Carbon dioxide absorption and physiological characteristics of selected tropical lowland tree species for revegetation

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Abstract. Biological diversity can make a significant contribution to reducing greenhouse gases in the atmosphere. Trees form an essential part of the functioning of the terrestrial biosphere, especially in the carbon cycle. Yet, tree photosynthesis is far less studied than crop photosynthesis. This research aims to assess CO₂ absorption-related physiological characteristics of selected tropical lowland trees that are curated in Cibinong Science Center-Botanical Garden (CSC-BG) Indonesia for revegetation prospecting. CO₂ absorption, stomatal conductance, and transpiration were measured using an infrared gas analyzer photosynthesis system. Meanwhile, leaf chlorophyll content was estimated using a SPAD chlorophyll-meter. CO₂ absorption rate ranged from 3.42 to 20 µmol m⁻² s⁻¹. The highest rate was observed in Teijsmanniodendron bogoriense followed by Tectona grandis (19.67 µmol m⁻² s⁻¹). The rate of transpiration ranged from 4.7 µmol m⁻² s⁻¹ to 7.82 µmol m⁻² s⁻¹. Diospyros discolor was the highest, followed by T. grandis (7.65 µmol m⁻² s⁻¹). CO₂ absorption and rate of transpiration were positively correlated to stomatal conductance. In contrast, the CO₂ absorption and chlorophyll content were very weakly correlated. The stomatal conductance ranged from 0.14 to 0.54 µmol m⁻² s⁻¹, with that of T. grandis was the highest, followed by Erythrina crista-galli (0.53 µmol m⁻² s⁻¹), whereas the chlorophyll content ranged from 31 up to 78.43 SPAD.

1. Introduction
Forest ecosystems can be both sources and sinks of carbon dioxide (CO₂). Deforestation and land-use change contribute to around 18% of global CO₂ emission annually [1]. Efforts to reduce these emissions must, therefore, be considered as part of the strategy for Indonesia to participate in global efforts to reduce greenhouse gas (GHG) emissions. Sustainable forest management, afforestation, reforestation, and agroforestry appear to be the best mitigation options [1]. Thus, trees in a forest stand to form an essential part in the functioning of the terrestrial biosphere, especially in the carbon cycle. Yet, tree photosynthesis is far less studied than crop photosynthesis due to a large number of species and difficulty in measuring photosynthesis of entire trees or forest stands.

The reduction of CO₂ from the atmosphere is mainly the absorption of CO₂ by plants through photosynthesis where with the presence of leaf chlorophyll, carbon dioxide, and water with the energy of solar radiation through various metabolic processes that are converted into sugar, oxygen, and water. The results of photosynthesis are then accumulated in the form of plant biomass such as wood, fruit, and tubers. Variation in the CO₂ assimilation rate is large among trees not only across the continental transect but also across the tropical climate regions [2]. Fast-growing trees often have relatively higher CO₂ assimilation rates in tropical climate zones suggesting that CO₂ assimilation rates can be an indicator for evaluating fast-growing characteristics [2, 3]. Variations in photosynthetic...
capacity are influenced by internal as well as external factors. External factors that influence photosynthesis include solar radiation, CO\(_2\) concentration in the atmosphere, temperature, wind speed, pressure vapor, and availability of water and nutrients. The rate of photosynthesis decreases when the sunlight intensity decreases, temperature decreases, water availability, and nutrients are low [4-9]. Internal factors affecting the capacity of photosynthesis include leaf characteristics (construction, area, stomata, weight-to-area ratio, N, and leaf chlorophyll content [10-14].

Trees that are suitable for carbon mitigation are fast-growing, highly adaptable, have pioneering properties to provide a high chance of success and have high carbon fixation capacity [15, 16]. However, tree ecological and physiological characteristics vary significantly between species. To achieve successful revegetation, we need to understand the ecological and physiological properties of plant species and the accuracy in selecting plant types based on expected characteristics [17]. This research aims to provide information on tree characteristics related to CO\(_2\) absorption by analyzing physiological characteristics, including CO\(_2\) assimilation, water transpiration, stomatal conductance, and chlorophyll content. This information can be used for selecting suitable trees for revegetation with maximum CO\(_2\) absorption.

2. Materials and methods

This research was conducted at Cibinong Science Center-Botanical Garden (CSC-BG), Indonesian Institute of Sciences (LIPI), from July to August 2019. Tree species which belong to tropical lowland type species were selected based on their valuable function, for example, potential wood producers such as jati (Tectona grandis), endangered species that produce valuable hardwood and resin such as gaharu (Aquilaria malaccensis) and damar (Agathis dammara), or Indonesian local fruit tree species such as menteng (Baccaurea racemosa) and bisbul (Diospyros discolor). The list of the selected tree species is shown in Table 1.

The measurement of environmental and physiological variables was conducted simultaneously. Light intensity was measured by using a lux meter (Luxor). Leaf chlorophyll content was measured using a chlorophyll meter Konica Minolta SPAD-502 (Konica-Minolta, Osaka, Japan). Simultaneous measurements of carbon dioxide (CO\(_2\)) assimilation, stomatal conductance, and transpiration were conducted by using a portable infra-red gas analyzer (IRGA)-based LCi ADC Photosynthesis System (ADC Bio scientific, London, United Kingdom). The measurement CO\(_2\) uptake is a direct method of measuring carbon exchange. The rate of CO\(_2\)-assimilation was measured under a certain range of CO\(_2\) concentrations, photon flux [18]. For the measurement of physiological characteristics, fully expanded young (third leaf from the tip of a twig) and older leaves (fifth or sixth leaf from the tip of a twig) were chosen. Three different individual plants of each species were measured as replications. Simultaneous measurements of microclimate (light intensity), photosynthesis, stomatal conductance, transpiration rate, and chlorophyll content were conducted. The measuring time for each species was between 09.00–11.00 AM under a completely clear sky. Besides, relative humidity and air temperature were measured using a thermo-hygrometer HTC-1 (HTC, China). Statistical analyses were performed using IBM SPSS Statistics ver. 26 (IBM, New York, USA) and Microsoft Excel 2016 (Microsoft Corporation, Washington, USA).

3. Results and discussion

3.1. Environmental variables

Absorption of CO\(_2\) is a physiological process known as photosynthesis that is determined by environmental factors, mainly solar radiation and CO\(_2\) concentration in the atmosphere. Solar radiation was measured as light intensity and quantum energy, reaching the leaf surface for photosynthesis (Qleaf). The fluctuation of radiation intensity that was measured by using Lux meter ranged between 49600–114133 Lux. The study was conducted during the dry season (July-August 2018) with 30-40% relative air humidity and temperature ranging from 27-31\(^\circ\)C. Whereas, the variable of Qleaf that represent quantum energy for photosynthesis ranged between 621.33 to 1342.33 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). Factors that determine CO\(_2\) absorption was measured as the concentration of CO\(_2\) inside the leaf chamber (Ci)
of the IRGA-based photosynthetic measurement instrument and CO\textsubscript{2} reference (Cref). The value of Ci ranged between 300.33–388 ppm, whereas the value of Cref was 385.33–462 ppm (Table 2).

### Table 1. List of selected tropical lowland species studied.

| Local Name (scientific name *) | Family * | Native range * | Uses * |
|-------------------------------|----------|----------------|--------|
| Gayam (Inocarpus fagifer)     | Fabaceae | Malaysia to South Pacific. | Food and drink, wood |
| Gaharu (Aquilaria malaccensis) | Thymelaeaceae | Assam, Bangladesh, Borneo, East Himalaya, Malaya, Myanmar, Philippines, Sumatera, Thailand, Vietnam. | Fragrant resin and heartwood for perfumery, incense, and medicine |
| Menteng (Baccaurea racemose)  | Phyllanthaceae | Borneo, Jawa, Lesser Sunda Islands, Malaya, Maluku, Sulawesi, Sumatera, Thailand. | Edible fruit |
| Eben (Diospyros celebica)     | Ebenaceae | Sulawesi | Wood and timber |
| Sawo Duren (Chrysophyllum cainito) | Sapotaceae | Panama | Edible fruit |
| Kateng (Cynometra ramiflora)  | Fabaceae | Tropical Asia to West Pacific | Wood |
| Tali Jiwa (Kopsia arborea)    | Apocynaceae | China to Malesia and North Queensland. | Decorative flower and medicine |
| Dadap Merah (Erythrina crista-galli) | Fabaceae | Brazil to North Argentina | Chemical product, medicine, and wood |
| Bisbul (Diospyros discolor)   | Ebenaceae | Borneo, Philippines, Taiwan. | Edible fruit |
| Gandaria (Bouea macrophylla)  | Anacardiaceae | Andaman, Jawa, Malaya, Sumatera, Thailand. | Edible fruit, shade tree |
| Jati (Tectona grandis)        | Lamiaceae | Indian subcontinent and South East Asia. | Wood and timber |
| Damar (Agathis dammara)       | Araucariaceae | Philippines to Maluku. | Dammar resin |
| Duk (Diospyros kaki)          | Meliaceae | Taiwan, Malesia to North Queensland. | Edible fruit |
| Entabuloh (Teijmanniodendron bogoriense) Koord. | Lamiaceae | Borneo, Maluku, New Guinea, Philippines, Sulawesi, Sumatera, Thailand. | Wood |
| Tanglar (Aglaia elliptica)    | Meliaceae | Indo-China to Malesia. | Edible fruit and medicine |

*Information about the plant’s scientific name, family, native range, and utilization is obtained from the POWO database [19].

### 3.2. Physiological characteristics related to CO\textsubscript{2} absorption

Physiological characteristics of tree species that determine CO\textsubscript{2} absorption, such as photosynthesis, stomatal conductance, and transpiration, were measured by using the photosynthesis measurement apparatus. The observed values of those physiological variables are presented in Figure 1 and Figure 2. The absorption of CO\textsubscript{2} varied between tree species. Variation of CO\textsubscript{2} absorption observed ranged between 3.42 \(\mu\text{mol} \text{m}^{-2} \text{s}^{-1}\) in ebin tree (D. celebica) up to 20 \(\mu\text{mol} \text{m}^{-2} \text{s}^{-1}\) in entabuloh tree (T. bogoriense) as the highest, followed by jati or teakwood (T. grandis) (19.67 \(\mu\text{mol} \text{m}^{-2} \text{s}^{-1}\)) and dadap merah (E. crista-galli) (15.49 \(\mu\text{mol} \text{m}^{-2} \text{s}^{-1}\)) (Figure 1). Rate of transpiration ranged between 4.7 mol m\textsuperscript{-2} s\textsuperscript{-1} in ebin (D. celebica) up to 7.82 mol m\textsuperscript{-2} s\textsuperscript{-1} in bisbul (D. discolor). The second highest transpiration was observed in jati (7.65 mol m\textsuperscript{-2} s\textsuperscript{-1}), followed by cainito (C. cainito) (7.64 mol m\textsuperscript{-2} s\textsuperscript{-1}) (Figure 1).

Variation in CO\textsubscript{2} absorption and rate of transpiration is closely related to variables of stomatal conductance and leaf chlorophyll content. The stomatal conductance ranged from 0.19 to 0.54 mol m\textsuperscript{-2} s\textsuperscript{-1}, with that of T. grandis was the highest, followed by E. crista-galli (0.53 mol m\textsuperscript{-2} s\textsuperscript{-1}) and D. discolor (0.48 mol m\textsuperscript{-2} s\textsuperscript{-1}) (Figure 1) whereas the variation in the leaf chlorophyll content ranged between 31 SPAD (B. racemosa) up to 78.43 SPAD (A. dammara) (Figure 2).
Table 2. The values of measured environment variables (mean ± standard deviation): Photon Flux Density (Q leaf), CO$_2$ inside the chamber (Ci) and CO$_2$ reference (Cref).

| Tree Species         | Leaf  | Qleaf ($\mu$mol m$^{-2}$ s$^{-1}$) | Ci (ppm)          | Cref (ppm)         |
|----------------------|-------|-----------------------------------|-------------------|-------------------|
| 1. Gayam (Inocarpus fagifer) | Young | 801.43                            | 346.33±12.04      | 435.00±12.83      |
| 2. Gayam (Inocarpus fagifer) | Old   | 1233.00                           | 311.00±67.86      | 445.67±10.78      |
| 3. Gaharu (Aquilaria malaccensis) | Young | 949.00                            | 341.33±5.91       | 439.33±466.00     |
| 3. Gaharu (Aquilaria malaccensis) | Old   | 954.67                            | 339.67±49.22      | 443.00±47.38      |
| 4. Menteng (Baccaurea racemosa) | Young | 695.67                            | 374.33±10.96      | 444.67±5.91       |
| 4. Menteng (Baccaurea racemosa) | Old   | 920.33                            | 320.00±66.97      | 462.00±18.06      |
| 5. Eben (Diospyros celebica) | Young | 1114.67                           | 336.00±14.31      | 453.33±24.14      |
| 5. Eben (Diospyros celebica) | Old   | 1156.33                           | 356.33±29.45      | 461.00±20.12      |
| 6. Sawo Duren (Chrysophyllum cainito) | Young | 1042.67                           | 343.67±21.48      | 428.67±10.96      |
| 6. Sawo Duren (Chrysophyllum cainito) | Old   | 1122.33                           | 363.00±6.38       | 459.00±31.03      |
| 7. Kateng (Cynometra ramiflora) | Young | 1238.00                           | 332.67±15.84      | 446.33±16.50      |
| 7. Kateng (Cynometra ramiflora) | Old   | 1186.33                           | 300.33±49.84      | 444.00±15.58      |
| 8. Tali Jiwa (Kopsia arborea) | Young | 1342.33                           | 313.33±14.38      | 431.00±4.55       |
| 8. Tali Jiwa (Kopsia arborea) | Old   | 1263.00                           | 318.00±21.21      | 423.33±6.02       |
| 9. Dadap Merah (Erythrina crista-galli) | Young | 621.33                            | 388.00±30.74      | 452.00±26.99      |
| 9. Dadap Merah (Erythrina crista-galli) | Old   | 747.33                            | 347.67±33.11      | 385.33±139.55     |
| 10. Gandaria (Diospyros discolor) | Young | 1135.33                           | 373.00±46.56      | 459.00±424.00     |
| 10. Gandaria (Diospyros discolor) | Old   | 837.00                            | 325.67±106.60     | 424.00±4.90       |
| 11. Jati (Tectona grandis) | Young | 949.00                            | 341.33±5.91       | 439.33±466.00     |
| 11. Jati (Tectona grandis) | Old   | 954.67                            | 339.67±49.22      | 452.00±47.38      |
| 12. Damar (Agathis dammara) | Young | 695.67                            | 374.33±10.96      | 444.67±5.91       |
| 12. Damar (Agathis dammara) | Old   | 920.33                            | 320.00±66.97      | 462.00±18.06      |
| 13. Duku (Dysoxylum parasiticum) | Young | 1114.67                           | 336.00±14.31      | 453.33±461.00     |
| 13. Duku (Dysoxylum parasiticum) | Old   | 1156.33                           | 356.33±29.45      | 448.00±20.12      |
| 14. Entabuloh (Teijsmanniodendron bogoriense) | Young | 665.33                            | 376.67±22.29      | 459.33±21.76      |
| 14. Entabuloh (Teijsmanniodendron bogoriense) | Old   | 403.33                            | 341.33±40.27      | 448.00±21.92      |
| 15. Tanglar (Aglaia elliptica) | Young | 1176.33                           | 341.00±27.90      | 435.67±13.02      |
| 15. Tanglar (Aglaia elliptica) | Old   | 980.00                            | 370.67±34.32      | 482.67±84.40      |

Leaf chlorophyll content determines leaf CO$_2$ assimilation [13, 14] – tree species with a lower rate of CO$_2$ assimilation appeared to show lower leaf chlorophyll content and vice versa. However, the CO$_2$ absorption across the fifteen tropical lowland species is very weakly proportionate to the chlorophyll content (Figure 2B). The difference in leaf structure and pigment composition across various plant species may cause different light reflection and scattering effects, affecting the values of
The 7th Symposium of JAPAN-ASEAN Science Technology Innovation Platform (JASTIP)  
IOP Publishing  
IOP Conf. Series: Earth and Environmental Science 591 (2020) 012039  
doi:10.1088/1755-1315/591/1/012039

SPAD chlorophyll meter. Thus, a calibration equation specific for each tree species of interest must be established to estimate the absolute chlorophyll content [20]. The use of actual chlorophyll content generated through calibration curve estimation will give a more accurate relationship with the CO$_2$ absorption variable. Furthermore, this relationship needs to be studied more thoroughly in a controlled environment.

**Figure 1.** Physiological characteristics of tree species related to photosynthesis. (A) CO$_2$ absorption, (B) transpiration, and (C) stomatal conductance of young and old leaves. Different letters indicate significant differences in the mean of variables in old leaves (ANOVA, Tukey post hoc test) at a significance level of 0.05 (n=3).

It is well-known that light intensity and air temperature affect stomatal opening and rate of transpiration. Transpiration rate increase with the increase of light intensity. In this study, there was an obvious correlation between these factors. Stomatal conductance varied with radiation intensities. The values of the conductance ranged from 0.14–0.54 mol m$^{-2}$ s$^{-1}$. In most tree species, stomatal
conductance was higher at a high light intensity. It means that leaf stomata opened more widely under higher light intensity up to a certain level. A higher value of stomatal conductance resulted in a higher transpiration rate and higher CO$_2$ absorption (Figure 3). Under normal environmental conditions, CO$_2$ assimilation was affected more by external factors, especially solar radiation than by the leaf stomatal character. However, some theory stated that stomatal conductance correlates with a photosynthetic capacity [21]. Abiotic factors, such as light, temperature, CO$_2$ concentration, vapor pressure deficit, and nutrient status, have a major effect on net photosynthesis, and thus on growth and productivity. All environmental conditions, which tend to reduce photosynthetic rates such as low light, low temperature, low nutrient availability, also reduce the photosynthetic carbon gain [22].

![Figure 2](image-url)

**Figure 2.** Leaf chlorophyll and the relationship between chlorophyll level and CO$_2$ absorption among the tree species. (A) Chlorophyll content of the young and old leaf. Different letters indicate significant differences in the old leaves chlorophyll content (ANOVA, Tukey post hoc test) at a significance level of 0.05 (n=3). (B) Very weak correlation between leaf chlorophyll content of the tree species and their CO$_2$ absorption.

Stomata are responsible for virtually all gas exchange, including CO$_2$, O$_2$, and water vapor, between the plant interior and the environment. The response of stomatal conductance to water transpiration varied across different plant species [23]. Low stomatal conductance limits and reduces CO$_2$ absorption into leaves, whereas high stomatal conductance promotes higher CO$_2$ assimilation, but
at the same time causes water loss through evaporation [23, 24]. To maintain an optimal trade-off between CO₂ assimilation and stomatal conductance, mechanisms exist to adjust stomatal aperture in response to environmental cues such as photosynthetic photon density, and to internal signals such as phytohormones [25, 26]. The ratio of photosynthetic rate to transpiration rate is the measure of instantaneous or photosynthetic water use efficiency [27]. Entabuloh (T. bogoriense) exhibited a significantly higher water use efficiency compared to eben (D. celebica), gaharu (A. malaccensis), and duku (B. macrophylla) (Figure 4). Other trees such as jati (T. grandis), dadap merah (E. crista-galli), gandaria (B. macrophylla), and damar (A. dammara) showed a relatively higher water use efficiency of above 2 µmol CO₂ mol⁻¹ H₂O (Figure 4). Interestingly, trees from the mint family, Lamiaceae, i.e., jati and entabuloh, fall into this high photosynthetic water use efficiency group. This finding opens a question for future study on the potential of the cultivation of important species from the family Lamiaceae for revegetation and carbon sequestration in the context of climate change.

![Stomatal conductance vs CO₂ absorption](image1)

**Figure 3.** Relationship between photosynthesis variables. A positive correlation between old leaves stomatal conductance and (A) CO₂ absorption; (B) Water transpiration.

High stomatal conductance is suggested to increase ventilation as a response to a high transpiration rate in the open site and acclimation to avoid the extreme increase in leaf temperature. Previous reports revealed that the variation of stomatal conductance was little between 0.03 mol m⁻² s⁻¹ and 0.263 mol m⁻² s⁻¹ in lowland environment and between 0.043 mol m⁻² s⁻¹ and 0.223 mol m⁻² s⁻¹ in highland environment condition [28, 29]. Other papers reported that stomatal conductance of fast-growing Shorea balangeran and Acacia mangium were 0.49 mol m⁻² s⁻¹ [30, 31] and 1.3 mol m⁻² s⁻¹ [2], respectively.

The results of this study agreed with some findings that leaf photosynthesis in trees fairly variable with maximum values under natural conditions ranged from 3–30 µmol m⁻² s⁻¹. The values varied between 2–25 µmol m⁻² s⁻¹ for deciduous broad-leaved trees; 2–10 µmol m⁻² s⁻¹ for coniferous trees; 3–6 µmol m⁻² s⁻¹ for certain broad-leaved species such as Quercus and Fagus; and more than 25 µmol m⁻² s⁻¹ for poplar, oil palms and eucalypt [22]. Photosynthesis rate of Shorea was reported of 7–21 µmol m⁻² s⁻¹, Shorea balangeran 21.9 µmol m⁻² s⁻¹, Acacia mangium 24.2 µmol m⁻² s⁻¹, Hopea odorata 16 µmol m⁻² s⁻¹, and Ochroma lagopus (27.8 µmol m⁻² s⁻¹) [2, 3, 32]. The photosynthesis rate of tropical woody plants for the first stage of succession ranged 10–20 µmol m⁻² s⁻¹, and very scarcely reached 25 µmol m⁻² s⁻¹ [33].
Figure 4. Photosynthetic water use efficiency (WUE) of various tree species. The WUE was determined as the ratio of absorbed CO$_2$ to the unit of transpired water of old mature leaves (n=3). Different letters indicate significant differences (ANOVA, Tukey HSD post hoc test) at a significance level of 0.05.

This study suggests that for evaluation of the appropriate tree species for a revegetation purpose, photosynthetic characteristics of leaves are suitable indicators. The degree of photosynthetic plasticity in response to changes in light regimes was high in the most-light demanding species. Therefore it is recommendable to select trees that have a higher CO$_2$ assimilation rate of sunlit leaf and a higher degree of plasticity [3]. Some reports revealed that the correlation between stomatal conductance and transpiration was closer than the correlation between stomatal conductance and CO$_2$ absorption [34, 35]. The increase of light intensity is accompanied by the increase in temperature and the increase of leaf transpiration. This positive correlation occurs up to a particular level of light intensity [36]. Some important remarks should be made about the correct interpretation of the values of photosynthetic rate. First, growth conditions, as well as the experimental methods, have important implications on the CO$_2$ exchange rate measured. Plants raised under natural conditions and/or measured in situ tend to have a higher CO$_2$ exchange rate than plants grown under the controlled environment, such as in the greenhouse condition.

4. Conclusion
The results of the study concluded that there was a wide range of variation in CO$_2$ absorption from 3.42–20 µmol m$^{-2}$ s$^{-1}$. The highest rate was observed in entabuloh (T. bogoriense) followed by jati (T. grandis) (19.67 µmol m$^{-2}$ s$^{-1}$). The rate of transpiration ranged between 4.7 mol m$^{-2}$ s$^{-1}$ up to 7.82 mol m$^{-2}$ s$^{-1}$ with bisbul (D. discolor) was the highest, followed by T. grandis (7.65 µmol m$^{-2}$ s$^{-1}$). The stomatal conductance is proportionate to CO$_2$ absorption and rate of transpiration. The stomatal conductance ranged between 0.19 mol m$^{-2}$ s$^{-1}$ up to 0.54 mol m$^{-2}$ s$^{-1}$ with T. grandis was the highest, followed by dadap merah (E. crista-galli (0.53 mol m$^{-2}$ s$^{-1}$). Whereas, the CO$_2$ absorption and chlorophyll content were weakly correlated. The leaf chlorophyll content ranged between 31 to 78.43 SPAD, in which the chlorophyll content of young leaves was lower than that of older leaves. Among all the selected tropical lowland species, T. bogoriense exhibited the highest photosynthetic water use efficiency (3.08 µmol CO$_2$ mol$^{-1}$ H$_2$O) while eben (D. celebica) showed the lowest value (1.03 µmol CO$_2$ mol$^{-1}$ H$_2$O).

Acknowledgment
We thank Indra Gunawan (Research Center for Biology, Indonesian Institute of Sciences) and Fanny Chairani Harahap (Department of Biology, North Sumatera University) for technical assistance during the field data collection and compilation.
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