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Typology of Cocoa Seedlings Derived from Orthotropic and Plagiotropic Cuttings Compared with Grafting and Hybrid Seeds

Teguh Iman Santoso[1,2], Endang Sulistyaningsih[1*], Eka Tarwaca Susila Putra[1] and Agung Wahyu Susilo[3]

[1]Department of Agronomy, Faculty of Agriculture, Universitas Gadjah Mada, Yogyakarta, Indonesia; [2]Laboratory of Agronomy, Indonesian Coffee and Cocoa Research Institute, Jember, Indonesia; [3]Laboratory of Plant Breeding, Indonesian Coffee and Cocoa Research Institute, Jember, Indonesia

[*]*Corresponding author:* endangsih@ugm.ac.id

Abstract

Cocoa derived from cuttings is expected to overcome the limitations of grafting and hybrid seed propagation. This study aimed to determine the typology of cocoa seedlings derived from cutting, grafting, and hybrid seeds and the similarity among propagations, and assess the biochemical content of budwood cuttings and its relationship with the success rate. This research was conducted at the greenhouse of the Indonesian Coffee and Cocoa Research Institute, East Java, from April to December 2022 by adopting a completely randomized design. A single-factor experiment was performed on propagation methods, namely hybrid seed (HS), orthotropic cutting (OC), plagiotropic cutting (PC), orthotropic grafting (OG), and plagiotropic grafting (PG). The growth characteristics, anatomical characteristics, and biochemical contents of cuttings were observed. Results showed that compared with PC, OC generated a larger root pith diameter that played a role in the improved growth performance. The leaf area, net assimilation rate, and relative growth rate in OC were similar to those in HS. The time to produce OC was similar to PG to meet the minimum standard requirements of ready-to-plant seedlings. However, the root volume, area, and length in OC were below those in HS and still needed to be improved. The cuttings derived from the budwood garden had higher sucrose contents than those from the production garden. Therefore, obtaining OC and PC samples from a budwood garden is recommended to achieve a high success rate.

Keywords: agronomic performance; cocoa clones; nursery; rootstock and scion

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INTRODUCTION

Indonesia is facing a substantial challenge of declining cocoa production, which is influenced by old plant age, pest disease attacks, nonstandard cultivation practices, and changing environmental conditions (Susilo et al., 2020). Current cocoa production in Indonesia only reaches 651,612 tons from an area of 1,421,009 ha, showing a productivity of 0.45 tons ha^{-1} year^{-1} (Statistics Indonesia, 2023). The actual cocoa productivity in Indonesia is only a quarter of its yield potential of 2 tons ha^{-1} year^{-1} (Daymond et al., 2020).

Among the commonly used cocoa clones in Indonesia, Sulawesi 01, Sulawesi 02, and MCC 02 are preferred due to their high productivity and tolerance to pests and diseases. MCC 02 has higher yield potential than Sulawesi 01 and Sulawesi 02 clones (Asman et al., 2024). It has a potential productivity of 3.1 tons ha^{-1} year^{-1} (Susilo et al., 2020). With the discovery of new varieties resistant to pests and diseases and the need to replace old cocoa plants, the adoption of superior cocoa planting materials has become

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urgent (Gomes et al., 2015; Olutegbe and Sanni, 2021). High-quality planting materials play a critical role in improving productivity (Gomes et al., 2015) without compromising biodiversity (Somarriba et al., 2021; Ocampo-Ariza et al., 2025). The adoption of improved planting materials can increase cocoa bean production without the need to expand cultivated land, thus helping to prevent deforestation and biodiversity loss (Mithöfer et al., 2017). This demonstrates the dual benefits of both agricultural productivity and ecological resilience, contributing to the achievement of sustainable agriculture goals (Ocampo-Ariza et al., 2025).

Cocoa has been propagated by seeds (65%), cloning (23%), and combination of planting materials (12%) in the major cocoa producers of Indonesia, such as West Sumatera, Lampung, East Java, West Sulawesi, Central Sulawesi, Southeast Sulawesi, South Sulawesi, and Papua (Daymond et al., 2020). The use of planting materials from seeds results in individual variation among a certain population due to segregation. This problem can be solved by vegetative propagation, which is preferred because it produces uniform plant characteristics and retains the parents' superior traits, such as high productivity (Gomes et al., 2015).

Plagiotropic grafting is a common vegetative propagation method used by farmers in Indonesia. However, this technique is associated with several problems. The harvest season of seeds as rootstocks is highly dependent upon the season and is mostly affected by weather conditions (Gomes et al., 2015). Furthermore, the cocoa plants obtained through plagiotropic grafting may show incompatibility between the rootstock and scion. The genetic variations of rootstock derived from hybrid seeds can also lead to diversity in the growth response of cocoa scions (Schmidt et al., 2021) and plant-growth barrier conditions. The incompatibility in plagiotropic grafting leads to the generation of a cocoa population with non-uniform conditions (N'zi et al., 2023). The growth of the plagiotropic grafting plant might be delayed due to the incompatibility of graft union (Adhikari et al., 2022). These abnormalities in plant growth usually occur a few years after grafting. Therefore, alternative propagation methods must be developed to address these problems.

Cocoa derived from cuttings is expected to be able to overcome the limitation of plagiotropic grafting. In general, cuttings do not use rootstock and are not affected by the incompatibility issues of plagiotropic grafting. Cuttings were a popular propagation method in Ecuador for producing CCN-51 clones (Gomes et al., 2015). Cocoa from cuttings has ability to produce a pure clonal population due to the absence of rootstock, and a typology close to seedlings derived from hybrid seeds (Sodré and Gomes, 2019). Cocoa cuttings can be developed using plagiotropic and orthotropic branches (Gomes et al., 2015). The planting material from plagiotropic cutting was previously developed in Indonesia in 1983 and in Bahia in 1999 but had an extremely low life percentage (Sodré and Gomes, 2019). Since 1984, the Institut de Recherches du Café et Cacao in Togo, West Africa, has exerted efforts to produce clonal planting materials with true-to-type character through orthotropic cuttings (Sodré and Gomes, 2019). However, their progress has been hindered by the limited availability of orthotropic scions at that time (Gomes et al., 2015).

Various efforts to solve these problems have been reported. Some researchers reported that developing a budwood garden (BG) could increase the production of scions and further increase the success rate of plagiotropic cutting and orthotropic cuttings planting materials (Gomes et al., 2015; Santoso and Zakariyya, 2022). A budwood scion has a high meristematic activity that will increase the success rate of cocoa cuttings (Sodré and Gomes, 2019). BGs are kept without producing fruit by regular pruning and narrow planting spacing. Assimilate production is concentrated for the growth of scions, which is predicted to be rich in sugars and phytohormones necessary to support the growth of cuttings.

The pseudoroots formed from orthotropic cuttings and plagiotropic cutting must be studied further because they are considered a growth limiter (Sodré and Gomes, 2019). Studies on the root characteristics in plagiotropic cutting and orthotropic cuttings lacked evidence on how these methods can support upper growth. The performance of cocoa planting materials from orthotropic cuttings and plagiotropic cutting has also been compared with hybrids and grafted seedlings as common propagation methods. The current research answers whether orthotropic cuttings and plagiotropic cutting have similarities and advantages over hybrid propagation and grafted seedlings. The production times of orthotropic cuttings and plagiotropic cutting to meet the minimum standards of ready-to-plant seedlings are evaluated and compared with those of hybrids and grafted seedlings. This study also

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examines the recommended sources of budwood materials that can produce a high success rate of orthotropic and plagiotropic cuttings based on their biochemical content. The information obtained from this study is expected to improve the existing cocoa propagation methods.

MATERIALS AND METHOD

Local conditions and experimental field

This research was conducted at the greenhouse in Kaliwining Experimental Station, Indonesian Coffee and Cocoa Research Institute, from April to December 2022. The research site is located in East Java, Indonesia, with an elevation of 45 m above sea level and classified into C-D Schmidt Ferguson climate type. The geographical position of the research site is 113.009° longitude and 8.004° latitude. The daily temperature ranges between 25.3 and 37.8 °C with an average light intensity of 95,600 lux during midday.

Plant materials and experimental design

This research adopted a completely randomized design with a single factor, namely propagation techniques of orthotropic cutting (OC), plagiotropic cutting (PC), orthotropic grafting (OG), plagiotropic grafting (PG), and hybrid seed (HS). Each treatment was performed in six replicates, and each replicate consisted of three samples. The scion material for cutting and grafting was MCC 02. The HS sample used in this research was obtained from the seedling of the half-sibs of MCC 02. The OG and PG planting materials were prepared using a rootstock derived from a seed of open-pollinated Sulawesi 1 x KEE 2. Top grafting was done using an orthotropic scion for OG and a plagiotropic scion for PG at 120 days after planting (DAP).

The cutting material used was a scion with a stem diameter of approximately 0.2 to 0.3 cm and two leaves. The cuttings were planted in a germination box covered using transparent plastic. Root induction was carried out for 30 days using a commercial root-promoting substance composed of 0.067% 1-naphthalene acetamide, 0.013% 2-methyl-1-naphthalene-acetamide, 0.033% 2-methyl-1- naphthaleneacetic acid, 0.057% indole-3-butyric acid, 4.04% thiram (tetramethyl thiuram disulfide) and 95.79% inert ingredients. After 30 days, the cuttings were planted in plastic bags with a size of 12 cm x 20 cm for observation up to 210 DAP. The planting media were soil, sand, and manure with a 1:1:1 ratio.

Biochemical profile and success rate determination

The biochemical content of cutting materials from a BG and a production garden (PRG) was determined. The sucrose content was measured using the Luff Schoorl method (Lubis et al., 2022). The total phenolic content for individual extracts was examined using the Folin-Ciocalteu method (Aryal et al., 2019). The auxin and cytokinin contents were determined using extraction and purification (Dobrev et al., 2017). The success rate was observed at 30 DAP.

Morphological characteristic determination

The cutting materials used in morphological characterization were obtained from the BG. Morphological characteristics such as plant height, number of leaves, and stem diameter were observed from 30 up to 210 DAP. A visual description of the plants was obtained using the phenological description method of cocoa growth developed by Niemenak et al. (2010). The vegetative growth under each treatment was then analyzed for growth speed to meet the minimum standards of seedlings ready for planting. The characteristics of the leaf such as thickness, area, and angle were observed at 210 DAP. The observation was conducted on fully expanded leaves. Leaf angle was observed as the inclination between the leaf blades toward the vertical line (Yang et al., 2023). The characteristics of the root such as volume, length, diameter, area, and fractal dimension were also observed at 210 DAP. The root length, area, and diameter were analyzed using an area meter and Image-J. The fractal dimension of the root was observed using the box-counting method.

The net assimilation rate (NAR) was calculated from T1 (150 DAP) to T2 (210 DAP) using Equation 1.

$$\mathrm{NAR} = \frac{W_2 - W_1}{T_2 - T_1} \times \frac{\ln L_2 - \ln L_1}{L_2 - L_1} \qquad (1)$$

Where W1 is the dry weight at 150 DAP, W2 is the dry weight at 210 DAP, L1 is the leaf area at 150 DAP, and L2 is the leaf area at 210 DAP.

The relative growth rate (RGR) was calculated from T1 (150 DAP) to T2 (210 DAP) using Equation 2.

$$\mathrm{RGR} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1} \qquad (2)$$

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Anatomical characteristic determination

The anatomical characteristics of the stem and root were analyzed at 210 DAP. Tissue samples were fixed using 70% alcohol, embedded in paraffin, sliced at a thickness of 6 µm using a rotary microtome, and observed under a light microscope (Olympus CX-21). The following anatomical characteristics were observed for the roots and shoots: epidermis thickness, phloem and xylem tissue width, xylem density, and pith diameter. The measurements were conducted using image raster software (Optilab Advance, Macinos, Indonesia).

Data analysis

The data were analyzed using analysis of variance with α = 5%. Tukey post-hoc test was carried out when significant differences were observed among the treatments. Clustering analysis for morphological characteristics was analyzed to determine propagation methods that had similarities with the hybrid seeds using cluster analysis dendrogram. The relationship among variables was analyzed using Pearson correlation and the results were shown using correlogram images. Data analysis was conducted using DSAASTAT and Jamovi data analysis software.

RESULTS AND DISCUSSION

Seedling typology

The visual observation of each propagation method was carried out at 210 DAP. In general, the OC materials had similar shoot morphology and growth performance to the HS. Both materials had a vertical growth direction of the shoots with similar leaf phyllotaxis. The PC material was shorter than the HS and more directed to horizontal growth with different leaf phyllotaxis (Table 1, Figure 1). Leaves show dimorphic characteristics corresponding to the stem on which they arise (Niemenak et al., 2010). The leaves on the OC had long petioles and were symmetrical, similar to those in the HS. Meanwhile, the leaves on the PC had short petioles and were slightly asymmetrical. The leaves on the OC were greater than those on the PC.

The roots produced from cuttings are usually pseudoroots. However, the roots produced from OC had a vertical downward growth direction similar to those from HS, albeit smaller in size. This finding is different from the propagation of PC materials with pseudoroots growing sideways (Table 1, Figure 2). Some researchers define pseudoroots as adventitious roots, which are plant roots formed from non-root tissues. In this case, adventitious roots are formed due to the presence of wounds in the tissues at the time of cutting. Cutting causes wounding that increases reactive oxygen species (ROS) production. The increase in ROS acts as a signal to enhance polyphenol production. Polyphenols play a role in preventing cell death due to ROS (Ghimire et al., 2022).

The production of polyphenols in plants occurs through the translocation of soluble sugars and carbohydrates from apical sites to the basal region. This increase also occurs with auxin following basipetal transport from the apical parts of the cuttings. The elevated auxin levels at the basal region acting upstream of nitric oxide to promote lateral root initiation (Steffens and Rasmussen, 2016). Furthermore, the degradation of local auxin in the basal region has been reported to be inhibited by the presence of polyphenols (Ghimire et al., 2022). The graft union is not obtained in OC and PC. This condition is an advantage for OC and PC because of the possibility of incompatibility between budwood and rootstock, which will not occur as in OG and PG propagation and, therefore, will not affect plant production (Adhikari et al., 2022).

Table 1. Description of cocoa seedlings

Description	HS	OC	PC	OG	PG
Propagation method	Generative	Vegetative	Vegetative	Vegetative	Vegetative
Source material	Seeds	Micro budwoods	Micro budwoods	Rootstocks and budwoods	Rootstocks and budwoods
Growth direction	Vertical	Vertical	Horizontal	Vertical	Horizontal
Phyllotaxis	3/8	3/8	1/2	3/8	1/2
Leaf angle	Erect	Erect	Horizontal	Erect	Horizontal
Roots	Tap roots	Pseudo tap roots	Sideways pseudoroots	Tap roots	Tap roots
Graft union	No	No	No	Yes	Yes

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting

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Figure 1. Visual comparison of the morphological characteristics of cocoa seedlings derived from different propagations at 210 DAP

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Bar length 20 cm

Figure 2. Morphological characteristics of plant roots derived from different propagations at 210 DAP

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Bar length 10 cm

A cluster analysis dendrogram was drawn based on the main characteristics of the shoots and roots at 210 DAP. The morphological characteristics of the tested planting material revealed three main groups: the first group showed close similarity (0.96) between OG and PG as indicated by the similar morphological characteristics. The second group showed that OC and HS shared similar morphological characteristics (0.91) but had similar morphological characteristics to the first group. The third group consisted only of PC (0.74). These samples had morphological characteristics different from those of the first and second groups (Figure 3).

In general, the OG and PG materials had joints connecting the rootstocks and scions. The heights of the OG and PG materials at 210 DAP were relatively similar due to the shoots being cut off at 120 DAP and used as rootstock for grafting. The growth in OC was similar to that in HS, with the same leaf phyllotaxis and vertical shoot directions at the age of 210 DAP. The typology of the OC seedlings had a high similarity to that of the HS seedlings based on cluster analysis. Therefore, OC can be developed as the main propagation method because it is clonal but has a close similarity to HS typology.

Meanwhile, the growth in PC is relative to the side and the leaf phyllotaxis is different. Although the morphological characteristics of PC differ from those of HS, PC can be considered an alternative technology for clonal propagation, especially since PC is known to enter the production phase more quickly than HS (Sodré and Gomes, 2019). Currently, PC technology may not be well-developed in Indonesia (Gomes et al., 2015) due to its low success rate, particularly when the scions are sourced from production plants (Santoso and Zakariyya, 2022). According to the findings of this research, the success rate of PC can be increased by

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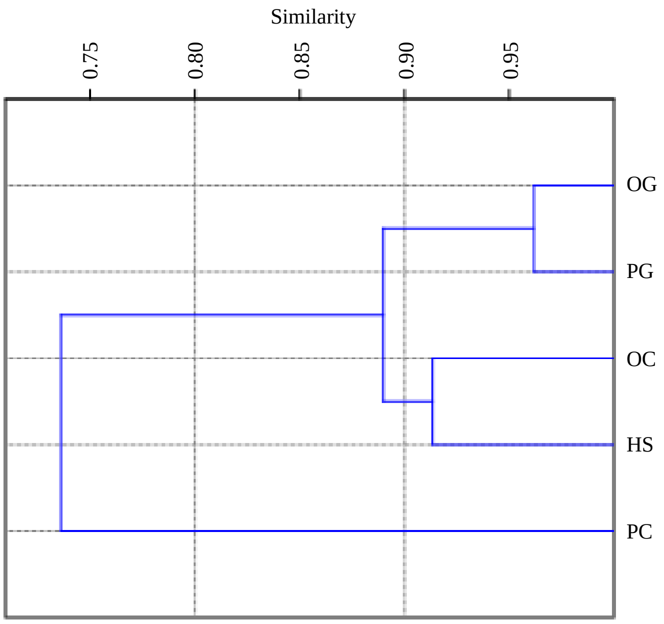

Figure 3. Cluster analysis dendrogram of cocoa seedlings derived from different propagation methods and growth variables

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting

using scions sourced from a budwood garden and maintaining them without producing fruit (Figure 4e).

Relationship between biochemical content and success rate

The biochemical content of the cutting materials was analyzed to determine how the indigenous phytochemicals in OC and PC materials affect the product's success rate. Ghimire et al. (2022) found that the biochemical content of cuttings determines their success rate. Previous studies have also suggested that various plant hormones play essential roles in the grafting process (Kawaguchi et al., 2024).

In this study, the cutting materials derived from the BG had higher sucrose concentrations than those derived from the PRG (Figure 4a). This result might be explained as follows. A BG is maintained without bearing fruit with the application of tight spacing, formation pruning, and frequent maintenance pruning. In contrast, PRGs are maintained to produce fruits. The fruit is a strong sink, so the partitioning of sucrose and other assimilates in PRGs is not only for the shoots. Flower formation, seed filling, and defense mechanisms against the pathogens in adult plants also affect the translocation of sucrose and phytohormones (Xue et al., 2020), causing the sucrose content in a PRG to be lower than that in a BG. In this study, the high sucrose content in the BG also had an impact on the high success rate of the cuttings (r = 0.97). Sucrose also promotes the expression of auxin-related genes in roots, leading to the accumulation of auxin in the root system (Zhang et al., 2020).

A BG is maintained by regular pruning to obtain the desired amount and size of scion. Pruning stimulates the growth of plant tissues. In this area, phytohormones are frequently produced in a meristematic cell before it is fully differentiated. Similarly, auxin is synthesized on the apical meristem, young leaf, and developing seed (Noah et al., 2021). The shoot apical meristem is a part of cytokinin production (Xue et al., 2020). Thus, the plants in a BG have more auxin and cytokinin contents than those in a PRG (Figure 4b and Figure 4c).

The biochemical content of the cutting materials significantly affected their success rate (Figure 4e). Except for PC-PRG, all the samples showed a success rate of more than 75%. The phenolic content of the PC-PRG sample was significantly higher ($p < 0.05$) than that of the PC sample derived from the BG (Figure 4d). Some phenolics, such as flavonoids, inhibit root development as a regulator of auxin transport (Babenko et al., 2019). Thus, the PC-PRG sample had the lowest success rate probably due to its phenolic content (r = -0.82). This result differs from the study that has also reported that phenolic

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compounds influence rooting promotion by inhibiting auxin degradation. It might be due to the levels of phenolic compounds. A previous study on *Chrysanthemum indicum* cuttings found that the accumulation of phenolic compounds in the cuttings helps protect auxins from oxidation and may play a role in promoting cell division and differentiation into root primordia regulated by auxin (Ghimire et al., 2022).

Minimum standard quality of seedlings

Plant height, stem diameter, and number of leaves are the main criteria for selecting cocoa seedlings for planting. Following Indonesian Government regulations, the selection and distribution of cocoa planting material to farmers can be evaluated using the minimum standards on age, plant height, leaf number, and stem diameter set by the Decree of the Minister of Agriculture of the Republic of Indonesia (Ministry of Agriculture, 2017). HS achieved the minimum standard requirement at 90 DAP, showing that this propagation was the fastest to reach the minimum standard among the other methods. OC and PC reached the requirement at 180 DAP, similar to

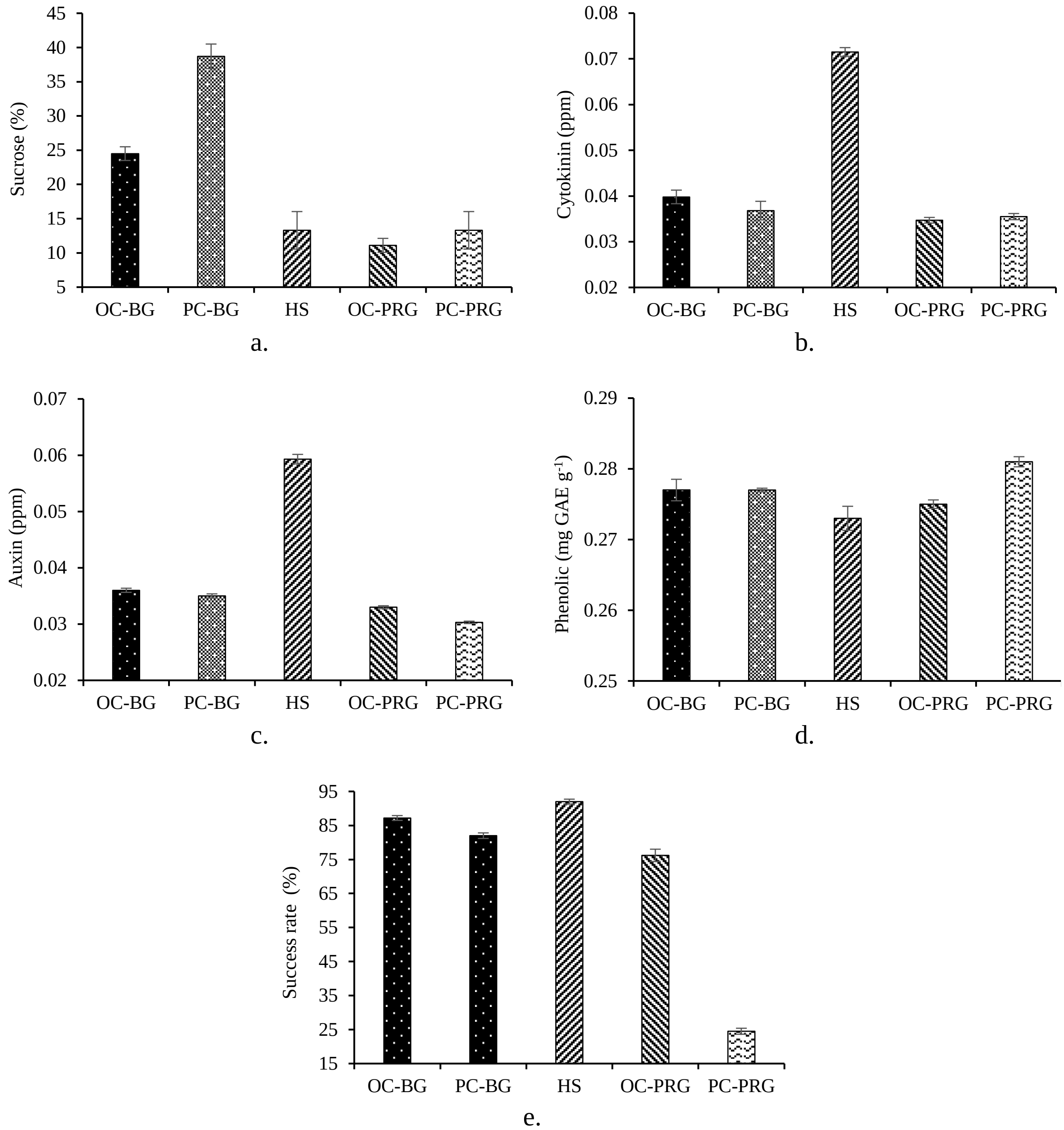

Figure 4. Biochemical content of cutting materials consisted of sucrose (a), cytokinin (b), auxin (c), and phenolic content (d). The success rate of different cutting source materials (e)

Note: OC = Orthotropic cutting, PC = Plagiotropic cutting, BG = Budwood garden, PRG = Production garden, HS = Hybrid seed. Bars indicate standard error of the mean (SE)

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Table 2. Comparison of the observation result and minimum standard for cocoa seedlings

Growth variable	HS		OC		PC		OG		PG	
	act	Min std.	act	Min std	act	Min std	act	Min std	act	Min std
Age (days)	90	90	180	150	180	180	180	180	180	180
Plant height (cm)	36.11	30.00	43.97	25.00	33.25	25.00	52.57	35.00	48.91	35.00
Stem diameter (mm)	5.11	5.00	6.14	4.00	5.50	4.00	6.38	5.00	5.89	5.00
Leaf number	9.79	6.00	14.75	8.00	13.16	8.00	14.16	6.00	14.76	6.00

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting, act = Actual, Min std = Minimum standard. Minimum standard of cocoa seedling based on Decree of the Minister of Agriculture of the Republic of Indonesia number 25/Kpts/ KB.020/5/2017

Table 3. Morphological characteristics of cocoa seedlings derived from different propagation methods at 210 DAP

Morphological characteristics	HS	OC	PC	OG	PG
Leaf characteristics					
Total leaf area (cm^2)	902.71^{a}	853.99^{ab}	367.29^{b}	591.60^{ab}	509.31^{ab}
Individual leaf area (cm^2)	46.08^{a}	44.91^{a}	21.96^{b}	35.60^{ab}	33.49^{ab}
Leaf angle (^{o})	60.50^{ab}	59.57^{ab}	62.74^{b}	52.16^{b}	60.33^{ab}
Leaf thickness (mm)	0.2^{a}	0.22^{a}	0.21^{a}	0.27^{a}	0.27^{a}
Root characteristics					
Volume (cm^3)	5.21^{a}	4.45^{ab}	2.30^{b}	4.35^{ab}	3.63^{ab}
Area (cm^2)	52.00^{a}	25.41^{b}	17.47^{b}	57.85^{a}	56.67^{a}
Length (cm)	544.42^{a}	318.44^{bc}	213.74^{c}	555.73^{a}	505.31^{ab}
Diameter (mm)	0.47^{ab}	0.40^{b}	0.40^{b}	0.52^{a}	0.56^{a}
Fractal dimension	1.45^{b}	1.47^{b}	1.61^{a}	1.49^{b}	1.50^{b}
Dry weight					
Shoot dry weight (g)	12.52^{a}	9.27^{a}	3.94^{b}	7.67^{ab}	8.08^{ab}
Root dry weight (g)	1.77^{ab}	1.37^{ab}	0.60^{b}	1.47^{ab}	1.25^{ab}
Total dry weight (g)	14.29^{a}	10.64^{a}	4.54^{b}	9.14^{ab}	9.33^{ab}
Root shoot ratio	0.141^{a}	0.147^{a}	0.152^{a}	0.191^{a}	0.154^{a}

Note: Numbers followed by the same letter in the same rows were not significantly different according to Tukey 5%. HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting

OG and PG (Table 2). On the basis of the production time required to meet the minimum standards, OC and PC require the same production time as OG and PG, the latter a clonal propagation method commonly used by farmers.

Plant height, stem diameter, and number of leaves were observed from 30 up to 210 DAP. The growth of the OC materials from 30 up to 210 DAP were not significantly different (p > 0.05) from those of the HS materials (Figure 5b and Figure 5c). The PC samples exhibited a slow growth, showing the lowest plant height observed in this study (Figure 5a). This condition might be related to the small leaf area on the PC materials (Table 3) that contributed to low total dry weight (r = 0.90) and low RGR (r = 0.92) (Table 4). These conditions hindered the growth of the PC material.

The plant height, stem diameter, and number of leaves of the OC material at 150 to 210 DAP showed no significant differences (p > 0.05) from those of the seeds as a control (Figure 5d-5f). Meanwhile, the PC material exhibited slower growth than the seeds but showed no significant differences (p > 0.05) from the PG and OG materials (Figure 5d-5f). On the basis of these results, the OC and PC planting materials at the age of 150 to 210 DAP are suitable because of their similarities to the material from PG, the clonal method commonly used by farmers. Although OC performs better than the others in height and diameter.

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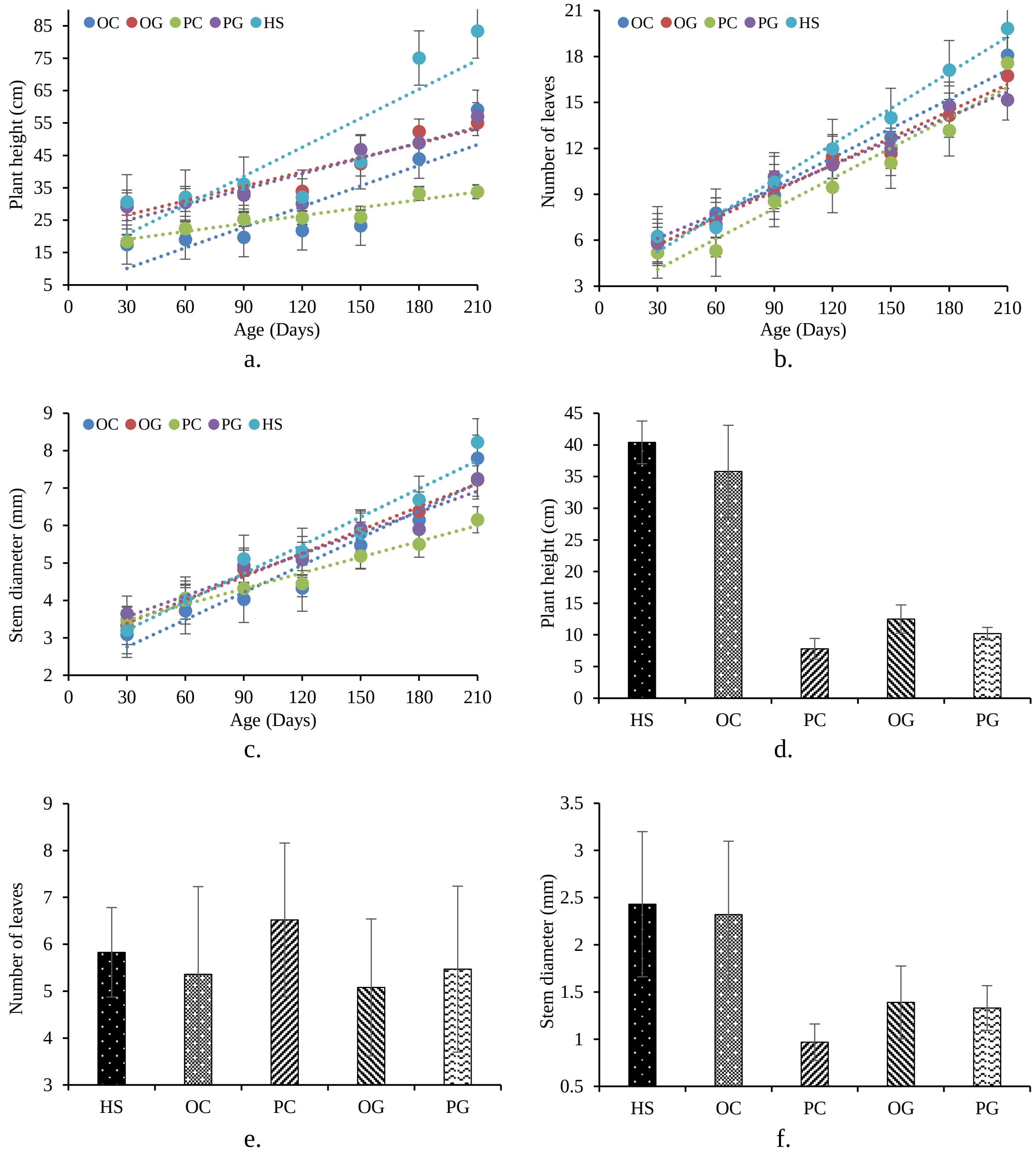

Figure 5. Plant height (a), number of leaves (b), and stem diameter (c) of seedlings derived from different propagations at 30 to 210 DAP and the growth increase of plant height (d), number of leaves (e), and stem diameter (f) between 150 to 210 DAP

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Bars indicate standard error of the mean (SE)

Morphological characteristics of shoots and roots

The leaf angles of the OC materials were not significantly different from those obtained from seed propagation. However, the leaf angles in OC materials were smaller than those observed in PC (Table 3). Leaves at an upright position make the canopy to be more efficient at capturing light, resulting in higher photosynthesis rates and growth yields compared with horizontal leaves in the canopy (Cao et al., 2022). Adjusting the leaf angle between vertical and horizontal is a plant's response to light, heat, and water availability (Yang et al., 2023). The leaf angle of the PC material was horizontal due to its branching types. Plagiotropic branching is more lateral than orthotropic branching, which shows upward growth characteristics (Gomes et al., 2015; Santoso and Zakariyya, 2022).

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The total leaf area of the OC materials was not significantly different from that under HS propagation (Table 3). This finding might indicate a similarity in photosynthesis between OC and HS propagation. Furthermore, the RGR and NAR in OC were not significantly different ($p > 0.05$) from those in HS propagation (Figure 6). The growth of the PC plants was inhibited until 210 DAP because of their smaller leaf areas and total leaf areas compared with the plants from other propagation methods (Table 3). Small leaf area (r = 0.90), small root volume (r = 0.80), and root area (r = 0.54) contributed to the lower dry weight of the PC plant (Table 4). A narrow leaf area leads to reduced cocoa photosynthesis (Santos et al., 2018) as confirmed by the low shoot, root, and total dry weight of the PC plant (Table 3).

Leaf area has a quadratic relation with cocoa growth, biomass production, and plant vigor. Santos et al. (2018) showed that an optimal leaf area leads to high biomass production and good growth performance of cocoa plants. In the present study, NAR was calculated based on the leaf area and plant dry weight to evaluate the impact of leaf area on plant photosynthesis ability. No significant differences in leaf thickness were observed among all the samples (Table 3), indicating that their chlorophyll content in mesophyll was relatively at the same level. Leaf thickness indicates the width of the leaf cell structure, such as the epidermis, mesophyll, and vascular tissue. It can also be used as a criterion to determine cocoa resistance toward drought stress, described cell turgidity, and water status in the leaf tissue (Santos et al., 2018).

Table 4. Pearson correlation among cocoa growth variables at 210 DAP

HS

	RPW	FD	RL	RA	RV	NAR	RGR	LA	DW
RPW	1.00								
FD	0.13	1.00							
RL	0.11	0.59	1.00						
RA	-0.11	0.61	0.86	1.00					
RV	0.10	0.79	0.91	0.83	1.00				
NAR	0.37	0.87	0.39	0.26	0.67	1.00			
RGR	0.12	0.80	0.63	0.44	0.85	0.89	1.00		
LA	0.14	0.92	0.60	0.47	0.83	0.94	0.97	1.00	
DW	0.16	0.82	0.61	0.38	0.80	0.91	0.99	0.97	1.00

OC

	RPW	FD	RL	RA	RV	NAR	RGR	LA	DW
RPW	1.00								
FD	0.22	1.00							
RL	0.90	0.53	1.00						
RA	0.83	0.53	0.98	1.00					
RV	0.83	0.33	0.89	0.93	1.00				
NAR	0.69	0.27	0.83	0.89	0.90	1.00			
RGR	0.82	0.11	0.86	0.89	0.93	0.95	1.00		
LA	0.81	0.29	0.86	0.90	0.99	0.89	0.93	1.00	
DW	0.81	0.19	0.86	0.91	0.98	0.95	0.98	0.98	1.00

PC

	RPW	FD	RL	RA	RV	NAR	RGR	LA	DW
RPW	1.00								
FD	0.74	1.00							
RL	0.26	0.80	1.00						
RA	-0.18	0.51	0.82	1.00					
RV	-0.11	0.51	0.64	0.93	1.00				
NAR	-0.30	-0.22	-0.16	0.24	0.37	1.00			
RGR	0.28	0.52	0.23	0.46	0.74	0.39	1.00		
LA	0.57	0.75	0.37	0.37	0.61	0.12	0.92	1.00	
DW	0.22	0.53	0.29	0.54	0.80	0.40	0.99	0.90	1.00

OG

	RPW	FD	RL	RA	RV	NAR	RGR	LA	DW
RPW	1.00								
FD	-0.49	1.00							
RL	0.04	0.83	1.00						
RA	0.03	0.81	0.99	1.00					
RV	0.03	0.84	0.99	0.98	1.00				
NAR	-0.59	0.50	0.30	0.32	0.32	1.00			
RGR	-0.30	0.95	0.92	0.90	0.90	0.52	1.00		
LA	0.26	0.64	0.92	0.94	0.93	0.07	0.72	1.00	
DW	-0.28	0.95	0.93	0.91	0.91	0.45	0.99	0.74	1.00

PG

	RPW	FD	RL	RA	RV	NAR	RGR	LA	DW
RPW	1.00								
FD	-0.57	1.00							
RL	-0.71	0.62	1.00						
RA	-0.70	0.98	0.65	1.00					
RV	-0.53	0.92	0.65	0.92	1.00				
NAR	-0.15	0.16	-0.28	0.24	0.01	1.00			
RGR	-0.50	0.73	0.09	0.77	0.54	0.68	1.00		
LA	-0.50	0.93	0.43	0.94	0.94	0.29	0.77	1.00	
DW	-0.42	0.96	0.41	0.94	0.91	0.29	0.79	0.98	1.00

1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting, RPW = Root pith width, FD = Fractal dimension of the roots, RL = Root length, RA = Root area, RV = Root volume, NAR = Net assimilation rate, RGR = Relative growth rate, LA = Leaf area, DW = Total dry weight

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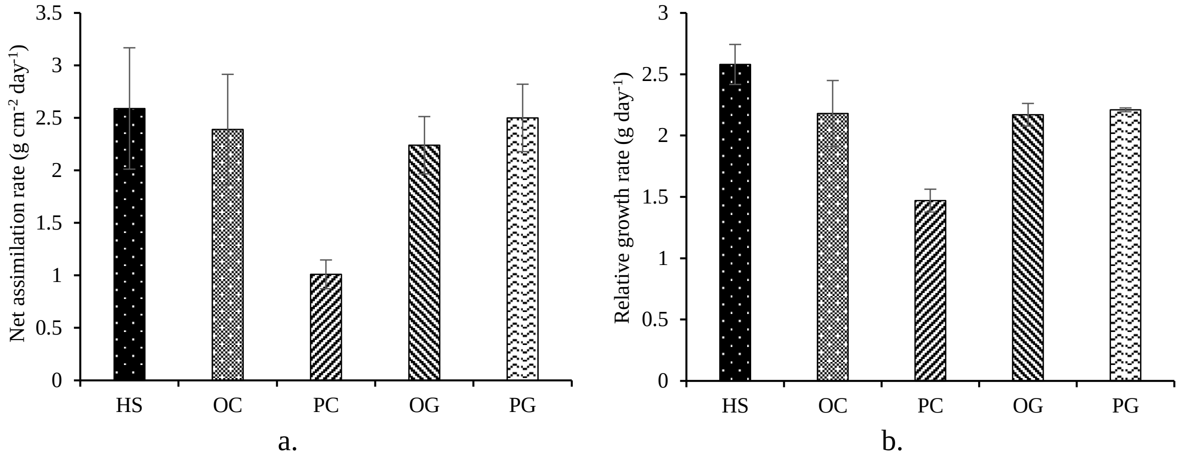

Figure 6. Net assimilation rate (a) and relative growth rate (b) of cocoa seedlings from different propagation methods from 150 to 210 DAP

Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Bars indicate standard error of the mean (SE)

Some root characteristics such as root volume, area, and length in OC were below those in HS (Table 3). Efforts to improve the root characteristics to be on par with HS are still warranted. Some researchers used organic fertilizers (Syamsiyah et al., 2023), dead-end trench (Maghfiroh and Putra, 2020), and arbuscular mycorrhiza fungi (De Vries et al., 2021), which are suspected of improving the root characteristics of plants. However, the fractal dimension of the OC root is similar to that of the HS root (Table 3).

The root fractal dimension in PC was higher than that in OC (Table 3). The fractal dimension was evaluated based on area dimension with a value of $1 \leq D \leq 2$ (Yang et al., 2022). A high fractal dimension indicates that the roots spread in a wide area (Chun et al., 2021). The PC root was more spread out, located at the soil surface, and not deep. In addition to genetic influence, the characteristics and architecture of the root can be used to predict plant responses to drought stress (Santos et al., 2018). Owing to the similarity of its root fractal dimension to HS propagation, OC materials might have better resistance than PC to drought stress.

The shoot, root, and total dry weight in OC were not significantly different from those in HS and were higher than those in grafting (Table 3). Dry weight describes the assimilation product of the plant (Santos et al., 2018) and reflects its productivity and resistance in suboptimal growing conditions (Maghfiroh et al., 2020).

The RGR in OC was not significantly different from that in HS and PG. The OC plant had better NAR and RGR than the PC plant (Figure 6). The large leaf area resulted in a significantly great photosynthetic capacity as indicated by the high total dry weight (r = 0.98), RGR (r = 0.93), and NAR (r = 0.89) (Table 4). High photosynthetic capacity leads to a high RGR. Plants with high RGRs have heavier dry weights than those with low RGRs (Table 3) due to the former's larger stem diameters and plant sizes (Figure 3). RGR and NAR can be used to measure the genetic responses of plants toward suboptimal conditions, especially drought. Resistant clones could maintain maximum biomass production under drought stress (Santos et al., 2018).

Anatomical characteristics of stem and root

The OC and PC materials obtained from BG were further tested to determine the anatomical characteristics of their stems and roots. The observation showed that the epidermis thickness, phloem and xylem tissue width, xylem density, and pith diameter of the OC material were similar to those of the plant derived from HS. Meanwhile, the anatomical characteristics of the roots and stems of the PC material differed from those of the plants derived from other propagation methods (Table 5, Figure 7, and Figure 8).

The anatomical characteristics of the root affect the plant's response to abiotic stress, especially drought stress. The plant responds to drought conditions by decreasing its xylem diameter and density (Qaderi et al., 2019). The PC plant had greater xylem density than the OC plant (Table 5), indicating that OC might provide better drought resistance than PC.

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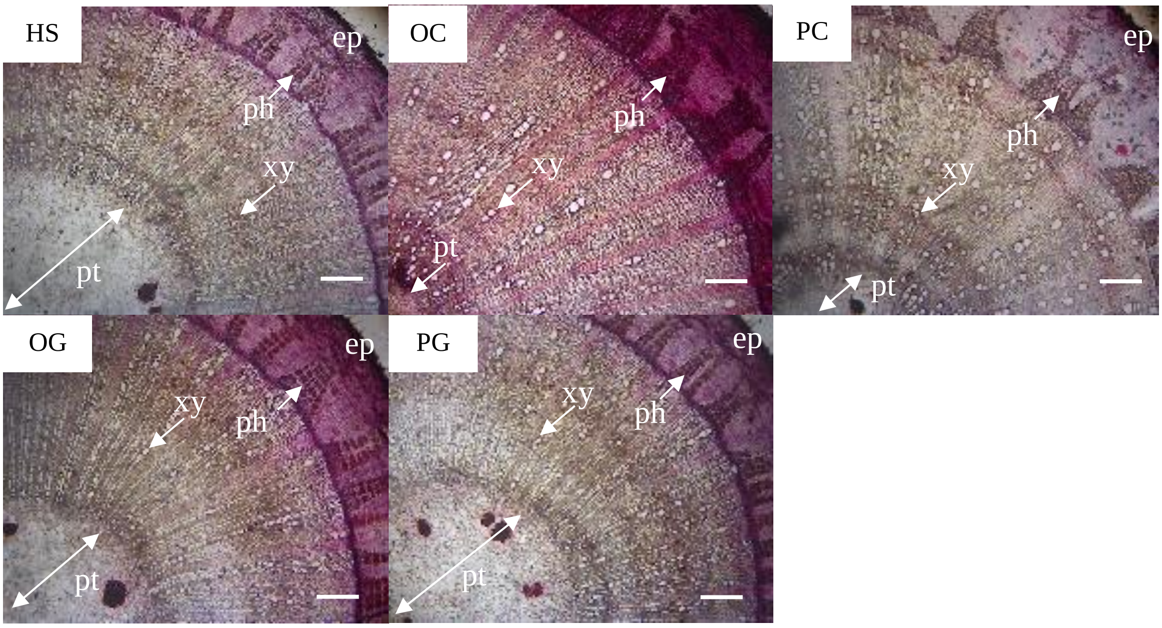

Figure 7. Stem cross-section of cacao seedlings derived from different propagation methods
Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Image caption: ep = Epidermis, ph = Phloem, xy = Yylem, pt = Pith. Bar length of 200 µm

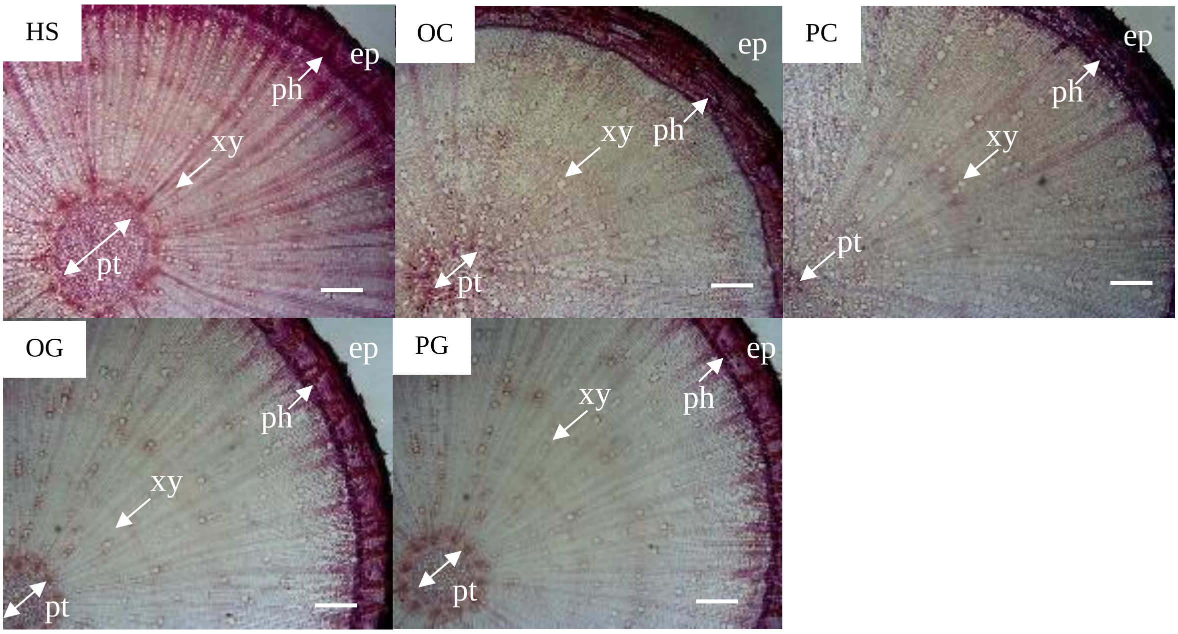

Figure 8. Root cross-sections of the plants obtained from different propagation methods
Note: HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting. Image caption: ep = Epidermis, ph = Phloem, xy = Yylem, pt = Pith. Bar length of 200 µm

The pith width of the root and stem in OC was not significantly different from those in HS propagation. Meanwhile, the pith width of the root and stem in PC was smaller than that in OC (Table 5). The pith is the deepest part of the roots and stems of plants. The pith tissue is composed of parenchyma tissues (Tomescu, 2021). The primary function of the pith is to store resources, such as water and food, so they can be transported by vascular tissues (Mendieta et al., 2021). The large root pith diameter of the OC material indicated its great ability to store water and food. This ability stimulated the growth of roots as reflected by the root length (r = 0.90), root area (r = 0.83), and root volume (r = 0.83). The pith diameter of the OC roots directly affected

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Table 5. Anatomical characteristics of cocoa derived from different propagation methods at 210 DAP

Anatomical characteristics	HS	OC	PC	OG	PG
Stem cross-sections					
Epidermis thickness (µm)	32.85[a]	31.83[a]	32.21[a]	27.63[a]	28.83[a]
Phloem tissue width (µm)	271.06[b]	266.56[b]	333.91[a]	256.79[b]	252.53[b]
Xylem tissue width (µm)	1,245.82[c]	1,057.40[d]	1,553.71[a]	1,428.54[b]	1,329.04[bc]
Xylem density (unit)	96.84[b]	78.59[b]	126.28[a]	73.92[b]	92.58[b]
Pith width (µm)	1,046.76[a]	1,111.09[a]	835.28[b]	1,098.61[a]	1,117.93[a]
Root cross-sections					
Epidermis thickness (µm)	44.35[a]	28.43[b]	37.32[ab]	35.95[ab]	32.34[ab]
Phloem tissue width (µm)	214.67[c]	267.30[b]	378.27[a]	178.22[c]	221.24[c]
Xylem tissue width (µm)	1,409.87[b]	1,475.04[b]	2,307.52[a]	1,310.24[b]	1,435.58[b]
Xylem density (unit)	115.37[b]	105.11[b]	137.02[a]	119.53[ab]	109.98[b]
Pith width (µm)	239.48[a]	152.40[b]	56.44[c]	270.03[a]	232.18[a]

Note: Numbers followed by the same letter in the same rows are not significantly different according to Tukey 5%. HS = Hybrid seed, OC = Orthotropic cutting, PC = Plagiotropic cutting, OG = Orthotropic grafting, PG = Plagiotropic grafting

the root growth and shoot performance as shown by the total dry weight (r = 0.81), total leaf area (r = 0.81), and RGR (r = 0.82) (Table 4 and Table 5).

CONCLUSIONS

The pseudo-taproots of the OC plant did not limit the plant growth as previously hypothesized. The OC method met the minimum standard requirements of ready-to-plant seedlings with production times similar to PG, a common clonal propagation method. The shoot morphological characteristics of the OC materials were similar to those of the HS, although the root characteristics remained different between OC and HS. Efforts to improve the root characteristics to be equal to HS are still warranted. Additional research is needed to optimize PC propagation due to its inferior performance compared with other propagation methods.

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REFERENCES

Adhikari, P. B., Xu, Q., & Notaguchi, M. (2022). Compatible graft establishment in fruit trees and its potential markers. *Agronomy*, *12*(8), 1981. https://doi.org/10.3390/agronomy12081981

Aryal, S., Baniya, M. K., Danekhu, K., Kunwar, P., Gurung, R., & Koirala, N. (2019). Total phenolic content, flavonoid content and antioxidant potential of wild vegetables from western Nepal. *Plants*, *8*(4), 96. https://doi.org/10.3390/plants8040096

Asman, A., Iwanami, T., & Rosmana, A. (2024). Effect of drought stress on dieback disease development under *Lasiodiplodia theobromae* infection in cocoa clone MCC 02. *Beverage Plant Research*, *4*, e034. https://doi.org/10.48130/bpr-0024-0023

Babenko, L. M., Smirnov, O. E., Romanenko, K. O., Trunova, O. K., & Kosakivska, I. V. (2019). Phenolic compounds in plants: Biogenesis and functions. *Ukrainian Biochemical Journal*, *91*(3), 5–18. https://doi.org/10.15407/ubj91.03.005

Cao, Y., Zhong, Z., Wang, H., & Shen, R. (2022). Leaf angle: A target of genetic improvement in cereal crops tailored for high-density planting. *Plant Biotechnology Journal*, *20*(3), 426–436. https://doi.org/10.1111/pbi.13780

Chun, H. C., Lee, S., Choi, Y. D., Gong, D. H., & Jung, K. Y. (2021). Effects of drought stress on root morphology and spatial distribution of soybean and adzuki bean. *Journal of Integrative Agriculture*, *20*(10), 2639–2651. https://doi.org/10.1016/S2095-3119(20)63560-2

Daymond, A. J., Prawoto, A., Abdoellah, S., Susilo, A. W., Cryer, N. C., Lahive, F., &

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Hadley, P. (2020). Variation in Indonesian cocoa farm productivity in relation to management, environmental and edaphic factors. *Experimental Agriculture*, *56*(5), 738–751. https://doi.org/10.1017/S0014479720000289

De Vries, J., Evers, J. B., Kuyper, T. W., van Ruijven, J., & Mommer, L. (2021). Mycorrhizal associations change root functionality: A 3D modelling study on competitive interactions between plants for light and nutrients. *New Phytologist*, *231*(3), 1171–1182. https://doi.org/10.1111/nph.17435

Dobrev, P. I., Hoyerová, K., & Petrášek, J. (2017). Analytical determination of auxins and cytokinins. *Methods in Molecular Biology*, *1569*, 31–39. https://doi.org/10.1007/978-1-4939-6831-2_2

Ghimire, B. K., Kim, S. H., Yu, C. Y., & Chung, I. M. (2022). Biochemical and physiological changes during early adventitious root formation in *Chrysanthemum indicum* cuttings. *Plants*, *11*(11), 1440. https://doi.org/10.3390/plants11111440

Gomes, A. R. S., Sodré, G. A., Guiltinan, M., Lockwood, R., & Maximova, S. (2015). *Supplying new cocoa planting material to farmers: A review of propagation methodologies*. Retrieved from https://hdl.handle.net/10568/68672

Kawaguchi, K., Notaguchi, M., Okayasu, K., Sawai, Y., Kojima, M., Takebayashi, Y., …, & Shiratake, K. (2024). Plant hormone profiling of scion and rootstock incision sites and intra- and inter-family graft junctions in *Nicotiana benthamiana*. *Plant Signaling and Behavior*, *19*(1), 2331358. https://doi.org/10.1080/15592324.2024.2331358

Lubis, N., Sofiyani, S., & Junaedi, E. C. (2022). Penentuan kualitas madu ditinjau dari kadar sukrosa dengan metode Luff Schoorl. *Jurnal Sains dan Kesehatan*, *4*(3), 290–297. https://doi.org/10.25026/jsk.v4i3.1050

Maghfiroh, C. N., & Putra, E. T. S. (2020). Morphological characters of root and yield of three cocoa (*Theobroma cacao*) clones in the field with dead-end trench. *Agricultural Science*, *5*(2), 58–65. https://doi.org/10.22146/ipas.51284

Maghfiroh, C. N., Putra, E. T. S., & Dewi, H. S. E. S. (2020). Root detection by resistivity imaging and physiological activity with the dead-end trench on three clones of cocoa (*Theobroma cacao*). *Biodiversitas*, *21*(6), 2794–2803. https://doi.org/10.13057/biodiv/d210656

Mendieta, K. A., Burleigh, J. G., & Putz, F. E. (2021). Pith width, leaf size, and twig thickness. *American Journal of Botany*, *108*(11), 2143–2149. https://doi.org/10.1002/ajb2.1800

Ministry of Agriculture. (2017). *Keputusan Menteri Pertanian RI nomor 25/Kpts/KB/020/5/2017 tentang pedoman produksi, serifikasi, peredaram dan pengawan benih tanaman kakao (*Theobroma cacao*)*. Ministry of Agriculture of Republic of Indonesia. Retrieved from https://drive.google.com/file/d/1ItRRrizGxy79FzSbQD7SjzQLCkAOSvg4/view

Mithöfer, D., Roshetko, J. M., Donovan, J. A., Nathalie, E., Robiglio, V., Wau, D., ..., & Blare, T. (2017). Unpacking sustainable cocoa: Do sustainability standards, development projects and policies address producer concerns in Indonesia, Cameroon and Peru. *International Journal of Biodiversity Science, Ecosystem Services and Management*, *13*(1), 444–469. https://doi.org/10.1080/21513732.2018.1432691

Niemenak, N., Cilas, C., Rohsius, C., Bleiholder, H., Meier, U., & Lieberei, R. (2010). Phenological growth stages of cacao plants (*Theobroma* sp.): Codification and description according to the BBCH scale. *Annals of Applied Biology*, *156*(1), 13–24. https://doi.org/10.1111/j.1744-7348.2009.00356.x

Noah, A. M., Casanova-Sáez, R., Ango, R. E. M., Antoniadi, I., Karady, M., Novák, O., ..., & Ljung, K. (2021). Dynamics of auxin and cytokinin metabolism during early root and hypocotyl growth in *Theobroma cacao*. *Plants*, *10*(5), 967. https://doi.org/10.3390/plants10050967

N'zi, J. C., Koné, I., M'bo, K. A. A., Koné, S., & Kouamé, C. (2023). Successful grafting elite cocoa clones (*Theobroma cacao*) as a function of the age of rootstock. *Heliyon*, *9*(8), e18732. https://doi.org/10.1016/j.heliyon.2023.e18732

Ocampo-Ariza, C., Müller, S., Yovera, F., Thomas, E., Vansynghel, J., Maas, B., ..., &

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Tscharntke, T. (2025). Cacao grafting increases crop yield without compromising biodiversity. *Journal of Applied Ecology*, *62*(3), 579–592. https://doi.org/10.1111/1365-2664.14851

Olutegbe, N. S., & Sanni, A. O. (2021). Determinants of compliance to good agricultural practices among cocoa farmers in Ondo State, Nigeria. *Caraka Tani: Journal of Sustainable Agriculture*, *36*(1), 123–134. https://doi.org/10.20961/carakatani.v36i1.44894

Qaderi, M. M., Martel, A. B., & Dixon, S. L. (2019). Environmental factors influence plant vascular system and water regulation. *Plants, 8*(3), 65. https://doi.org/10.3390/plants8030065

Santos, E. A. D., Almeida, A. A. F. D., Branco, M. C., Santos, I. C. D., Ahnert, D., Baligar, V. C., & Valle, R. R. (2018). Path analysis of phenotypic traits in young cacao plants under drought conditions. *PLoS ONE*, *13*(2), e0191847. https://doi.org/10.1371/journal.pone.0191847

Santoso, T. I., & Zakariyya, F. (2022). Field performance of plagiotropic cocoa in two clonally propagation methods: Vegetative and early production phase. *AIP Conference Proceedings*, *2563*, 020002. https://doi.org/10.1063/5.0104501

Schmidt, J. E., DuVal, A., Puig, A., Tempeleu, A., & Crow, T. (2021). Interactive and dynamic effects of rootstock and rhizobiome on scion nutrition in cacao seedlings. *Frontiers in Agronomy*, *3*, 754646. https://doi.org/10.3389/fagro.2021.754646

Sodré, G. A., & Gomes, A. R. S. (2019). Cocoa propagation, technologies for productions of seedlings. *Revista Brasileira de Fruticultura*, *41*(2), 1–22. https://doi.org/10.1590/0100-29452019782

Somarriba, E., Peguero, F., Cerda, R., Orozco-Aguilar, L., López-Sampson, A., Leandro-Muñoz, M. E., ..., & Sinclair, F. L. (2021). Rehabilitation and renovation of cocoa (*Theobroma cacao*) agroforestry systems: A review. *Agronomy for Sustainable Development*, *41*(5), 64. https://doi.org/10.1007/s13593-021-00717-9

Statistics Indonesia. (2023). *Indonesian cocoa statistics 2022*. Retrieved from https://www.bps.go.id/en/publication/2023/11/30/ef4419ba62e6ec7d4490218e/indonesian-cocoa-statistics-2022.html

Steffens, B., & Rasmussen, A. (2016). The physiology of adventitious roots. *Plant Physiology*, *170*(2), 603–617. https://doi.org/10.1104/pp.15.01360

Susilo, A. W., Anita-Sari, I., & Setyawan, B. (2020). Yield performance of promising cocoa clones (*Theobroma cacao*) in dry climatic conditions. *Pelita Perkebunan*, *36*(1), 24–31. Retrieved from https://scholar.google.co.id/scholar?cites=11510613434984316174&as_sdt=2005&sciodt=0,5&hl=id

Syamsiyah, J., Minardi, S., Herdiansyah, G., Cahyono, O., & Mentari, F. C. (2023). Physical properties of Alfisols, growth and products of hybrid corn affected by organic and inorganic fertilizer. *Caraka Tani: Journal of Sustainable Agriculture*, *38*(1), 99–112. https://doi.org/10.20961/carakatani.v38i1.65014

Tomescu, A. M. F. (2021). The stele a developmental perspective on the diversity and evolution of primary vascular architecture. *Biological Reviews*, *96*(4), 1263–1283. https://doi.org/10.1111/brv.12699

Xue, Z., Liu, L., & Zhang, C. (2020). Regulation of shoot apical meristem and axillary meristem development in plants. *International Journal of Molecular Sciences*, *21*(8), 2917. https://doi.org/10.3390/ijms21082917

Yang, Q., Cheng, W., Hao, Z., Zhang, Q., Yang, D., Teng, D., ..., & Lei, S. (2022). Study on the fractal characteristics of the plant root system and its relationship with soil strength in tailing ponds. *Wireless Communications and Mobile Computing*, *1*, 9499465. https://doi.org/10.1155/2022/9499465

Yang, X., Li, R., Jablonski, A., Stovall, A., Kim, J., Yi, K., ..., & Lerdau, M. (2023). Leaf angle as a leaf and canopy trait: Rejuvenating its role in ecology with new technology. *Ecology Letters*, *26*(6), 1005–1020. https://doi.org/10.1111/ele.14215

Zhang, S., Peng, F., Xiao, Y., Wang, W., & Wu, X. (2020). Peach PpSnRK1 participates in sucrose-mediated root growth through auxin signaling. *Frontiers in Plant Science*, *11*, 506553. https://doi.org/10.3389/fpls.2020.00409

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