

Ecophysiological and growth characters of ten woody plant species in determining their carbon sequestration

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Manuscript received: 15 January 2018. Revision accepted: 21 March 2018.

Abstract. Rindyastuti R, Rachmawati D, Sancayaningsih RP, Yulistyarini T. 2018. Ecophysiological and growth characters of ten woody plant species in determining their carbon sequestration. *Biodiversitas* 19: 660-669. Tree planting and ecosystem restoration is one of mitigation program of global climate change scheme to reduce CO₂ in the atmosphere by sequestering carbon. Carbon storage in the living plant varies among species due to ecophysiological and growth characters of their photosynthesis. Ecophysiological properties of tropical plant species related to carbon sequestration was lack of investigation. The study in this area will be the significant knowledge contribution to C-sink project especially species-level management which has been agreed globally and nationally. The objectives of this research were to study the ecophysiological and growth factors affecting carbon sequestration and to select plant species with high carbon sequestration using 16 months-old-seedling of ten woody plant species. Biomass, carbon storage, the whole plant photosynthetic capacity, total chlorophyll content, stomatal index, and Leaf Area Index (LAI) were significantly different among species. The LAI, total chlorophyll content, whole plant photosynthetic capacity, stem height and stem diameter were positively correlated to biomass and carbon storage. Multivariate correlation test ($P > 0.05$) revealed that the total of chlorophyll content was the ecophysiological factor most contributes to carbon sequestration. The total of chlorophyll content correlates to the stem height, while the whole plant photosynthesis correlates to leaf area in determining plant carbon sequestration. Moreover, two mangrove species, *H. littoralis* and *B. asiatica* have the highest carbon sequestration among species studied. For priority in tree planting program in dry lowland habitats, the local species, i.e., *S. cumini* and *D. discolor* were more recommended than any others species observed in this study.

Keywords: Ecophysiology, growth, chlorophyll, woody, carbon sequestration, CO₂

INTRODUCTION

Carbon dioxide (CO₂) is one of the greenhouse gases produced by the organic material burning, such as wood during the deforestation and the emission of burned fossil fuel (Reitze 2001; Jacobson 2012). The concentration of CO₂ in the atmosphere increases greenhouse gases significantly that cause global temperature rise. The rising global temperature interferes human health, water cycle, coastal ecosystems, agriculture, biodiversity, other environmental aspects and communities (Field et al. 2009). Several scheme efforts to reduce greenhouse gas emissions has been developed, which are by preventing the forest destruction and restoring degraded area through tree planting and ecosystems restoration (Diaz et al. 2009). The reduction of carbon emissions through forest ecosystem restoration could be conducted through the valuation of carbon absorption by forest vegetation as a carbon stock (Dewwar and Cannel 1992). Indonesia through The Ministry of Forestry signed the international agreement, i.e., Kyoto Protocol to conduct the C-sink project including research on carbon sequestration by various vegetation and land use (Potter and Lee 1998; Kirby and Potvin 2007; IPCC 2006).

As consequences of international agreements ratifications, Indonesian policymakers develop tree planting program on degraded areas as one of mitigation to reduce carbon emission. However, Potter and Lee (1998) reported that tree planting activities were conducted with a perspective gap between society and government. One planting activity by society was dedicated to their advantage especially economic benefits, while the other, it were continuously conducted because of government or donor subsidy. The complex background of tree planting activities indicated that the selection of tree species has not become the consideration of the program. The major tree planting activities were designated as production or conversion forest with species used have been predominantly timber trees such as *Acacia mangium*, *Pinus merkusii*, *Falcataria moluccana* (known locally as sengon), *Gmelina arborea*, *Tectona grandis* (teak) and *Swietenia macrophylla* (mahogany). On the other hand, maintaining high species richness including native species is becoming the important topic in ecosystem management. Many research results showed a linear relationship between diversity and carbon storage, either in tropics and temperate ecosystems (Kumar 2011; Kirby and Potvin 2007; Quijas et al. 2010; Diaz et al. 2009). Therefore, more

diverse species planted for the program will make benefits to the ecosystem, because greater biodiversity may ensure longer-term stability of C storage in fluctuating environments (Kumar 2011).

Carbon sequestration is the ability of a reservoir especially vegetation to absorb and store CO₂ from the atmosphere, which is different among types of vegetations and tree species (Kirby and Potvin 2007; Chaturvedi et al. 2011). Dry climate forest, for example, tends to experience higher water loss through transpiration. The vegetations of this habitat have a lower plant density than those of tropical rainforest. Therefore, the carbon fixation of the deciduous forest is relatively low in certain seasons (Janzen 1988; Holdridge et al. 1971). At species-level, a research result revealed that some species such as *Acacia catechu*, *Buchanania lanzan*, *Hardwickia binata*, *Shorea robusta* and *Terminalia tomentosa* have more potential carbon accumulation rather than other species in the dry tropical forest in India (Chaturvedi et al. 2011). Therefore, the ecosystem management on the C-sink project in further stage should consider the species-level management, whereas, to select plant species with high potential for carbon storage.

The selection of plant species for tree planting program should be developed because, besides the differences of carbon sequestration among species, the beneficial traits of plant species in carbon sequestration are usually accompanied by other unfavorable properties of plant's carbon allocations (Jack and Evans 1993; Larcher 2001). Plants store most of the photosynthetic products such as carbon and other nutrients for their growth in the form of dry weight or biomass. The biomass of plant species varies in size, efficiency, and distribution. The carbon storage relates to growth and ecophysiological factors and is determined by the factors that are more dominant compared to other factors. Some research on subtropical plants indicated that photosynthesis, respiration, and NAR (Net Assimilation Rate) correlated with RGR (Relative Growth Rate). Many previous types of research, especially for woody plants, resulted in the factors associated with leaf areas such as SLA (Specific Leaf Area) and LAR (Leaf Area Ratio) has stronger and more consistent correlation with RGR compared to NAR (Lambers et al. 1998; Pugnaire and Valladares 1999).

The ecophysiological and growth factors of woody plants in the tropics are still lack of investigation. It causes the unplanned tree planting program conducted in tropics area especially developing countries. The study in this area will be the significant knowledge contribution to C-sink project, especially to species-level management. Because it will be the basic knowledge to select high potential carbon sequestered by plant species. Therefore, research on the dominant factor in carbon sequestration and the selection of plant species for recovering the degraded lands in tropics habitat need to be established. Ten species studied were woody plant species either native and non-native to Indonesia, which commonly planted in secondary forest and the garden in lowland habitats. The ten species represents woody plants from various habitats which were planted for the revegetation program in Java through plant

development program of ex situ conservation. The questions of this study are: (i) What is the dominant factor in woody plant species grow in dry lowland habitats affecting their carbon sequestration?. (ii) Which plant species with high carbon sequestration could be selected for priority in tree planting program in dry lowland habitat?. The results of this study are expected to explain the factors correlating to plant carbon sequestration in the tropics region and recommend selected plant species for restoration ecosystem-based carbon sequestration.

MATERIALS AND METHODS

Materials

The seedlings of ten woody plant species were grown in Purwodadi Botanic Gardens, Pasuruan, East Java until the age of 16 months. According to Pugnaire and Valladares (1999), the seedling stage is a growth phase which is commonly observed to highlight the knowledge of environmental constraints and ecophysiological adaptations of tropical forest under the natural experiments. Three individuals were used as replication for each species. All species used in this study are C3 woody plant species (Rindyastuti and Hapsari 2017) which are commonly adapted to the dry lowland habitats, the most degraded ecosystem in Java, Indonesia. They are *Barringtonia asiatica*, *Dracontomelon dao*, *Heritiera littoralis*, *Diospyros discolor*, *Calophyllum inophyllum*, *Antidesma bunius*, *Schleichera oleosa*, *Syzygium cumini*, *Madhuca longifolia*, *Adenantha pavonina* (Table 1). The seedlings were grown in polybags with a diameter of 10 cm and are transferred into a polybag with 20 cm in diameter at the age of 14 months. Purwodadi Botanic Gardens, Pasuruan, East Java has a temperature range during the rainy season from 26.2 to 30.8°C and at the dry season from 28.7 to 34.6°C. After 4 months, the seedlings were grown in a greenhouse at Faculty of Biology, Gadjah Mada University, Yogyakarta with a temperature range from 29.3 to 35.2°C.

Methods

Biomass, carbon storage, the whole plant photosynthetic capacity, total chlorophyll content, stomatal index, and Leaf Area Index (LAI) were measured in this study.

Measurements of biomass and carbon storage

Biomass and carbon stock of plant seedlings were measured at 0, 4 and 8 months. Biomass is measured over a period of 8 months, which are in October 2014, February 2015 and June 2015. Each seedling is divided into root, stem, and leaves that were weighted and put into the oven at a temperature of 80°C until reach a constant weight. The dried plant materials are weighted to obtain the dry weight. The data of total biomass (B) were converted into the stored carbon (C) using a formula according to IPCC (2006):

$$C \text{ (kg)} = B \times 0.5.$$

Table 1. List of species, local name, habitat, distribution, type of plant and shade tolerance of ten woody plant species observed in this study

Species	Local name	Habitat	Distribution	Type	Shade tolerance
<i>Barringtonia asiatica</i> (L.) Kurtz	Keben	Mangrove, tropical coast	East Africa, South Asia, Southeast Asia, Northern Australia to Pacific Islands.	Evergreen woody	Intermediate to tolerant
<i>Dracontomelon dao</i> (Blanco) Merr. & Rolfe	Dau	Monsoon forest (deciduous and semi-)	South Asia, Southeast Asia, Northern Australia to Pacific Islands.	Semi-deciduous, hardwood	Tolerant
<i>Heritiera littoralis</i> Aiton	Dungun	Mangrove, tropical coast	East Africa, South Asia, Southeast Asia, Northern Australia to Pacific Islands.	Evergreen hardwood	Tolerant
<i>Diospyros discolor</i> A. DC.	Bisbul	Dry lowland tropic	Southeast Asia, Taiwan, and tropical regions.	Evergreen hardwood	Tolerant
<i>Calophyllum inophyllum</i> L.	Nyamplung	Coast-lowland tropic	East Africa, South Asia, Southeast Asia, Northern Australia to Pacific Islands.	Evergreen hardwood	Intolerant
<i>Antidesma bunius</i> (L.) Spreng.	Buni, Wuni	Highland tropic	South Asia, Southeast Asia, Northern Australia to Pacific Islands.	Evergreen hardwood	Tolerant
<i>Schleichera oleosa</i> (Lour.) Merr.	Kesambi	Dry low-highland mix deciduous forest	Himalaya, Srilanka, India and China. Introduced in Malaysia, naturalized to Indonesia.	Deciduous hardwood	Tolerant
<i>Syzygium cumini</i> (L.) Skeels	Duwet, Juwet	Dry and moist tropical-deciduous forest	East Asia, Southeast Asia to Australia. Cultivated in tropics and subtropics regions.	Evergreen hardwood	Tolerant
<i>Madhuca longifolia</i> (J.Koenig ex L.) J.F. Macbr.	Nyatoh	Dry lowland tropics	India, naturalized to countries in Southeast Asia.	Evergreen-semievergreen, hardwood	Tolerant
<i>Adenanthera pavonina</i> L.	Saga	Evergreen-deciduous forest	South Asia, Southeast Asia to Pacific Islands. South Asia, Naturalized and cultivated in Africa.	Evergreen-deciduous, woody	Tolerant

Note: Verheij dan Coronel (1992); Soerianegara dan Lemmens (1994); Lemmens et al. (1995); Sosef et al. (1998); Kundu (2011); Sikarwar (2002)

Measurements of ecophysiological factors

Ecophysiological factors including whole plant photosynthetic capacity, stomatal index, the total chlorophyll content and Leaf Area Index (LAI) were investigated in this study.

Measurements of whole plant photosynthetic capacity

Whole plant photosynthetic capacity was obtained by measuring the photosynthetic rate using *Portable Infrared Gas Exchange System* (LICOR 6400XP) during the day between 10-12 am. Three data for each plant individual are taken as replications. The whole plant photosynthetic capacity was obtained by multiplying the value of photosynthetic rate by leaf area (LI-COR Biosciences 2013; Jeki 2013).

Measurements of Stomatal Index

The measurements of the stomatal index were established when the seedlings are at the age of 20 months. The epidermic layers of leaf which contain stomata were removed using alteco glue. The epidermal layer of the leaf was taken using alteco glue applied to the surface of the leaves. Therefore, the sample was observed under a light microscope with a magnification of 10 x 10 and 10 x 40. The number of stomata was averaged and index of stomata (IS) was calculated using the following formula (Royer 2001):

$$IS = \frac{S}{S+E}$$

Where,

S : Stomata number/mm²

E : Epidermic cell number/mm²

Measurements of the total chlorophyll content

Measurement of the total chlorophyll content was carried by spectrophotometric method. A total of 1 g of leaves was taken from each species with three replications. The leaves were extracted with acetone 80%. Leaf samples and the reference solution were measured for the absorbance using a spectrophotometer at a wavelength of 645 nm and 663 nm. Then the total chlorophyll content was calculated by the following formula (Islam et al. 2009):

$$\text{Total of chlorophyll (mg/g)} = (20.2 \times A_{645} + 8.02 \times A_{663}) \times a / (1000 \times b)$$

$$\text{Chlorophyll a (mg/g)} = (12.7 \times A_{645} - 2.69 \times A_{663}) \times a / (1000 \times b)$$

$$\text{Chlorophyll b (mg/g)} = (22.9 \times A_{645} - 4.68 \times A_{663}) \times a / (1000 \times b)$$

Where,

A₆₄₅ = The absorbance at a wavelength of 645 nm

A₆₆₃ = The absorbance at a wavelength of 663 nm

a = The volume of acetone (mL)

b = Leaf dry weight (g)

Measurements of Leaf Area Index (LAI)

LAI measurement was carried out by gravimetric which is a conversion weight value to a broad measure of the

weight ratio of the paper with a particular area. Leaf area was calculated by comparing the proportion of an area of 16 cm² paper weight with the weight of the entire paper using comparison formula (Chaudhary et al. 2012; Irwan and Wicaksono 2017):

$$L2 = \frac{L1 \times W2}{W1}$$

Where,

L2 : Leaf area

L1 : Area of sample paper

W2 : Paper weight

W1 : Weight of sample paper

LAI calculations were performed by the following formula (Blanco and Folegatti 2003) :

$$LAI = \frac{LA}{Lt}$$

Where,

LAI : Leaf Area Index

LA : Leaf Area

Lt : Area per planting unit

Data analyses

Ecophysiological and growth data were analyzed using ANOVA with Completely Randomized Design (CRD) ($\alpha=0.05$) with a variation of species as its treatment. Data analysis was followed by a further test DMRT (Duncan's Multiple Range Test). The data analysis was conducted to find out the significant difference of ecophysiological and growth factors on the variation of plants and study the species which has a high value in carbon sequestration. Carbon sequestrations of plant species were determined from plants biomass. Ecophysiological and growth factors were analyzed using correlation both bivariate and multivariate analyses ($\alpha=0.05$). These analyses were used to study the relationship between growth and ecophysiological with biomass and carbon storage and the relationship between these factors and the dominant factors affecting biomass and carbon storage. Therefore, the factor most contribute to high biomass was classified as a dominant factor in plant carbon sequestration (Gomez and Gomez 1984).

RESULTS AND DISCUSSION

Biomass and carbon storage

The biomass increase of month 0, 4 and 8 (Figure 1). In general, increasing of biomass in the first 4 months was higher than the second 4 months because the nutrients in the second 4 months have been reduced. The biomass of *S. cumini* was decreased in the second 4 months due to the leaf fall. *H. littoralis*, *C. inophyllum*, and *S. oleosa* could reach high biomass at 4 months of first and second. This result suggested that these species have high productivity and physiological resistance to the environmental changes

especially temperature. Based on the ANOVA ($P < 0.05$), the final biomass of 10 plant species studied were different significantly among species. Based on the mean value and further test results of DMRT ($P < 0.05$), *B. asiatica*, *H. littoralis*, *S. oleosa* and *A. pavonina* were classified as having high biomass whereas biomass of *D. discolor*, *M. longifolia* and *A. bunius* have low total biomass. *H. littoralis* had the highest biomass while *M. longifolia* has the lowest biomass. Carbon storages of ten woody plant species were shown in Figure 2. Carbon storage of plant species studied varies among species. Based on the ANOVA test ($P < 0.05$), carbon storage of 10 species studied was different significantly. *H. littoralis* has the highest carbon storage while *M. longifolia* has the lowest carbon storage.

Growth characters

Two growth factors measured in this study were stem height and stem diameter. Based on the ANOVA ($\alpha = 0.05$), the differences in the stem height and stem diameter among ten woody plant species are significant (Table 1). *S. oleosa* has the highest stem while *D. discolor* has the lowest stem. *B. asiatica* has the biggest stem diameter while *D. discolor* has the smallest stem diameter. The significant difference in stem height and diameter showed that growth characters might influence the difference of carbon storage in woody plant species. Figure 1 showed the descriptive relationship between the growth characters and carbon storage. It indicated that plant species with high carbon storage have high stem diameter. The relationship between these factors should be ensured using correlation test.

Based on the Varian test ($\alpha = 0.05$), ecophysiological factors including whole plant photosynthetic capacity, the total of chlorophyll content, Stomatal Index and LAI of ten woody plant species are different significantly among species (Table 2). It indicated that the ecophysiological factors of plant species might influence the differences of plant carbon storage. Figure 4 showed that plant species with high sequestered carbon tend to be supported by their ecophysiological factors. The species which tend to have high carbon storage are supported by ecophysiological factor i.e., whole plant photosynthetic capacity which is described in a mangrove species, *H. littoralis*. The species which tend to have low whole plant photosynthetic capacity, have low chlorophyll content and high leaf area index (Figure 4).

Correlation between ecophysiological factors with growth factors

Based on the bivariate correlation test, both total of chlorophyll content and the whole plants photosynthetic capacity has a positive correlation with the stem height with P value of 0.0001 and 0.00002, respectively. It showed that in the early stage of growth, woody plants in the present study tend to rise the ecophysiological component which is total of chlorophyll content and the whole plant photosynthetic capacity to rising productivity. Moreover, to help plants reach the sunlight for photon absorption, stem height was supposed to be high, associated with the rise of chlorophyll content and

photosynthetic capacity, as a strategy in plant growth than to enlarge the stem or to allocate plant mass to increase stem diameter.

Correlation between ecophysiological and growth factors with carbon storage

Based on the bivariate correlation test between ecophysiological factors and carbon storage, the factors such as the LAI, total of chlorophyll and photosynthetic capacity correlate positively to carbon storage ($P = 0.042$, 0.0002 and 0,001 respectively ($P < 0.05$). It indicated that the difference of LAI, total of chlorophyll content and photosynthetic capacity influence the different carbon storage of woody plant species. Based on the bivariate correlation test between ecophysiological factors and carbon storage, stem height and stem diameter positively correlated with the carbon storage ($P = 0.002$ dan 0.0001 ($P < 0.05$) (Table 4). This result indicated that the growth factors might influence plant carbon storage. The growth factors influencing the formation of plant carbon storage revealed that carbon storage could be estimated from stem height or stem diameter. However, the factors which possess stronger correlation with the carbon sequestration should be investigated through multivariate analysis.

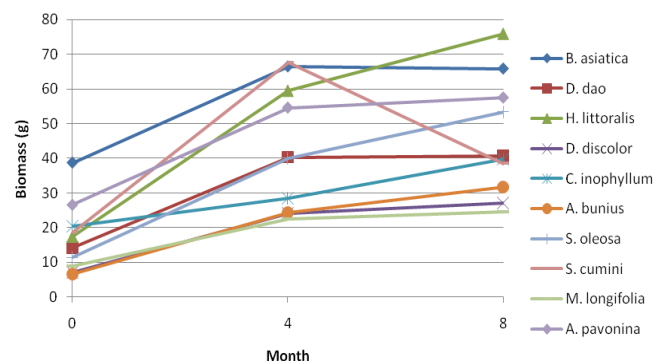


Figure 1. Biomass of seedlings of ten woody plant species in the month of 0, 4 and 8

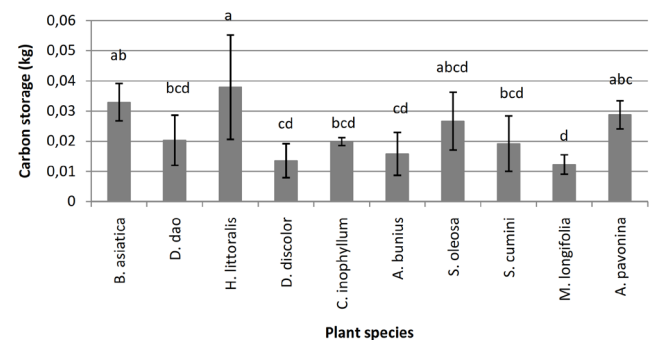


Figure 2. Carbon storage of seedling of ten woody plant species after 8 months of observation. Error Bars with different letters indicated significant differences among plant species at $P < 0.05$ based on DMRT

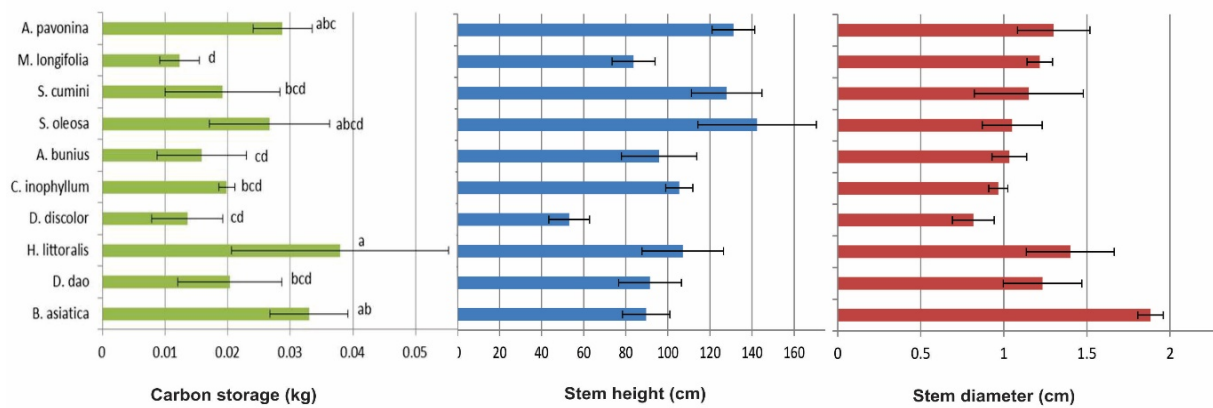


Figure 3. The carbon storage and growth characters (stem height and stem diameter) of ten woody plant species. Error Bars with different letters indicated significant differences among plant species at $P < 0.05$ based on DMRT

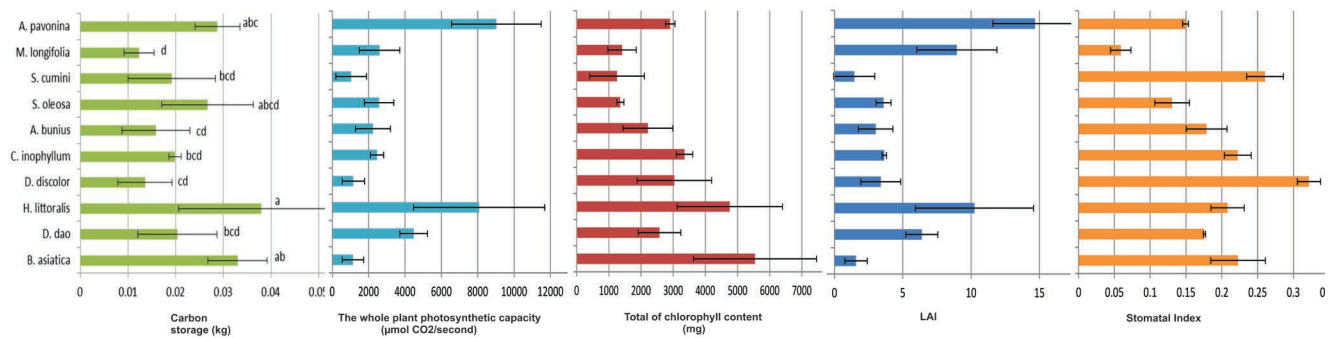


Figure 4. The carbon storage and ecophysiological characters (the whole plant photosynthetic capacity, total of chlorophyll content, LAI and Stomatal Index) of 10 woody plant species. Error Bars with different letters indicated significant differences among plant species at $P < 0.05$ based on ANOVA and DMRT

The species with high carbon storage tend to be supported by a high total of chlorophyll content, photosynthetic capacity and stomatal indexes such as two mangrove species, *H. littoralis* and *B. asiatica*. A species with low photosynthetic capacity tend to has a high total of chlorophyll and LAI. Furthermore, the stomatal index has a weak correlation with the plant carbon storage in all species studied. Based on the comparison study, the total of chlorophyll was considered as very important factors which influence the plant carbon storage. However, the correlation between the total of chlorophyll content and carbon storage should be confirmed through the multivariate correlation test to ensure the dominant factor influence carbon storage.

Dominant factors contribute to carbon storage

The multivariate correlation test was established to study the most dominant factors correlated to carbon sequestration which are revealed into two parameters: biomass and carbon storage. The dominant factors which

contribute to plant carbon sequestration (biomass and carbon storage) are stem height, the total of chlorophyll content and whole plant photosynthetic capacity with P value of 0.002, 0.0004 and 0.043, respectively (Table 5). The stem height is the growth factor which more affects carbon sequestration in plant species studied rather than stem diameter. Based on these results, the estimation of carbon storage using stem height is accurate to compare the carbon deposits on the seedlings. Therefore, the selection of fast growing plant species that have tall stems in the early stage of growth can be prioritized in the tree planting program.

Ecophysiological factors which contribute to carbon sequestration are the total of chlorophylls and whole plant photosynthetic capacity at $P = 0.0004$ and 0.043 ($P < 0.05$) with correlation coefficient of 0.52 and 0.533 (Table 5). The smaller P value, the stronger the relationship between two factors. Based on the P values, the total of chlorophyll content is stronger in contributing to carbon sequestration than the total of photosynthesis.

Table 2. The growth factors, biomass and C storage of ten woody plant species

Plant species	Total chlorophyll content (mg)	Stomatal Index	The whole plant photosynthetic capacity ($\mu\text{mol CO}_2/\text{second}$)	Leaf Area Index
<i>B. asiatica</i>	5,544.2 \pm 191.2 ^a	0.22 \pm 0.04 ^{cb}	1,140.82 \pm 588.5 ^c	1.58 \pm 0.82 ^d
<i>D. dao</i>	2,575.06 \pm 662.24 ^{cd}	0.18 \pm 0.02 ^{ed}	4,481.36 \pm 757.54 ^b	6.39 \pm 1.17 ^{bc}
<i>H. littoralis</i>	4,756.76 \pm 1639.15 ^{ab}	0.21 \pm 0.02 ^{cd}	8,079.06 \pm 3601.72 ^a	10.25 \pm 4.31 ^b
<i>D. discolor</i>	3,037.53 \pm 1159.45 ^{bcd}	0.32 \pm 0.03 ^a	1,157.8 \pm 610.34 ^c	3.40 \pm 1.46 ^{cd}
<i>C. inophyllum</i> □	3,352.51 \pm 254.71 ^{bc}	0.22 \pm 0.02 ^{cb}	2,464.59 \pm 362.12 ^{bc}	3.65 \pm 0.16 ^{cd}
<i>A. bunius</i>	2,215.39 \pm 774.59 ^{cd}	0.18 \pm 0.03 ^{de}	2,237.41 \pm 960.58 ^{bc}	3.02 \pm 1.26 ^{cd}
<i>S. oleosa</i>	1,356.67 \pm 110.7 ^d	0.13 \pm 0.02 ^f	2,573.37 \pm 808.21 ^{bc}	3.60 \pm 0.54 ^{cd}
<i>S. cumini</i>	1,256.66 \pm 849.49 ^d	0.26 \pm 0.03 ^b	1,040.84 \pm 839.81 ^{bc}	1.45 \pm 1.5 ^d
<i>M. longifolia</i>	1,412.12 \pm 440.19 ^d	0.06 \pm 0.01 ^g	2,600.52 \pm 1115.9 ^{bc}	8.96 \pm 2.93 ^b
<i>A. pavonina</i>	2,907.33 \pm 147.49 ^{bcd}	0.15 \pm 0.004 ^{ef}	9,021.84 \pm 2459.74 ^a	14.68 \pm 3.09 ^a

Note: Different letters indicated significant differences among plant species at $p < 0.05$ based on ANOVA and DMRT

Table 3. Ecophysiological factors of ten woody plant species

Plant species	Stem height (cm)	Stem diameter (cm)	Stem elongation (cm)	Stem enlargement (cm)	Biomass (g)	C Storage (kg)
<i>B. asiatica</i>	89.67 \pm 11.24 ^{cd}	1.88 \pm 0.076 ^a	27.83 \pm 18.9 ^c	0.617 \pm 0.063 ^{ab}	65.93 \pm 6.29 ^{ab}	0.033 \pm 12.36 ^{ab}
<i>D. dao</i>	91.5 \pm 14.91 ^d	1.23 \pm 0.24 ^{bc}	35.57 \pm 19.8 ^{bc}	0.13 \pm 0.07 ^c	40.66 \pm 7.1 ^{bc}	0.02 \pm 16.58 ^{bcde}
<i>H. littoralis</i>	107.1 \pm 19.37 ^{bcd}	1.4 \pm 0.26 ^b	57.9 \pm 17.1 ^{abc}	0.68 \pm 0.06 ^a	75.86 \pm 6.66 ^a	0.038 \pm 34.6 ^a
<i>D. discolor</i>	53.1 \pm 9.68 ^e	0.82 \pm 0.13 ^d	32.6 \pm 9.7 ^{bc}	0.52 \pm 0.03 ^{abc}	27.12 \pm 3.8 ^c	0.014 \pm 11.3 ^{de}
<i>C. inophyllum</i> □	105.4 \pm 6.44 ^{bcd}	0.97 \pm 0.058 ^{cd}	32.23 \pm 5.35 ^{bc}	0.2 \pm 0.025 ^{bc}	39.73 \pm 3.9 ^{bc}	0.020 \pm 2.6 ^{cde}
<i>A. bunius</i>	95.8 \pm 17.9 ^d	1.03 \pm 0.1 ^{cd}	54.43 \pm 17.14 ^{ab}	0.6 \pm 0.058 ^{ab}	31.73 \pm 5.6 ^c	0.016 \pm 14.2 ^{abcd}
<i>S. oleosa</i>	142.4 \pm 28.15 ^a	1.05 \pm 0.18 ^{cd}	73.47 \pm 25.8 ^a	0.63 \pm 0.04 ^{ab}	53.38 \pm 5.4 ^{bc}	0.027 \pm 19.15 ^{abcd}
<i>S. cumini</i>	127.9 \pm 16.75 ^{abc}	1.15 \pm 0.33 ^{bcd}	59.83 \pm 19.16 ^{ab}	0.48 \pm 0.058 ^{abc}	38.45 \pm 12.3 ^c	0.019 \pm 18.3 ^{bcde}
<i>M. longifolia</i>	83.7 \pm 10.23 ^d	1.22 \pm 0.076 ^{bc}	40.37 \pm 6.79 ^{bc}	0.48 \pm 0.05 ^{abc}	24.62 \pm 9.3 ^c	0.012 \pm 6.4 ^e
<i>A. pavonina</i>	131.17 \pm 10.15 ^{ab}	1.3 \pm 0.22 ^{bc}	60 \pm 10.4 ^{ab}	0.27 \pm 0.025 ^b	57.55 \pm 14.6 ^{abc}	0.029 \pm 9.39 ^{abc}

Note: Different letters indicate significant differences among plant species at $P < 0.05$ based on ANOVA and DMRT

Table 4. Ecophysiological and growth factors correlated to carbon storage based on bivariate correlation test ($P < 0.05$)

Factors	Correlation with C storage P value	Correlation
Stem height	0.002	Strong correlated
Stem diameter	0.00001	Strong correlated
Number of leaves	0.161	Not correlated
LAI	0.042	Correlated
Total of chlorophyll content	0.000	Strong correlated
Whole plant photosynthetic capacity	0.001	Strong correlated
Stomatal Index	0.916	Not correlated

Note: The factors correlated in $P < 0.05$ and strong correlated in $P < 0.01$

Table 5. Growth and ecophysiological factors correlated to carbon storage based on multivariate correlation test ($P < 0.05$)

Factors	P value	Correlation
Stem height	0.002	Strong correlated
Total of chlorophyll content	0.0004	Strong correlated
Whole plant photosynthetic capacity	0.043	Correlated

Note: The factors correlated in $P < 0.05$ and strong correlated in $P < 0.01$

Discussion

The very strong correlation between the total of chlorophyll content and carbon storage showed that the chlorophyll was an important factor in plant productivity. Chlorophyll was the compound which absorbs a photon of sunlight and transports the electron from photosystem to the first electron acceptor in the photosynthetic path in thylacoid membrane in the process of photophosphorilation. The photophosphorilation yield the ATP and NADPH which are needed by carbon fixation in Calvin Cycle. The more ATP available, more carbon fixed by photosynthetic enzyme (Hopkins 1995; Lambers et al. 1998; Meyer and Anderson 1952). The difference of chlorophyll content among plant species showed the combination of physiological adaptation, especially to shade environment and the gene expressions especially for the chloroplast formation.

The results of previous research on the 24 non-woody plant species showed that photosynthetic factor is not the only factor contributing to carbon storage (Poorter et al. 1990). Furthermore, the correlation between photosynthetic rate and growth rate was not found for several species in this previous study. This is in line with the results of this study that the total of photosynthetic capacity weakly correlates with the carbon storage, weaker than the correlations between the total of chlorophyll and carbon

storage. This condition might be because the photosynthesis which physiologically depends on the enzyme activity is genetically controlled by genes. Thus, photosynthetic factors tend to be more stable in terms of plant adaptation to the environment. In contrast, most of the plant species are more sensitive to light conditions compared to other factors such as nutrients. It indicated that the total of chlorophyll, a compound of leaf that absorbs light, becomes one of the important factors which associate to the plant's adaptation through time (Hopkins 1995; Pugnaire and Valladares 1999). In line with those studies, Poorter et al. (1990) also indicated that leaf growth was the main variable of plant carbon budget, which differentiates between slow- and fast-growing species. In this previous study, the fast growing species allocate more carbon to leaf growth than to any other plant bodies.

All species studied and most woody plant species are C3 plants. Consequently, all these species have a similar path of photosynthesis (Rindyastuti and Hapsari 2017). This result could support the analysis why chlorophyll content among species is more dynamic among woody plant species rather than the photosynthetic capacity. Overall, C3 plants have lower CO₂ uptake than C4 plants, such as grass (Larcher 2001; Leopold and Kreidemann 1975). Furthermore, the significant difference of carbon storage influenced by photosynthetic capacity will be diagnosed by plants from different photosynthetic types (C3, C4, CAM), while plants with the similar type of photosynthesis will share similar photosynthetic capacity, relatively.

Chlorophyll is a green compound which has a function to catch up a sunlight quantum or energy called photon as an electron acceptor to induce a photochemical reaction in photosynthesis. There are two kinds of chlorophylls i.e., chlorophyll a and b. The presence of chlorophyll a (C₅₅H₇₂O₅N₄Mg) is more universal than chlorophyll b (C₅₅H₇₀O₆N₄Mg), because it occurs in all photosynthetic organisms (Meyer and Anderson 1952). The chlorophyll formation is limited by many factors such as genetics, light, Oxygen (O₂), Carbohydrates, N, Mg, Iron, other mineral elements, temperature, and water (Jack and Evans 1993). Thus, the differences in chlorophyll content among woody plants in this study are caused by the different adaptation to the sunlight. Chlorophyll content is important because it correlates with the light intensity which has been identified as the main limiting factor for seedling growth and establishment in tropical forest (Pugnaire and Valladares 1999). Some species are the sun-loving plant (*B. asiatica* and *C. inophyllum*) while other species are shade-adapted plants (Table 1). Larcher (2001) reported that shade and sun adapted plants have the different total of chlorophyll content. Shade adapted plants tend to have higher chlorophyll content in leaf or dry matter, for example in *Fagus sylvatica*. It indicated that carbon sequestration is also related to light tolerance of plant species.

The whole plant photosynthetic capacity is related to the leaf area in determining the carbon sequestration of woody plants studied. The whole plant photosynthetic capacity is a requirement for a positive carbon gain. Besides the chlorophyll content, it is the other fundamental

understanding of seedling survival (Pugnaire and Valladares 1999). When the plant has high leaf area, the photosynthetic capacity of either their carbon storage was becoming higher. Consistent relationships between the whole plant photosynthetic capacity and leaf area in determining the carbon storage are shown in several dry lowland species such as *C. inophyllum*, *S. cumini*, *S. oleosa* and *M. longifolia* (Figure 4). While, the inconsistent relationship between these two factors was shown in a mangrove species, *B. asiatica*.

Chlorophyll content correlates to the stem height to determine the carbon sequestration of woody plants in the tropics area. It is also influenced by the shade adaptation of plant species. Plant species on the early stage of growth especially shade-adapted plants and fast-growing tend to rise chlorophyll content to catch more sunlight because sunlight was known as a limitation factor for the growth of the plant in the tropical area (Pugnaire and Valladares 1999). It is shown by most of the dry lowland species in this study, such as *D. discolor*, *S. oleosa*, *M. longifolia* and *A. pavonina*. Moreover, one sub-montane species, *A. bunius* tend to have a similar adaptation with the other dry lowland species. The result is in line with the result of previous study on the pattern of adaptation of plant species studied to dry climate showed that *A. bunius* were adapted in dry lowland habitat (Rindyastuti and Hapsari 2017). Moreover, plants tend to maximize the increasing of stem height to compete with other plants to reach the sunlight which is shown by the positive correlation between stem height with biomass or with carbon storage. The stem height influences plant carbon sequestration by elongating the stem to maximize the function of chlorophyll in catching photons during photosynthetic activity (Lambers et al. 1998; Pugnaire and Valladares 1999). The results of this study are expected to explain the factors that correlate to carbon sequestration and contribute a recommendation on plant selection for restoration ecosystem-based carbon sequestration.

The different capacity to accumulate carbon has important implications for tree planting programs and ecosystem restoration based on the C-sink framework. The species richness should be maintained for landscape-level management, yet the selection of trees planted for the program could become one way for sequestering carbon high at the species level. At landscape-level, forest with certain species component with high carbon sequestration was more protected rather than another forest (Chaturvedi et al. 2011).

Two plant species studied, i.e., *H. littoralis* and *B. asiatica* have the highest carbon storage. However, both species were mangrove plants which have very specific coastal habitats. Therefore, they have low implications for ecosystem restoration in dry lowland habitats. Two other species of *S. oleosa* and *A. pavonina* have high carbon storage, thus were more recommended for tree planting programs in dry lowland habitats. *S. oleosa* is a deciduous hardwood and shade tolerant species which grows in dry low-highland mixed deciduous forest. *A. pavonina* is an evergreen-deciduous woody and shade tolerant species which could grow in evergreen-deciduous habitat (Verheij

dan Coronel 1992; Lemmens et al. 1995; Sosef et al. 1998). Most deciduous species has lower carbon storage compare to evergreen species (Janzen 1988; Holdridge et al. 1971). However, *S. oleosa* was naturalized in the tropics including in Indonesia, while *A. pavonina* were exotic to Indonesia and tended to have rapid growth (Orwa et al. 2009). Exotic plant with rapid growth potentially invades the area. It is commonly called as invasive alien species (IAS) which are not recommended to be grown in many types of habitats to protect the ecosystems (CBD 2010). Thus, *S. oleosa* could be more recommended for priority in tree planting program than *A. pavonina*.

Two other species, i.e. *S. cumini* and *D. discolor* have high carbon storage in the seedling phase. Both species were classified as slow-growing plants like local plants commonly well-known. *S. cumini* is local plant species belongs to Myrtaceae family. It is a source of edible fruits with the local name of Juwet or Duwet (Javanese), Jamblang (Sundanese) and Dhuwak (Madura) (Lemmens et al. 1995; Verheij and Coronel 1992). Other local species *D. discolor* (Ebenaceae), is well-known as *Bisbul* or *Buah Mentega* in Indonesia. It is one of an important timber group of Ebony and an iconic persimmon originated from Southeast Asia (Lemmens et al. 1995). Based on this study, two important local species is known to have high carbon storage for local and slow growing and should be the priority for tree planting and ecosystem restoration. It will be in line with other research results of Chaturvedi et al. (2011) which recommended to protect forests with the dominant constituent of *Acacia catechu*, *Buchanania lanzan*, *Hardwickia binata*, *Shorea robusta* and *Terminalia tomentosa* because they showed high potential carbon sequestration in a dry tropical forest in India. In recent years, since the global climate change become a global environmental issue, the ability to sequester carbon is important additional values for plant conservation besides of food source and timber use.

In conclusion, among species studied, two mangrove species, i.e., *H. littoralis* dan *B. asiatica* have high carbon sequestration. For recommendation in tree planting program, two local species, i.e., *S. cumini* and *D. discolor* were better to restore the degraded ecosystems in dry lowland habitats than other species. There are two ecophysiological factors which influence carbon sequestration of woody plant, which is the total of chlorophyll content and the whole plant photosynthetic capacity. The total of chlorophyll content is more strongly influence the carbon sequestration rather than the whole plant photosynthetic capacity. The total chlorophyll content is also associated with the stem height in influencing the plant's carbon sequestration. Woody plants studied in the early stage tend to elongate the stem to maximize the function of chlorophyll in catching sun energy during photosynthesis.

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