, more and more forest area is being exposed to these effects and it is necessary to study them carefully.

4.4 LIMITATIONS OF THIS STUDY

Above ground biomass growth is usually a good indicator for carbon sequestration rates in tropical rainforests. In the presented study, biomass was calculated on the basis of height data that only measured bole height, not full crown height. Consequently, the analysis is oblivious to any changes in biomass storage on the branch or leaf level and may thus overlook an important part of the trees' carbon storage capacity. Nevertheless, carbon stored in the bole is the most long-lasting, as it may not be returned to the atmosphere for several decades, while leaves are dropped and degraded, readily releasing their carbon. It could be argued that the carbon cycling in leaves occurs at rates too fast to be relevant for the forest's long term storage capacity. The estimates also do not take into account below ground biomass, which amounts to approximately 20-30% of the entire biomass of a tree and

significantly contributes to soil carbon, even after tree death (Kuyah et al. 2012, Sinacore et al. 2017). This is a clear weakness of this study.

Another limitation is presented regarding the temperature parameter. Temperature was calculated as deviation from the mean local temperature, as described in section 2.3.2. When the group mean is subtracted, the variance between plots is lost. It is therefore assumed that plots in an area with already high temperature are affected the same way by a temperature increase as plots with low baseline temperatures. Considering the non-linear relationship between temperature and plant productivity, this is likely not the case. This loss of between plot variability can be avoided by 'reintroducing the mean', however, in the study at hand this was not done due to the correlation between logging and between plot temperature differences. In a follow up study, these effects could be disentangled through an experimental design which includes temperature measurements at higher spatial resolutions in order to distinguish between local and temporal temperature deviations.

V. CONCLUSIONS

In this study, logging has been shown to exert a positive effect on individual tree growth rates. However, this effect was relativized by a higher vulnerability of trees in logged forest to rising temperatures, causing their productivity to drop off quickly in a warmer climate. Further it was shown that on the stand level, logged forest was less productive than old growth forest due to demographic differences. A possible explanation for the higher vulnerability of logged forest plots to warming may be the disturbance of the microclimate through canopy openings in logged plots. However, no clear answer could be found using just the data at hand. A closer examination of this relationship with special focus on the subcanopy microclimate could shine light on the vulnerability of logged over rainforest plots to global warming. This is a pressing issue, as both forest degradation and rising temperatures are problems we will face for many years onwards.

The findings of this study further hint towards an increased sensitivity of suppressed tropical trees to rising temperatures. While woody biomass productivity decreased for the entire study area, the largest growth inhibition took place in shaded and suppressed trees. Dominant trees exhibited a higher resilience when faced with hot temperatures. Some initial explanations have been discussed for this observation, however, they remain highly speculative as mechanical and experimental evidence is lacking. If the adverse effects can be linked to specific functional groups or phyla, future management techniques may need to consider elevated temperatures when selecting tree species for reforestation. Logging cycles may also be affected by the retardation of understory tree growth, impacting management decisions of the timber industry. To verify and deepen the implications of these results, more research is needed.

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VII. APPENDIX

Simulating tree height

Because tree height was not available for the full dataset, missing height values had to be simulated using the overall diameter to height relationship found in the study area. This was done by fitting an asymptotic regression on the available tree height data and simulating the missing height values on the basis of each year's tree diameter. The constants fitted during asymptotic regression are $a = 28.09$, $b = 4.22$ and $c = -3.89$ the resulting formula therefore is:

$$H = 28.09 - (28.09 - 4.22) * \exp(-\exp(-3.89)*D)$$

For trees for which an initial measured measure was available, simulating the following height values led to positive and negative jumps in biomass, as the expected height sometimes deviated quite largely from the measured one. The equation was therefore adjusted using that original height measure in order to achieve a better representation of each individual tree's growth trajectory. The formula was fine tuned by adding the difference between original and simulated height to constants a and b , resulting in the following formula:

$$H = a + (H_{\text{orig}} - H_{\text{sim}}) + (a - b) * \exp(-\exp(c)* D)$$

Logging effect excluding pioneer species

The effect of pioneer species on tree growth was assessed in order to investigate the possibility that not tree growth rates are affected by logging activity, but instead the frequency of fast growing pioneer trees. Figure 1 shows the resulting charts of A - the entire dataset and B - the dataset excluding pioneer trees. No significant differences were found in the analysis.

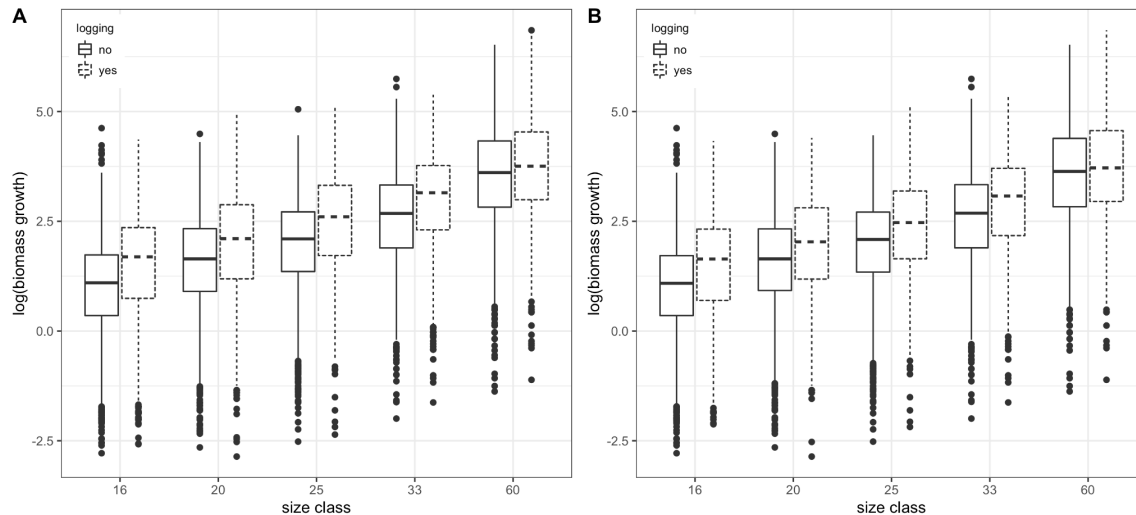


Fig. A1 Effect of logging on tree growth for the entire dataset (Fig. 1. A) and for a subset from which typical pioneer species were removed (Fig. 1. B). A positive effect of logging is visible in trees across all size classes regardless whether pioneer species were included or not.

Wood density distributions across forest strata

Different strata experienced varying growth impacts across a temperature gradient. However, the different strata may also comprise different species communities and thus functional groups. In order to investigate the role of functional groups in this understory warming effect, wood density distributions were compared for each light availability class (from 0% crown illumination to 100%) and are shown in Figure A2 below.

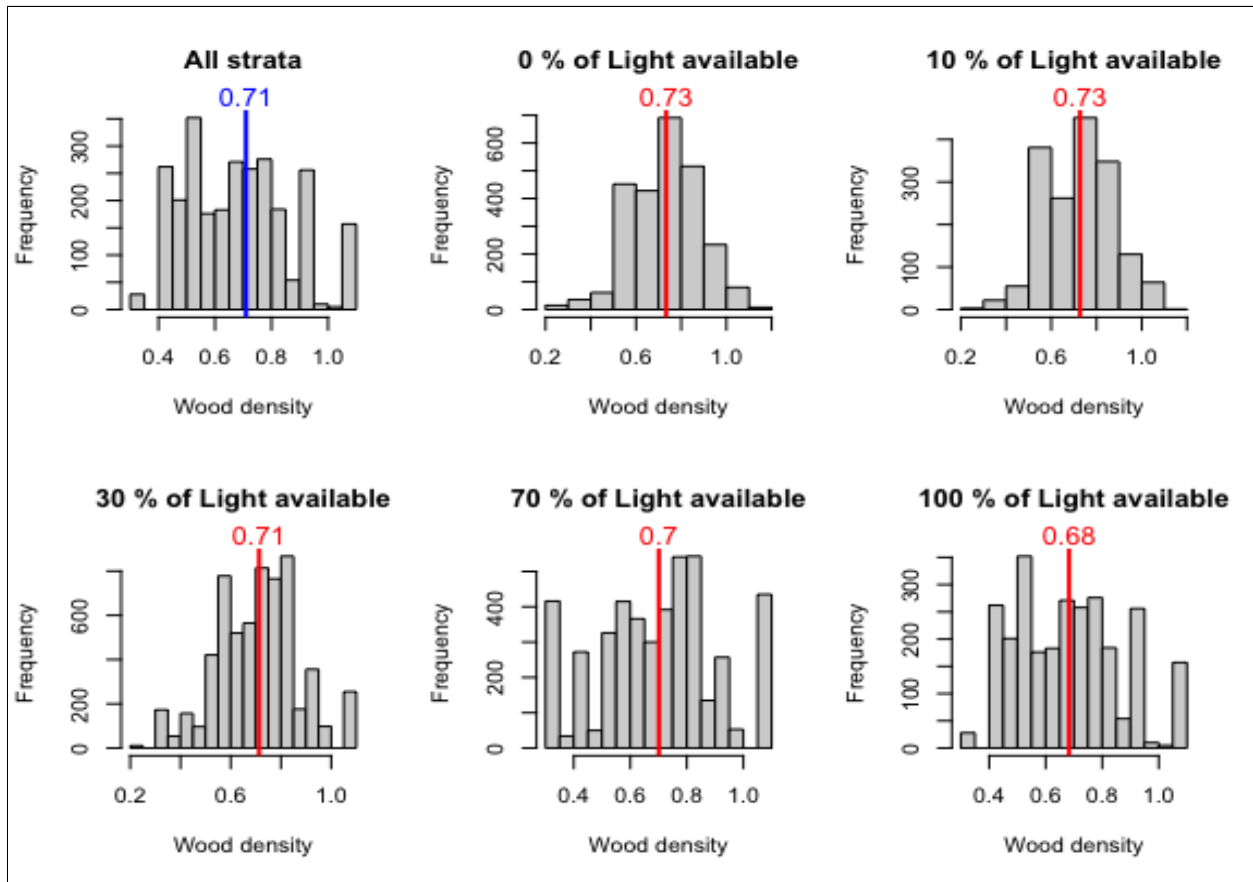


Fig. A2 Mean wood densities and frequency distributions of wood density values within each light availability class. The red lines and the blue line indicate the mean values.

The mean wood density across all trees is 0.71 with only slight deviations across the different strata. The highest mean wood density is found in the understory which has the lowest light availability. This can be explained by the fact that hardwood trees are often more shade resistant and can thus remain in the understory layer for longer, while softwood species either grow rapidly to the top or die off. In addition, the dominating dipterocarp vegetation on borneo leads to the increased occurrence of relatively low wood density trees in the canopy layer.

Predictions for today's climate

As was shown in section 3.2.2, temperature exerts a negative impact on tree growth rates in all forest strata. The model that was developed during this analysis, could potentially also be used to predict the reaction of trees to unprecedented temperature values, such as those governing the area today. Figure A3 visualises the results of this prediction for which temperatures were simulated to be consistently rising until they reach 1° higher in 2020 than they were in 1970.

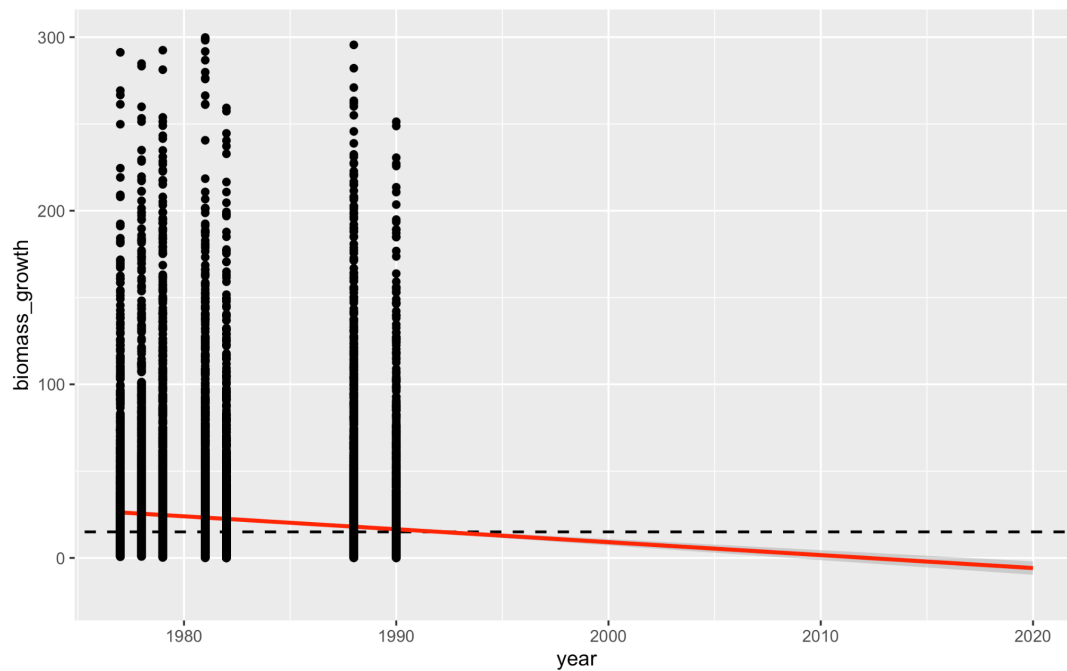


Fig. A3 The red line presents the model's predictions for mean yearly tree growth under increasing temperatures. The dashed black line indicates expected growth rates if the temperature would stay at the level of 1990. The temperature in the year 2020 was 1° higher than at the beginning of the study period in 1970.

This is already a conservative estimate, as temperatures have risen more than 1° in the past 50 years. However, as can be seen in the figure below, growth rates were predicted to decrease so drastically, that the mean biomass gain is predicted to be negative after the year 2012. This indicates that a linear model does not describe the real relationship between temperature and biomass growth. The effect of temperature on tree growth is most likely non-linear with growth rates saturating at a low level outside of optimum temperatures for a long time, until temperature extremes lead to tree mortality.

