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Photosynthesis in tropical forests in Rwanda

-an ecophysiological characterization of tropical mountain rainforest and tree plantations.

Johanna Gårdesten

Uppsats för avläggande av naturvetenskaplig magisterexamen i Biologi
30 hp

Institutionen för Växt- och miljövetenskaper
Göteborgs universitet

GÖTEBORGS UNIVERSITET

Preface

Temperate ecosystem is relatively studied, although ecosystems in the tropics is quite uninvestigated, especially those in Africa. Tropical ecosystems are important in many ways, as a local source to the people and as an important role in the global carbon cycle. Hopefully this project will enhanced the knowledge of the ecophysiological characters of some tropical tree species. The focus of the project is the photosynthesis and gas exchange of the plants with the aim to contribute with data to climate models. The study is linked to an ongoing collaboration between the University of Gothenburg and the University of Rwanda where the carbon flow between atmosphere, plants and soil is considered.

The field work was done during eight weeks in January-March 2009 in Butare and Nyungwe of Rwanda. The Minor field study was financed through SIDA (Swedish Internationally Development Cooperation Agency).

Acknowledgements

This study in Rwanda wouldn´t have been able to go through with if there haven´t been supported by some several persons. I am very thankful to following people.

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Among the people in Rwanda helping me with all the practical things I would also like to give special thanks to Ph. Student Donat Nsabimana, Department of Biology at the University of Rwanda for his welcoming, advice and big help. Together with his assistant Etienne Sebera, they helped me to manage to collect all data needed in field for this thesis. The students Eric and Felix at the Department of Biology the University of Rwanda helped me with my fieldwork when they had time free from school. I also would like thank the climbers Emanuel and Jeremiah with company, who did the impressing job of climbing the trees and the collecting of the leaves. From the University of Rwanda I received a warm welcome and the University gave me access to laboratory and car with drivers.

I also would like to thank Rwanda Office of Tourism and National Park (ORTPN) for giving permission of doing research in Nyungwe.

At the Department of Plant and environmental sciences of Gothenburg University I would like to thank you Dr. Henrik Tjellsström and Research Engineer Mats Räntfors for helping me with the leaf samples analyses.

Also thanks to SIDA (Swedish Internationally Development Cooperation Agency) and the University of Gothenburg for giving me this opportunity and financed this study with MFS scholarship

Finally I would like to thank you all for giving me a worthwhile, interesting and enjoying time in Rwanda. The land of thousands hills with amazing nature and its people will always keep a special place in my heart and mind.

Sammanfattning

Tropiska regnskogar är viktiga ur flera olika perspektiv, inte enbart som en naturresurs till lokalbefolkningen utan de innehar även en stor roll i ett regionalt och globalt perspektiv. Världen står idag inför kommande klimatförändring och den kommer att påverka alla levande organismer. Tropiska regnskogar har stor inverkan på globala flöden av kol och atmosfärens stigande koldioxidhalt, således även på det regionala klimatet och hydrologin. Då kunskap om tropiska ekosystem är relativt begränsad, i synnerhet regnskogarna i Afrika, ämnar den här studien till att utföra en ekofysiologisk karaktärisering av några tropiska trädarter i Rwanda. Studien är finansierad av SIDA och är kopplad till ett större projekt där kolomsättningen i tropiska skogar studeras.

Fotosyntesens reglering och parametrar togs fram för den biokemiska fotosyntesmodellen av Farquhar m. fl för att förstå gasutbytet mellan vegetation och atmosfär. Mätningar av fotosyntesen gjordes hos sammanlagt sju olika trädarter i en bergsregnskog och en trädplantering i Rwanda av mätinstrumentet Licor. De sex arter som studerades i bergsregnskogen i Nyungwe skiljdes åt i två grupper; klimaxarter och pionjärer. Tre arter studerades i arboretumet Ruhande, varav två även fanns i Nyungwe. Mätningar och data mättes hos både solblad och skuggblad och samtliga blads torrvikt av kväve- och fosforhalt analyserades i lab.

Resultaten av data visade en signifikant skillnad mellan klimax och pionjärarter, där pionjärer visade sig ha ett högre värde av parametrarna V_{cmax} (maximala hastigheten av karboxylationen) och J_{max} (maximala hastigheten av elektrontransporten). Ingen signifikant skillnad fanns mellan sol- och skuggblad. Jämförelserna av de båda arterna *E.e* och *P.f* som fanns på båda platserna visade att det var en signifikant skillnad hos arten *P.fulva*. Värdena av V_{cmax} var högre i Nyungwe än i Ruhande Arboretum.

Fotosyntesen visade sig ha ett positivt samband av näringsämnena kväve och fosfor, dock inte av sådan hög grad. Genom korrelationskoefficienten visade det att parametrarna V_{cmax} och J_{max} var ena aning mer korrelerade med kväve. Genom att genomföra linjär regression av näringsämnena kväve och fosfor visade sig att kvävet hade högst signifikant effekt på V_{cmax}.

Det finns olika ekofysilogiska karaktärer hos trädarter i tropisk skog i Rwanda. Fortfarande är kunskapen om fotosyntesens regleringar och parametrar i tropiska ekosystem förhållandevis liten. Då tropiska ekosystem är komplexa behövs det fler och större studier, men genom den här uppsatsen fylls en liten lucka av kunskap igen.

Content

Introduction

1.1 Background

Global environmental change is in focus of the world today and it will affect every living organism in the world. The change of land use together with the change of atmospheric composition is a major contributor to the climate change. CO_2 is the largest single contributor and the rate of photosynthetic CO_2 uptake by leaves is not yet saturated. (Körner, 2003)

Historically the concentration of CO_2 in the atmosphere is believed to have been higher in the early Cenozoic (~60 million years ago) than the currently one. The concentration is assumed to have been as high as 2000 p.p.m about 60-55 Myr ago but there are disagreements of the exactly concentration and when the decline of it began, but approximately 55- 40 Myr ago. Since the early Miocene (~24million year ago) the concentration seems to have been below 370 p.p.m (Pearson, 2002). The concentration of CO_2 has been anthropogenic affected since the pre industrial time. According to the report from the IPPC (2007) the concentration of CO_2 in 2005 was 379 p.p.m and the annual increase of CO_2 emissions grew with 80% from 1970- 2004.

Changing the composition of the atmosphere will affect all aspects of plant life. The plants, in turn will give feed-back to the atmosphere and climate by their photosynthesis and respiration. The plants affect the flow of carbon and the transpiration regulates the local/regional hydrologic balance. The interactions between plants and atmosphere are important in models to foresee the climate and stability in ecosystems in the future and during changed condition. (Körner, 2003)

Forests occupy roughly 30 percent of the terrestrial biosphere and the ecosystems are important in environmental, sociologic and economic ways. The forest supplies not only food and products, but also works as protection against soil erosion and a regulator of the hydrological cycle. In total the forest store ~45% of terrestrial carbon. (Bonan, 2008)

There are different levels of vulnerability to climate change of forest ecosystems. The vulnerability depends on the diversity both genetic and the richness in species. Also of the size of the forest area and how it´s affected of natural and anthropogenic factors. The most vulnerable are those systems which already exist under high pressure from humans. (IPPC, 2007)

The tropical forest are mostly located in countries with limited economics and the forest here is being degraded, deforested and exploited through anthropogenic activities which weakens the resilience of the forest to the climate change. The need of building materials, food and fuel wood are mostly the drivers for forest degradation. Tropical domain is predicted to experience a higher temperature with an overall decrease in precipitation although it differs between regions (Malhi et al. 2005). The forest systems in mountains are predicted to be more vulnerable. They are facing biodiversity degradation, induced drought and with this risk for more fires. (IPPC, 2007)

1.2 Definition of tropical rainforest

The tropical domain plays an important role in the global energy budgets and the general circulation of the atmosphere. The tropics are located approximately between the Tropic of Cancer 23^0 N and the Tropic of Capricorn 23^0 N and takes up 40 per cent of the total global surface area. The Old world, often called the Palaeotropical, consists the regions in Africa and Asia meanwhile the New world, Neotropical, is the region in Central and South America. The vegetation in the tropical domain is highly variable, with evergreen rain forest to arid deserts. Although tropical environment is different from each other, even at local scale; some common things can be said about it (Kellman et al. 1997).

Due to the Koppen- Geiger classification system tropical climates should be determined as those systems having no month with mean temperatures below 18^0 C. The soils that dominate tropical regions are oxisols (ferralsols) and ultisols (acrisols); both highly weathered soils and dominated by kaolinites and iron and aluminium oxides which give low CEC but some AEC (Eriksson et. al, 2005). The primary limiting nutrient on very old soils seems to be phosphorus rather than nitrogen. Nitrogen appears to have a fast cycling in tropical forests and is not the limiting on plant growth. (Lüttge, 2008)

Tropical forest is one of the two major plant formations in the tropics, the other one is savannah. The tropical rainforest is distributed along the geographical regions of the tropics, the Neotropics, Africa and the Asia-Pacific area. Forests within these regions often share common structural traits and plant forms but few common species (Kellman et al. 1997). The climate is warm to hot and frost are absent throughout the whole year. No forest type or habitat has as high diversity and endemic species as the rainforest. The tropical forest contains 70 per cent of the plants and animals in the world. Not less than 70 % of the world´s vascular plants, 30 % of all birds and >90% of all invertebrates are found here (Sands, 2007).

The classification of tropical rain forest can sometimes be difficult and often you determine the forest types depending on the length and severity of the dry season. The further distance from the equator you come, less precipitation falls and rainfall becomes more seasonal and there is longer time with longer dry seasons. Where you have an increased precipitation and cloudiness in tropical mountains the trees become loaded with mosses and other epiphytes, and other plants that are dependent on moisture (Kellman et al. 1997). Due to the diversity of tree species, there is no species dominating the rainforests thereby the most frequent tree species hardly ever represent more than 15% of all species of trees present (Sands, 2007).

1.3 Rwanda

Rwanda, the land of the thousands hills, is situated landlocked in Central Africa with border to Tanzania, Uganda, Burundi and DRC (Democratic republic of Congo). The landscape of Rwanda is unique, created by its position in the Albertine Rift which has made the land rich in diversity. The land is dominated of mountain ranges and highlands plateaus with great watershed between the Nile and the Congo River basins (ORTPN, 2009). African tropical rainforests are usually at higher elevation with drier and cooler climate than the rainforests of other continents (IPPC, 2007)

1.4 Farquhar model

In year 1980 Farquhar et al. published the article "A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species" The model of the photosynthesis described in the article was an attempt to describing the responses of CO_2 exchange by leaves taking the environmental conditions (temperature, CO_2 concentration, light intensity, humidity and oxygen concentration) in consideration (Long, S.P and Bernacchi, C.J, 2003).

The mathematical model is describing the Rubisco kinetics, linking the equations of the photosynthetic carbon reduction cycle and the photo respiratory carbon oxidation cycle together. The models of photosynthesis and stomatal conductance can be placed into larger models trying to understand the global carbon cycle and the land surface feedback on climate (Sharkey et al. 2007).

1.5 Physiological ecology of tropical plants

Environmental factors can become a stress factor if its quantity is too high or too low, and the most important factors are; nutrients, water, CO_2, light and temperature. The interactions and variation in time and space of these factors cause competition and stress in the tropical forest and thereby determine the species composition. The light penetration relays to Lambert- Beer´s law, which means that the irradiance decrease exponentially from the main canopy layer to the forest floor (Lüttge, 2008).

The organisms in the forest influence the carbon- dioxide concentration through their photosynthesis and respiration. There are diurnal and seasonal dynamics of the CO_2 concentration in the vertical profile in the tropical rainforest and the plants within in the canopy may photosynthesize at higher concentrations of CO_2 than the average in the atmosphere outside the forest, at least in the morning (Lüttge, 2008).

The soil is often poor in mineralized nutrients, and phosphorus is often the most limiting plant nutrient. The different species in the tropical forest varies their leaf longevity from month to years, with high variety in investments of nutrients to the leaves. The plant can either allocate nitrogen recourses to obtain a higher photosynthetic assimilation from large leaves to fragile leaves or to provide a resistant physical structure which leads in a lower rate of CO_2 assimilation over a longer time (Lüttge, 2008).

Individual trees have both shade and sun leaves, thus the part of the foliage is shaded or exposed to the sun. The variability in the climate in the tropical forests makes it important for the plants to have different aspects. The photosynthesis of shades leaves at light saturation is lower (Lüttge, 2008).

The classification of climax and pioneer species focuses on light, and the resource of light is strongly limiting in forests (Meir et al. 2007). Comparing fast-growing pioneers to slow-growing climax species shows that the pioneers have the characteristic of sun plants. The climax species show a more intermediate behaviour as they can both be exposed in the sun and shaded in the lower canopy layer. The pioneers and the climax species regulate their gas exchange in different ways. The pioneers often have higher rates of the maximum photosynthesis the shade plant. The shades leaves in climax species have lower leaf

Conductance to water vapour which leads to lower gas exchange and growth. Comparison to the climax species; the pioneers have a greater stomata conductance, supplying CO2 to photosynthesis at a higher rate. (Lüttge, 2008)

Nitrogen plays an important role in the photosynthetic apparatus, as Rubisco and cytochrome contain much of it. There is a linear relationship between the Farquhar et al. model and nitrogen in temperate tree species grown in ambient or elevated CO_2 concentrations. The relationship depends on the enzyme of Rubisco, which is the key to the carboxylation, and affects the maximum rate of carboxylation (V_{cmax}). Rubisco contain 30% of the protein in photosynthesising leaves (Meir et al. 2007).

In ecosystems where N is the limiting (for example in the northern hemisphere), the nutrient is expected to influence V_{cmax} strongly. There are few measurements of photosynthesis made in tropical forests. In tropical ecosystems the amount of nitrogen is usually not the limiting factor and the relationship could have more variety. Instead it is said that the amount of phosphorus that is the limiting nutrient, although its influence on the photosynthesis is rarely investigated in tropical forests (Meir et al. 2007).

1.6 The aim

The purpose with this Minor field study is to do an ecophysiological characterisation of some tree species in a tropical rainforest with respect to the photosynthesis and gas exchange between plants and atmosphere with the aim to contribute to the estimation of the total account of carbon taken up by a mountain rainforest in Rwanda. While temperate areas are relatively well studied, this knowledge is missing in tropical ecosystems, especially in Africa. There is a need of enhanced understanding of tropical ecosystems, now more than ever since facing the global climate change and threat of deforestation. The interactions between plants and atmosphere are important in models to foresee the climate and stability in ecosystems in the future and during changed land use or environmental conditions both on global and regional scale. The project is a part of the ongoing collaboration between the Department of Plant and Environmental Sciences at Gothenburg University and the National University of Rwanda and includes close collaboration with researches in Rwanda and Sweden. This Minor Field Study, financed through SIDA (Swedish International Development Cooperation Agency), is a part of a larger project to contribute to research and development in progress of the area.

The main questions are:

- What kind of variations in the leaves are there of the photosynthesis and gas exchange of tropical tree species in Rwanda.
  - i) Are there any differences between species or between climax and pioneers?
  - ii) Are there any differences between sun or shade leaves?
  - iii) Are there any differences depending on where they are distributed, rainforest or Arboterum?
- Is the photosynthesis in tropical forests limited by nitrogen or phosphorus?

2. Methods and material

2.1 Study sites

The fieldwork was made at the two sites Ruhande Arboretum and Nyungwe between 24th of January-10th of March 2009.

Ruhande Arboretum

The Arboretum of Ruhande is located in the South of Rwanda (2^{0}36´S, 29^{0}44´E, 1638-1737m elevation), nearby the University of Rwanda in the city of Butare. The forest plantation was initiated in year 1933 and has a size of 200 ha, divided into 504 plots. The Arboretum consist over 207 indigenous and exotic tree species where each species is planted into plots of the size 50x50 meters. Both deciduous and conifer trees are planted here and there are many different trees within the family of Eucalyptus. The Arboretum of Ruhande work as an area for research and education purposes, but also supplies trees seeds at national level. All the tree nurseries in Rwanda and various development projects get their seeds from here (FAO, 2009).

The precipitation mainly falls during two rainy seasons, where the major rainy season occurs from March to May and the second one from September to December. The long-term average of the precipitation (between years 1967-1993) was 1246.4 mm and the annually mean temperature is $19.6^{0}C$ (WCS, 2002). During wet season the relative humidity lies between 77 and 86% and during dry seasons it ranges between 59 and 65%.(Nsabimana, 2009) The soil type of the area is Ferralsoil which is characteristically an old and highly weathered soil. This soil often occurs in tropical regions where you have a distinct rainy and dry season. The access to nutrients is quite limiting and the pH low due to the low cation exchange capacity. (Eriksson et al. 2005) The pH is between 3.9 and 5.4 in the topsoil (Nsabimana, 2009).

The species we studied were *Entandrophragma exelsum, Euacalyptus maculata, Polyscia fulva. E. exelsum* and *P. fulva.* These are indigenous species to the tropical mountain forests in Africa. *E. exelsum* is also called the African mahogany and valuable for its timber. *P. fulva* is used in agro forestry due to its timber and the umbrella like canopy feature makes it a good species intercropping with bananas, coffee and cacao. The fast-growing exotic species of *Eucalyptus maculata* was introduced from Australia and commonly used in agro forestry worldwide. (FAO, 2009) Euacalyptus species occupy 65% of the planted forest in Rwanda (Nsabimana, 2009).

The plots of the forest stands were randomly distributed and replicated three times, although for E. *maculata* only two plots were available. In total 11 plots were used for measurements in the Arboretum. A comparison between two types of *P.fulva* stands was also made, where the protected area is without annually cutting from scrubs and herbaceous plants. These plots have not been investigated in their photosynthetic activity before.

Nyungwe

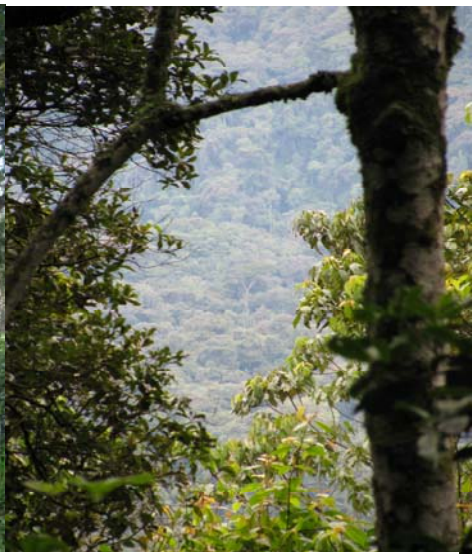
Nyungwe National Park is situated in Southwest of Rwanda ($2^{0}15'$- $2^{0}55'$ S, $29^{0}00'$- $29^{0}30'$ E, and 1600-2950 m elevation) and is the largest mountain rainforest in Africa with a size of 1000 km^2. The forest serves as an important habitat for different species and was initiated as a forest reserve year 1933, although back then still utilized by human. The diversity in flora and fauna is rich and many endemic species can be found here. At least 260 species of trees and scrubs together with at least 275 species of birds and 13 types of primates are reported from here (ORTPN, 2009). Ecological processes and the position in the Albertine Rift have given the area rich diversity, with a variety of topography, and different soil types. The mosaic of different structure and layers of the forest together with the high elevation makes it a good place for epiphytes and cryptogams. The National park is also home for the rare western Chimpanzee (WCS, 2002).

The climate is quite cool with annually average of the maximum temperature is 19^0 C and the minimum temperature is 10.9^0C (WCS, 2002). The mean annually precipitation is 1744mm according to the climate station in Nyungwe. The main dry season takes place between July and August and the smaller one between December and January (Nsabinama, 2009).

The selected species used in this area were; *Carapa grandiflora, Entandrophragma exelsum, Hagenia abyssinica, Macaranga kilimandscharica, Polyscia fulva, Suzugium guineense.* You can divide these six species into two groups; the climax (*C. grandiflora, E.exelsum S. guineense)* and the pioneer (*H. abyssinica, M. kilimandscharica, P.fulva)* species. The distribution of species is dominated by *Macaranga kilimandscharica* and *Suzugium guineense,* which together accounted for 35.7 percent of the inventory of large trees (≥ 30 cm DBH). The third species was *C. grandiflora* with a relative density of 6.6 percent. The density of rest of the species were following; *H. abyssinica* 4.2, *Polyscia fulva* 1.2, *E. exelsum* 1.0.

The study site here was situated in Uwinka, a research station and a part of Nyumgwe National Park. The selected stands were located nearby three distinct plots; the yellow, blue and green plot. The species of *Hagenia abyssinica* and *Polyschia fulva* were not present in these plots; the trails of green, grey and yellow colors leading to the plots with same colors were thereby used. All *E. exelsum* trees were found at one site, outside but nearby blue plot. The measurements were replicated three times and in total 18 trees were considered. Two species in Nyungwe is overlapping within the Arboretum; *Entandrophragma exelsum* and *Polyschia fulva.*

Picture 1, Plantation of P.fulva in Ruhande Arboretum.



Picture 2, View over the mountain rainforest of Nyungwe.

2.2 Field measurements

Measurements were made at the sites by the instrument LI-6400XT, which is a portable gas analyzer. The gas analyzer has two non- dispersive infrared gas analyzers and the infrared radiation passes through a chopping filter wheel and into the sample analyzer detector. The instrument measurements give no delays when measuring and it's possible to measure the absolute concentrations of both CO2 and H20. The instrument is robust and reliable even in tough conditions but a preparation check-list of the most important sensors and functions of the instrument was made every day before measuring. (Licor, 2009)

Picture 3, Shows the instrument LICOR measuring the species P.fulva.

Two branches, approximately about the size of 2 meters, were cut down by a professional tree climber from the tree, one each from canopy position in sun and in shade. Two sun leaves and two shade leaves of each were measured. The leaves were in good conditions and not damaged. Measurements were only conducted if the value of the conductance was over 0.05 µmol m^{-1} s^{-1}. VPD was not allowed to be over a certain level (1.0 in Ruhande and 1.5 in Nyungwe). RH was checked during the entire measurement. The photosynthesis was measured at different temperatures at the sites. The cooler climate in Nyungwe made it better to set the temperature to 20^0 C, meanwhile at the Arboretum 25^0 was more suitable. Depending on the value of conductance and its stability, A-Ci curves with somewhat different CO_2 were made. Some data points were excluded due to falling conductance.

2.3 Leaf physical and chemical determinations

Other data from the leaf were collected after measurement. Thickness, length and width of the leaf were noted and the content of the chlorophyll was measured by the SPAD technique. Different numbers (3-6) of leaf discs of known area was taken from the leaves and the leaf material was dried at 70^0 C to constant mass, thereafter weight on a balance before grounding. The grounded leaves were taken to Sweden in Ependorf tubes for further analyzes of the N and P content.

2.4 Data analyzes

The maximum rate of the carboxylation, V_{cmax}, and the maximum rate of the electron transport, J_{max}, was calculated in the ACi curve fitting mode of Sharkey et al. (2007). In the biochemical model of Farquhar et al. (2001), the limiting factors can either be; the amount of Rubisco enzyme (Ac), the RuBp-generation (Aj) or trios phosphate limitation (ATPU). This fitting model with the parameters of V_{cmax}, J_{max}, TPU, Rd and gm, requires pair of data of An (net CO_2 assimilation) and Ci (CO_2 intercellular of the leaf). The amount of Rubisco is usually the limiting factor when CO_2 level is low and the RuBp-generation when the CO_2 level is higher. Using a non-linear relationship curve fitting model in Excel you can minimize the differences between the observed photosynthesis and the predicted one and the model is an important tool to see changes of A due to environmental changes. Some assumptions and adjustments must be taken by the researcher and in some cases potentially co-limited data points from the analysis need to be excluded. The limit points were assigned in the order that all points below 17.5 Pa at chloroplast as Rubisco-limited, points above 35 as RuBp-regeneration and those in between these numbers as co-limited. The points at higher levels that are constant or declining with CO_2 are assigned as TPU-limited. (Sharkey et al. 2007)

The N and P content in the leaves were determined through analysis in lab and are given on a dry mass basis as well as leaf area basis. The leaf mass area ratio (LMA) was also calculated. The N concentration was achieved directly by gas chromatography and together with the LMA (leaf mass per area), the N content in g/m^{-2} could be calculated. For methods for P concentration determination see Tjellström et al.

The variables were correlated with photosynthetic capacities each (V_{cmax} and J_{max}) and linear regression was used to analyze the dependence of V_{cmax} and J_{max} on leaf nutrient N and P concentration. See inserted Table 2 for further details on tree and leaf data.

3. Results

The climax and pioneers species in Nyungwe had a significant difference comparing their J_{max} to each other (Figure 1a). In Nyngwe the climax species had significant lower photosynthetic rates of J_{max} with values between 76.1- 108 µmol m^{-2} s^{-1}. The pioneer species had significantly higher values of J_{max} in the range of 131.4 - 218.6 µmol m^{-2} s^{-1}. There were differences also between the pioneer species, were *Macaranga kilimandscharica* and *Hagenia abyssinica* differed. There was also a significant difference among the values of Vc_{max} between the pioneers and climax species, with the exception of the climax species *Suzugium guineense* (Figure 1b). *S. guineense* only showed significant difference to the pioneer species *Hagenia abyssinica* within the pioneers. The values of Vc_{max} of the climax species ranged between 37.9- 69.0 µmol m^{-2} s^{-1}. The pioneers had significantly higher values of J_{max} in the range of 93.6- 178.0 µmol m^{-2} s^{-1}.

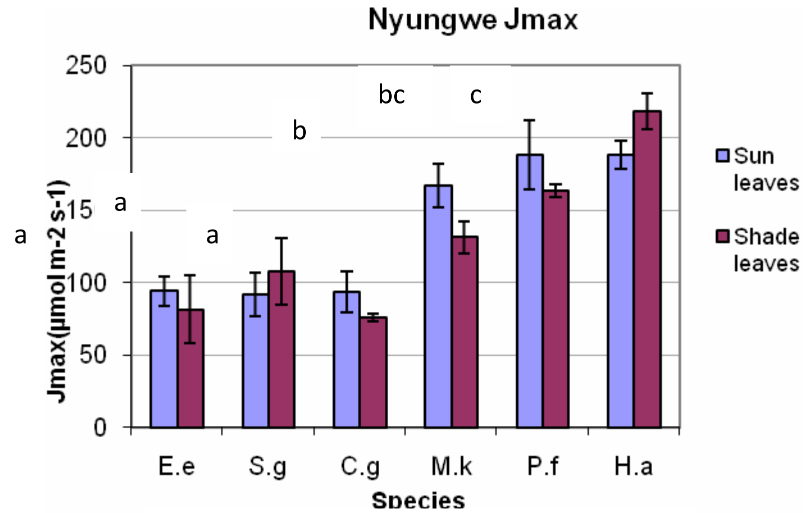


Figure 1a. The maximum rate of electron transport J_{max} (µmol m^{-2} s^{-1}) of the species in Nyungwe. Different letters indicate significant difference (P<0.05) between species.

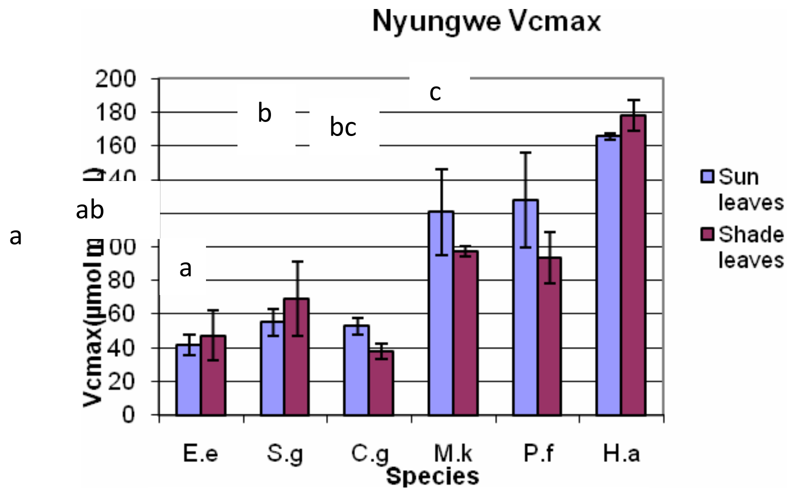


Figure 1b. The maximum rate of carboxylation V_{cmax} (µmol m^{-2} s^{-1}) of the species in Nyungwe. Different letters indicate significant difference (P<0.05) between species.

The species in the Arboretum had values of J_{max} in the range of 71.1-111.8 µmol m^{-2} s^{-1} and the values of V_{cmax} between 38.4-87.4 µmol m^{-2} s^{-1} (Figure2). The species of *E.e* had significantly lower values of J_{max} and V_{cmax} than the species of *P.f*

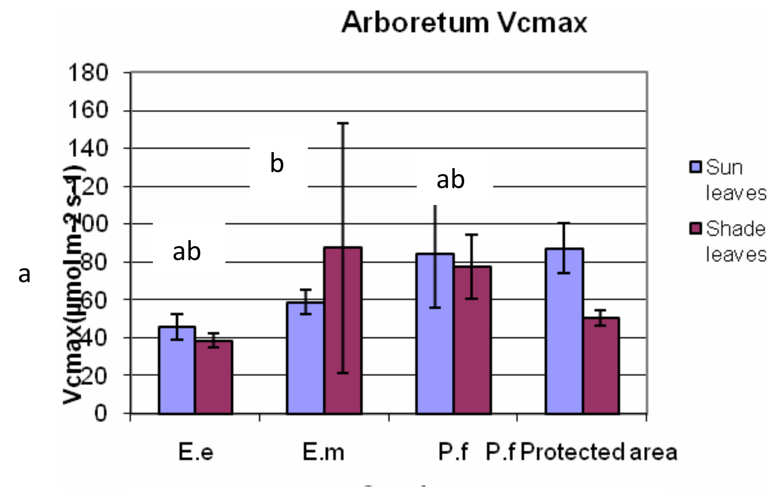


Figure 2a, the maximum rate of electron transport Vc_{max} (µmol m^{-2} s^{-1}) of the species in Arboretum. The diagram shows no significant difference among species.

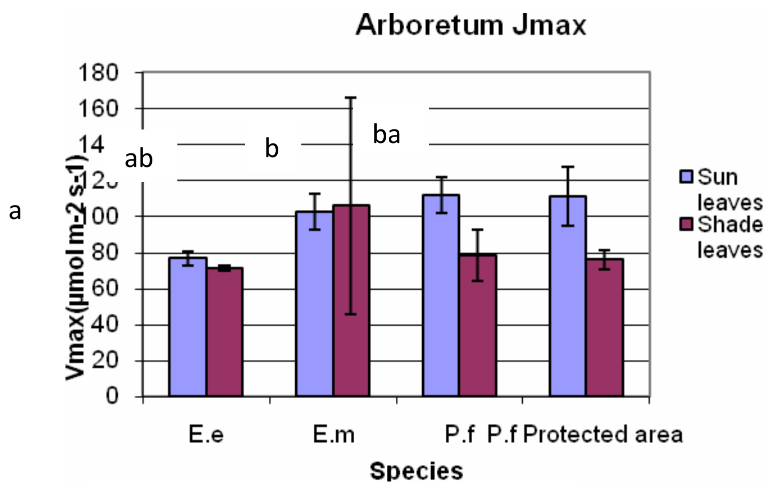


Figure 2b. The maximum rate of electron transport J_{max} (µmol m^{-2} s^{-1}) of the species in Arboretum. The diagram shows no significant difference among species.

The comparison between the two overlapping species of *Polyscia fulva* and *Entandrophragma exelsum* between the sites of Nyungwe and the Arboretum showed no significant difference of V_{cmax}, but there was a significant different in the values of J_{max} between *P. fulva* in the Arboretum to the *P. fulva* in Nyungwe. *P. fulva* in Nyungwe exhibited higher values of J_{max}.

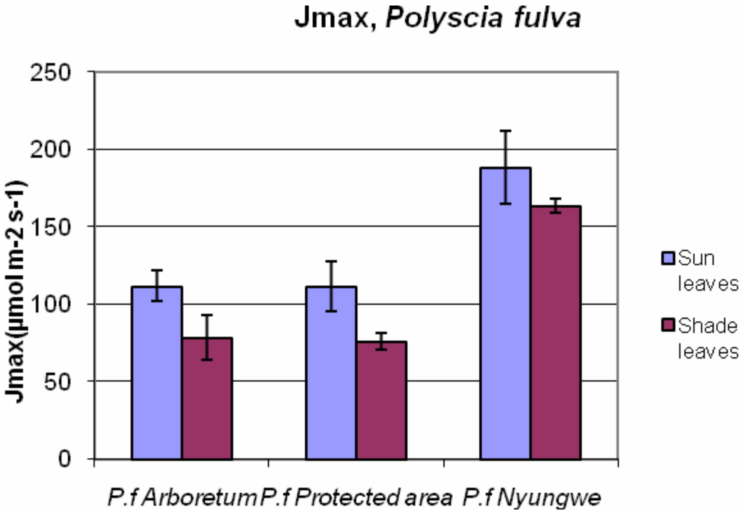


Figure 3. Significant difference of J_{max} between P.fulva in Nyungwe and the Arboretum.

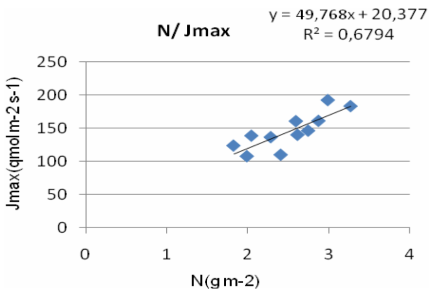
The result of doing a t-test with paired two samples for means exposed no overall significant differences between sun leaves and shaded leaves between all species.

Coefficients of determinations are shown in Table 1a. The table shows that there is a positive correlation. But there is little difference between the nutrients in the degree of correlation. The highest correlation was in the climax species of *E.e* where the correlation between J_{max} and P was 0.5448 and in the pioneer species *M.k* where the correlation between J_{max} and N was 0.6333(Figure4). Both V_{cmax} and J_{max} seemed to have a slightly higher grade of correlation to N rather to P. There was no correlation in the species of *H.a* and *E.m*; all the values were close to zero.

Species	Vcmax/P	Jmax/ P	Vcmax/N	Jmax/N
Climax Correlation/*p-values*				
E.exelsum	0.2514 / 0.04	0.5675 /0.00048	0.3065/ 0.02	0.3395 /0.014
S.guineense	0.2626 /0.07	0.075/0.32	0.3966/0.021	0.2588/0.075
C.grandiflora	0.1911/0.15	0.1799/0.16	0.3066/0.061	0.3711/0.035
Pioneer				
M.kilimandscharica	0.1706/0.21	0.2177/0.038	0.3011/0.029	0.6497/0.0018
P. fulva	0.1585/0.021	0.4196/0.00046	0.1108/0.058	0.1955/0.0099

H.abyssinica	0.0349/0.61	0.0112/0.77	0.007/0.81	0.0669/0.47
E.maculata	0.0009/0.95	0.00007/0.98	0.0035/0.72	0.0165/0.59

Table 1. Partial correlation coefficients for regressions of V_{cmax} and J_{max} on N and P content. Highest degree of correlation was between the species of E.e where the correlation between J_{max} and P was 0.5448 and in the pioneer species M.k where the correlation between J_{max} and N was 0.6333. The p-values shows the most significant effect ($p<0.05$) on V_{cmax} to be N.



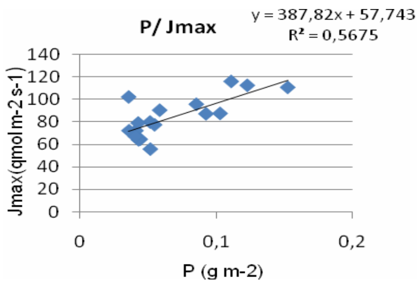


Figure 4.. Scatter plots showing the highest correlation in the pioneer species M.k where the correlation between J_{max} and N was 0.6794 in the climax species of E.e where the correlation between J_{max} and P was 0.5675.

The power of different variables was examined by linear regression (Table 1). The linear regression identified the most significant effect ($p<0.05$) on V_{cmax} to be N in our sites and species. The effect of N and P in the species of *H.a* and *E.m* was not shown at all. There was also most significant effect on J_{max} by N in our sites and species.

Discussion

There are few data of V_{cmax} and J_{max} available for species in tropical rainforests and especially for those in Africa. The values found in this study are around the reported range from an earlier study in tropical forests in Africa (Meir et. al 2007).

Comparing the climax species and the pioneer species in Nyungwe showed a significant difference. The fast growing pioneer species tend to have higher rate of V_{cmax} and J_{max}. The different values show differences of the capacity of photosynthesis. Climax species show more intermediate behaviour as they can be exposed to both sun and shade. (Lüttge, 2008) There were some differences within the group of pioneers, where *Macaranga kilimandscharica* and *Hagenia abyssinica* differed. Explanation to this can be that the species are different kinds of pioneers. *Macaranga kilimandscharica* grew more inside the dense forests compared to *Hagenia abyssinica* which grew in more open gaps nearby trails and roads where there had been more severe disturbances. An assumption could be that the *Macaranga kilimandscharica* is something between the climax and pioneer species or that they shift during their lifetime. There was also a significantly differences between the climax species *E.e* and the pioneer *P.f* in the Arboretum.

There was a significant difference of V_{cmax} between the *P. fulva* in Nyungwe compared to the Arboretum. This could depend on that the environmental conditions are better in Nungwe. *P.f* is a pioneer and likes disturbances, for example gaps. The gaps of bigger trees inside the forests make it possible for fast-growing species to establish and the gaps have fast rates of decomposition and releasing of nutrients. In the Arboretum on the other hand there are generally no naturally gaps, so the decomposition and releasing of nutrients are lower here.

Comparing the sun leaves to the shades leaves showed that there was no significant difference between them. If the leaves would have been compared within the species, maybe some significant difference would have occurred. In some of the species it was hard to determine if the leaves were distinct sun or shade leaves.

According to the nitrogen and phosphorus content to J_{max} and V_{cmax}, there was a positive correlation between them, although small in the degree. The highest degree of correlation was in the climax species of *E.e* where the correlation between J_{max} and P was 0.5448 and in the pioneer species *M.k* where the correlation between J_{max} and N was 0.6333. Both V_{cmax} and J_{max} seemed to have a slightly higher grade of correlation to N rather to P. According to Meir, nitrogen is usually not the limiting nutrient in the tropics and that the relationship could have more variety compared to other biomes. The influence of N and P on the photosynthesis in tropical ecosystems might in that way be more complex and have a variety in different types of rain forest but also among species.

The linear regression indicate that the photosynthesis was constrained more by N than P in this thesis, although there´s also significant effect on V_{cmax} by P in some of the species. The lack of clearly shown V_{cmax}- leaf N relationship could be that there´s uncertainty in the small data set or that the understanding of allocating of N to different uses in tropical leaves is missing (Meir et al. 2007). Maybe there´s also a bigger variation between species than what is believed. The data in the species of *E.m* could have been affected by the small data set collected; the species was only replicated twice.

5. Conclusions

Data of the photosynthesis was collected from 7 different species in total, 6 species in Nyungwe National Park and 3 species from Arboretum. The data indicate that there is a significant difference of V_{cmax} and J_{max} between climax and pioneer species. There is no significant difference between sun and shaded leaves. For *P.fulva* growing in Nyungwe and the Arboretum, there was no difference in V_{cmax} while the J_{max} was higher in Nyungwe.

The data weakly suggest that the photosynthesis is more limited by N in tropical mountain rainforest and plantations in Rwanda. The relationship between the photosynthesis and nutrients still needs to be more investigated.

These data and project add to a more understanding of some ecophysiological characters in tropical ecosystems of Rwanda. However, more data is needed from tropical rain forest to be able to increase certainty of the model parameters of the photosynthesis and gas exchange to use in climate models.

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Table 2, Tree and leaf data

Species	Plot	DBH	Height of sun leaves (m)	Height of shade leaves (m)	Thickness (cm)	Length (cm)	Width (cm)	SPAD	LMA g/m2	N_%dwt	P_%dwt
Rain forest, Nyungwe											
E. exelsum	Muruli Tree No.1	33.4	27	13							
	Sun leaf 1				0,30	28,90	15,10	80,80	126,00	2,36	0,03
	Sun leaf 2				0,29	31,50	12,30	74,90	134,84	2,50	0,11
	Shade leaf 1				0,24	29,20	14,10	73,60	100,21	2,29	1,17
	Shade leaf 2				0,29	37,10	14,60	78,30	128,94	2,28	0,76
	Muruli Tree No.2	27.1	20	18							
	Sun leaf 1				0,27	27,90	11,20	64,10	103,89	2,04	0,71
	Sun leaf 2				0,25	26,50	8,60	60,10	103,89	2,04	0,71
	Shade leaf 1				0,26	28,70	9,50	68,80	137,05	2,14	0,08
	Shade leaf 2				0,30	31,60	12,10	66,30	117,16	2,14	0,08
	Muruli Tree No.3	19.6	19	16							
	Sun leaf 1				0,27	27,40	12,00	62,70	123,05	2,04	0,07
	Sun leaf 2				0,26	21,30	9,80	54,90	108,31	2,04	0,09
	Shade leaf 1				0,28	27,10	11,20	67,50	126,73	2,30	0,10
	Shade leaf 2				0,29	30,50	14,40	73,10	121,58	2,39	0,10
S. guineense	Blue plot	59	15	15							
	Sun leaf 1				0,34	12,00	4,50	65,20	107,84	2,81	0,10
	Sun leaf 2				0,28	10,40	3,60	64,50	109,13	2,85	0,07
	sun leaf 3				0,29	10,90	3,80	56,60	118,23	2,85	0,07
	Shade leaf 1				0,32	11,30	4,30	59,50	109,13	2,88	0,08
	Shade leaf 2				0,33	11,20	3,90	66,80	98,74	2,85	0,07
	Yellow plot	33.1	15	15							
	Sun leaf 1				0,28	6,20	3,30	42,80	160,78	1,77	0,04

	Sun leaf 2				0,27	8,40	3,80	49,00	142,91	1,84	0,05
	Shade leaf 1				0,22	9,50	4,50	43,30	107,84	1,87	0,06
	Shade leaf 2				0,27	8,40	5,70	48,70	110,43	1,69	0,05
	Green plot	46	20	4							
	Sun leaf 1				0,33	7,00	3,10	49,20	162,40	1,80	0,05
	Sun leaf 2				0,27	6,70	3,30	47,40	142,91	1,88	0,06
	Shade leaf 1				0,20	11,50	3,50	52,10	103,94	1,96	0,05
	Shade leaf 2				0,21	7,70	2,90	35,80	89,32	1,87	0,05
C. grandiflora	Blue plot	26	13	7							
	Sun leaf 1				0,26	27,10	8,10	83,50	124,52	2,24	0,07
	Sun leaf 2				0,34	21,30	6,10	74,20	165,79	2,20	0,09
	Shade leaf 1				0,22	14,30	61,10	72,80	105,37	2,33	0,11
	Shade leaf 2				0,25	26,80	8,20	73,90	112,00	2,48	0,08
	Shade leaf 3				0,34	21,30	5,60	78,60	157,68	1,99	0,07
	Yellow plot	80.3	20	7							
	Sun leaf 1				0,33	25,10	6,60	50,10	102,42	1,18	0,15
	Sun leaf 2				0,34	21,30	5,60	78,60	150,31	1,93	0,08
	Shade leaf 1				0,24	25,50	6,40	40,90	83,26	1,65	0,15
	Shade leaf 2				0,25	25,20	7,00	69,40	127,47	2,24	0,08

	Green plot	36.2	12	5							
	Sun leaf 1				0,38	23,50	6,70	85,50	145,89	1,97	0,08
	Sun leaf 2				0,37	23,80	7,70	75,80	168,00	1,88	0,08
	Shade leaf 1				0,34	22,00	6,20	80,10	148,84	1,82	0,07
	Shade leaf 2				0,24	29,50	7,50	71,40	73,68	1,99	0,10
P.fulva	Near blue plot	46	15	13							
	Sun leaf 1				0,45	15,00	4,50	50,00	138,52	2,38	0,11
	Sun leaf 2				0,46	9,60	3,20	49,60	149,41	2,22	0,10
	Shade leaf 1				0,43	11,00	5,70	44,30	120,84	2,41	0,10
	Shade leaf 2				0,45	12,90	3,20	49,60	148,11	2,22	0,09
	Near green plot	48.5	18	16							
	Sun leaf 1				0,39	19,10	6,20	44,10	99,47	2,04	0,11
	Sun leaf 2				0,35	18,00	5,90	46,80	96,52	2,13	0,10
	Shade leaf 1				0,41	16,20	5,70	48,40	108,31	2,19	0,10
	Shade leaf 2				0,37	16,20	5,00	46,30	97,26	1,91	0,07
	Near grey trail	20	20	20							
	Sun leaf 1				0,41	15,60	5,50	50,80	149,58	2,11	0,10
	Sun leaf 2				0,40	16,50	5,40	46,50	130,42	1,94	0,09
	Shade leaf 1				0,38	15,40	5,00	45,90	123,05	1,78	0,08
	Shade leaf 2				0,38	16,70	5,50	46,10	118,63	1,69	0,07
M. kilimandscharica	Blue plot	16.2	15	8							
	Sun leaf 1				0,33	10,00	5,10	51,20	132,52	1,72	0,08
	Sun leaf 2				0,27	11,20	4,30	48,20	118,23	2,33	0,07
	Shade leaf 1				0,24	11,30	4,70	52,80	109,13	2,40	0,07
	Shade leaf 2				0,23	12,40	5,40	52,60	94,84	2,54	0,07
	Yellow plot	26.1	14	8							
	Sun leaf 1				0,34	12,50	6,60	49,10	125,26	2,29	0,07

	Sun leaf 2				0,33	15,50	8,30	57,60	124,52	2,40	0,09
	Shade leaf 1				0,29	14,10	7,00	47,60	106,54	2,44	0,10
	Shade leaf 2				0,33	14,20	7,50	54,60	119,53	2,30	0,10
	Green plot	32	20	12							
	Sun leaf 1				0,35	10,90	4,90	39,10	127,32	1,79	0,08
	Sun leaf 2				0,27	10,40	6,30	42,10	106,54	1,92	0,07
	Shade leaf 1				0,25	10,50	7,00	47,60	102,64	1,78	0,11
	Shade leaf 2				0,25	11,00	7,50	54,60	111,73	1,78	0,07
H. abyssinica	Near blue trail	39	5	3							
	Sun leaf 1				0,24	19,20	5,80	39,30	58,95	3,15	0,11
	Sun leaf 2				0,24	17,80	5,90	40,80	62,63	3,36	0,12
	Shade leaf 1				0,24	16,70	5,40	39,40	51,58	3,74	0,17
	Near yellow trail	40	8	5							
	Sun leaf 1				0,22	15,40	5,00	36,50	45,47	3,87	0,21
	Sun leaf 2				0,22	15,40	5,00	32,50	43,31	3,89	0,21
	Shade leaf 1				0,22	13,80	4,60	35,00	50,89	3,73	0,18
	Shade leaf 2				0,21	14,20	4,90	35,40	44,39	3,27	0,17
	Near grey trail	22.6	7	4							
	Sun leaf 1				0,18	16,60	5,20	30,70	44,95	3,83	0,18
	Sun leaf 2				0,20	17,40	5,50	31,50	50,84	3,20	0,17
	Shade leaf 1				0,21	17,80	5,20	32,80	41,26	3,75	0,17
Arboretum, Ruhande											
E. exelsum	#44	43.2	25	8							
	Sun leaf 1				0,33	22,60	11,20	57,20	158,42	1,69	0,03
	Sun leaf 2				0,33	22,40	10,50	55,60	160,63	1,66	0,03
	Shade leaf 1				0,26	19,50	8,80	57,90	111,26	1,57	0,04
	Shade leaf 2				0,28	26,70	11,50	55,50	110,52	1,66	0,03
	#54	45.2	30	10							
	Sun leaf 1				0,34	19,60	10,60	62,00	161,37	1,79	0,03

	Sun leaf 2				0,35	25,00	11,60	71,10	152,52	1,94	0,03
	Shade leaf 1				0,32	22,20	7,70	59,10	112,73	1,91	0,04
	#78	44.2	30	12							
	Sun leaf 1				0,36	19,00	8,60	58,20	172,42	1,63	0,03
	Sun leaf 2				0,31	18,00	8,00	51,10	168,00	1,64	0,03
	Shade leaf 1				0,24	20,90	9,10	61,70	114,21	1,83	0,04
	Shade leaf 2				0,24	21,80	9,20	63,30	113,47	1,68	0,04
E. maculata	#6	19.5	30	15							
	Sun leaf 1				0,34	10,20	2,40	57,90	228,66	1,40	0,02
	Sun leaf 2				0,36	11,90	2,30	55,20	226,06	1,35	0,03
	Shade leaf 1				0,25	13,80	2,30	51,10	87,68	1,33	0,02
	#446	17.5	20	8							
	Sun leaf 1				0,34	14,30	2,90	46,20	201,38	1,52	0,03
	Sun leaf 2				0,33	14,20	3,50	44,40	203,55	1,50	0,02
	Shade leaf 1				0,31	18,10	3,60	50,70	126,02	1,69	0,03
P. fulva	#240	35.1	26	22							
	Sun leaf 1				0,69	14,30	6,10	50,50	154,73	1,54	0,04
	Sun leaf 2				0,57	16,40	5,80	49,80	158,42	1,43	0,05
	Shade leaf 1				0,41	19,00	8,40	47,30	78,10	2,15	0,06
	Shade leaf 2				0,42	20,00	9,60	49,60	71,47	2,35	0,09
	#262	57.2	35	27							
	Sun leaf 1				0,46	16,60	5,50	52,00	148,10	1,80	0,07
	Sun leaf 2				0,43	10,60	5,60	54,50	161,37	2,10	0,06
	Shade leaf 1				0,40	17,40	7,00	51,70	124,52	2,08	0,07
	Shade leaf 2				0,57	13,00	5,80	54,80	294,92	1,92	0,07
	Shade leaf 3				0,46	14,10	5,50	55,20	131,89	2,10	0,07
	#268	26	38	36							
	Sun leaf 1				0,53	9,80	4,20	51,30	183,52	1,50	0,05
	Sun leaf 2				0,49	8,60	5,00	53,90	151,03	1.946	0,05

	Shade leaf 1				0,37	12,50	8,70	48,40	128,94	1,54	0,05
	Shade leaf 2				0,38	10,30	7,30	49,30	108,31	1,88	0,06
P. fulva	PA1	61.9	13	10							
	Sun leaf 1				0,59	13,60	7,20	62,40	175,37	1,79	0,05
	Sun leaf 2				0,55	12,10	8,20	57,20	157,68	1,88	0,06
	Shade leaf 1				0,34	15,00	9,30	49,90	77,37	2,30	0,07
	Shade leaf 2				0,28	18,60	9,10	46,40	67,79	2,18	0,09
	Shade leaf 3				0,34	13,50	8,00	42,60	61,89	2,68	0,26
	PA2	45.2	25	16							
	Sun leaf 1				0,55	11,60	5,10	55,20	128,84	2,30	0,06
	Sun leaf 2				0,40	15,10	5,90	53,00	132,09	2,06	0,04
	Shade leaf 1				0,38	14,10	5,40	47,80	102,86	2,03	0,05
	PA3	36.1	32	22							
	Sun leaf 1				0,48	8,10	8,00	60,40	109,79	2,13	0,09
	Sun leaf 2				0,40	19,30	8,70	59,20	120,10	2,43	0,07
	Shade leaf 1				0,32	15,60	6,70	49,50	58,95	2,74	0,16
	Shade leaf 2				0,22	16,80	4,00	42,20	25,79	2,82	0,15