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Establishing breeding house of superior sandalwood in Gunung Sewu, Indonesia: Preserving the 27 selected genotypes grafted onto two types of rootstocks

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Abstract. *Ratnaningrum YWN, Faridah E, Utama INS, Prastyo B. 2022. Establishing breeding house of superior sandalwood in Gunung Sewu, Indonesia: preserving the 27 selected genotypes grafted onto two types of rootstocks. Biodiversitas 23: 3488-3497.* Developing methods for vegetative propagation of sandalwood (*Santalum album* Linn.) is important for the mass production of selected genotypes. Previous research has selected the superior genotypes of sandalwood in Gunung Sewu based on seed production, crossing-ability, santalol content and/or the rare alleles characters. This study estimates the grafting compatibility of 27 selected genotypes of sandalwood, which are grafted onto two types of rootstock. In the peak rainy season in February 2021, scions were picked from the 27 genotypes originating from four landraces (Imogiri, Bejiharjo, Bleberan and Petir) in Gunung Sewu. Scions were then grafted onto two types of rootstock using the top-cleft technique. The first rootstock type is the 8 months old seedlings of the red-big-flower sandalwood variant planted in a polybag (Type 1); while the second one is the root-suckers that emerged from horizontal roots (Type 2). Results revealed Petir genotypes as the most surviving scions (100% in Type 2 and 75% in Type 1 rootstock), followed by those originating from Imogiri. All four genotypes originating from Petir (Pt1, Pt2, Pt3 and Pt4) achieved the highest scores in most of the parameters observed. The Type 2 rootstock survived more grafts (57%) compared to those of Type 1 (49%). The number of shoots and the height increment of grafting showed significant differences. The top-cleft grafting technique is considered effective in conserving the superior genotypes of sandalwood and to provide a copy of those genotypes for materials of the crossing units. The use of Petir and Imogiri genotypes as the scions, and the red-big flower variant root-suckers as the rootstocks, are highly recommended for the best grafting success.

Keywords: Compatibility, grafting, Gunung Sewu, sandalwood, selected genotypes

INTRODUCTION

Santalum album Linn. (East Indian Sandalwood), the most commercial semi-parasitic species for its oil contents, is endemic to South India, Indonesia, New Guinea, Australia and the Pacific islands (Subasinghe 2013; da Silva et al. 2016; Arunkumar et al. 2019; Page et al. 2021; Pullaiah et al. 2021). The center of sandalwood origin is the Eastern Islands of Indonesia (Harbaugh and Baldwin 2007; da Silva et al. 2016; Arunkumar et al. 2019), while in Gunung Sewu which extends from East to Central Java, sandalwood developed as new landraces (Ratnaningrum et al. 2015). Since 1994, the International Union for Conservation of Nature (IUCN) has declared sandalwood as *vulnerable* due to habitat loss and degradation. Moreover, it stated that it is *critically endangered* at the local level in Indonesia (Ratnaningrum et al. 2015; Seran et al. 2018; Arunkumar et al. 2019). Accordingly, the occurrence of new landraces in Gunung Sewu sounds promising to provide genetic materials for rehabilitation efforts (Ratnaningrum et al. 2015, 2017a).

Studies on sandalwood in Gunung Sewu were initiated in 2010 with the assessment of population structures (Ratnaningrum et al. 2015, 2018), genetic diversity (Ratnaningrum et al. 2015, 2017a, 2021; Putri et al. 2020), gene flow (Ratnaningrum et al. 2017a, 2021), phenotypic traits (Ratnaningrum et al. 2017b, 2018; Arifriana et al. 2017; Ratnaningrum and Kurniawan 2019), pollination events (Ratnaningrum et al. 2018; Fathin and Ratnaningrum 2018), reproductive biology and mating systems (Ratnaningrum et al. 2015, 2017b, 2018; Ratnaningrum and Kurniawan 2019), and both sexual and asexual reproductive systems (Ratnaningrum et al. 2016, 2018; Prastyo et al. 2022). Later on 2014 to 2022, the superior parents were then selected based on the contents of rare alleles (Ratnaningrum et al. 2015, 2017a, 2021; Putri et al. 2019; Pratiwi 2019), the reproductive ability (Ratnaningrum et al. 2015, 2017b, 2018; Ratnaningrum and Kurniawan 2019; Sawiyati 2019), and/or the level of santalol (Haryjanto et al. 2017; Ratnaningrum et al. 2021).

Developing methods for vegetative propagation is important for the mass production of selected genotypes, as well as for providing the materials for hedge orchards. In addition, establishing the breeding units requires the superior genotypes which able to flower earlier (Page et al. 2020). Grafting connects part of plants in such a way that perform a new individual; aimed at preserving the genes of superior and/or rare plants (Page et al. 2020, 2021), improving the stem performance (Huang et al. 2019), accelerating the achievement of reproductive age, and providing ready-to-flower mature plants for breeding purpose (Page et al. 2020; Pullaiah et al. 2021). Grafting is also reported to improve plant resistance, productivity, and fruit quality (Kumar et al. 2017; Belmonte-Urena et al. 2020). The survival rate, plant morphology, plant growth, reproductive and yield parameters of *Solanum* spp. in India were significantly affected by grafting (Kumar et al. 2017). Within the developed graftings, several traits were transferred by rootstock to scion, as was reported in *Solanum melongena* in Greece. Rootstocks controlled the nutrient deposition which affected the composition and nutritional value of the fruits; as well as transferred the resistance of fusarium wilt from the rootstocks to the fruits (Krommydas et al. 2018).

The survival rate in the grafted sandalwood was mostly affected by the genotypes, as well as the age and size of both rootstocks and scions (Page et al 2012, 2020; Pullaiah et al. 2021). The initial study on sandalwood grafting in Wanagama Gunung Sewu showed that the seedlings raised from a red-big flower variant are the best for rootstock (Prastyo et al. 2022). In several sites on Pacific Islands, wild seedlings and root-suckers are also common for rootstock materials (Page et al. 2012, 2021). In Tanzania, the *Allanblackia stuhlmannii* grafting might also be applied using in-situ rootstocks, both on-farm or in the natural environment (Munjuga et al. 2013).

In addition, the grafting techniques and the skill of propagators are also important (Huang et al. 2019; Pullaiah et al. 2021; Page et al. 2012, 2021). The top-cleft grafting techniques are considered effective for sandalwood. In India and Australia, the top-cleft grafting on 12-month-old rootstock gave 60% success (Page et al. 2012, 2020, 2021; Pullaiah et al. 2021). The grafting of *S. austrocaledonicum* is best achieved using a top-cleft grafting with actively growing semi-hardwood stems; and the trained propagators improved the success of grafting (60% to 90%) (Page et al. 2020). The top-cleft grafting is also considered the most effective method for *Allanblackia stuhlmannii* in Tanzania (Munjuga et al. 2013), *Vitex payos* in Kenya (Bala et al. 2017), *Carica papaya* in Taiwan (Nguyen and Chung-Ruey 2018), *Juglans regia* in India (Singh et al. 2019), *Mangifera indica* in Ethiopia (Beshir et al. 2019), and *Handroanthus* spp. in Brazil (Simões et al. 2021). However for some other species, different grafting methods were also promising. In Turkey, the side graft of *Castanea sativa* performed high compatibility (74% success) (Kulaç et al. 2021), while *Pistacia lentiscus* and *P. atlantica* gained more success with the chip-budding method (Parlak 2018).

The environmental factors are also crucial; the grafted plants preferred a humid condition during the development of grafting, since a drier environment might have a negative impact due to heat shock (Huang et al. 2019). However, the excess humidity might increase the fungal attack which reduces survival (Pullaiah et al. 2021). Winter is considered the best time for the grafting of sandalwood (Pullaiah et al. 2021) and *Juglans regia* in India (Singh et al. 2019), apple in Nepal (Devkota et al. 2020), and *Mangifera indica* in Ethiopia (Beshir et al. 2019). The early spring gave the best result for the grafting of *Pterocarpus santalinus* in China (Huang et al. 2019), and *Pistacia lentiscus* and *P. atlantica* graftings in Turkey (Parlak 2018). However in Malawi, the higher temperature at the end of the dry season was more suitable for *Anacardium occidentale* graftings (Chipojola et al. 2013). A mild summer is more suitable than autumn for cleft grafting of *Carica papaya* in Taiwan (Nguyen et al. 2018). In the arid regions of Kenya, the peak of dry winter is considered the best season for graftings. However plants grafted in the peak of summer gave poor survival due to a heat shock, and on the contrary, those grafted in the peak of the rainy season experienced grafting rots due to the excess humidity (Bala et al. 2017).

This study estimates the grafting compatibility of scions obtained from 27 selected genotypes of sandalwood, which are grafted onto two types of rootstock. The 27 genotypes were collected from four landraces representing each zone and landscape in Gunung Sewu: Imogiri in the mountainy area of Western Zone, Bejiharjo in the caves area and Bleberan in the riparian area of the Middle Zone, and Petir in the hilly karst of Eastern Zone. The two rootstock types were the 8 months old seedlings of the red-big-flower sandalwood variant planted in a polybag (Type 1) and the root-suckers naturally emerged from the horizontal roots (Type 2). The grafted materials will provide superior individuals which produce flowers in an earlier period (8 months), whereas those originating from generative seedlings take 3-5 years to flower.

MATERIALS AND METHODS

Study sites

At the end of the rainy season in February 2021, scions were collected from 27 selected genotypes originated in four landraces representing each zone in Gunung Sewu: Imogiri (the highland area in the Western Zone), Bejiharjo (the cave area in the Middle Zone), Bleberan (the riparian catchment area in the Middle Zone), and Petir (the hilly karst area in the Eastern Zone) landrace, respectively. Scions were grafted onto rootstocks which were planted in Petir (Figure 1).

Imogiri Village (7°56′45.0” S; 110°23′20.9” E; 252–328 MASL), Imogiri District, is a part of the Batur Agung Formation in the South-Western Zone of Gunung Sewu. The recent landscapes originated from the fluvial processes, a geological formation influenced by ancient volcanic activities. The fluvial landforms containing alluvium are now located along the ancient Opak River, representing the wavy, hilly to mountainous forms. Imogiri represents a tropical mountain ecosystem under the *Am* of the Schmidt and Fergusson climatic type. Since the oldest sandalwood specimens (dated 1853) were collected from Imogiri, hence this landrace is considered the oldest on Java Island. Recently, sandalwood grew dispersedly in small groups on the rugged terrain, rocky inclines, or the verge of cliffs following the catchment area of the Opak River. These groups are separated by natural barriers such as hills and cliffs, which might inhibit gene flow and seed germination (Putri et al. 2019).

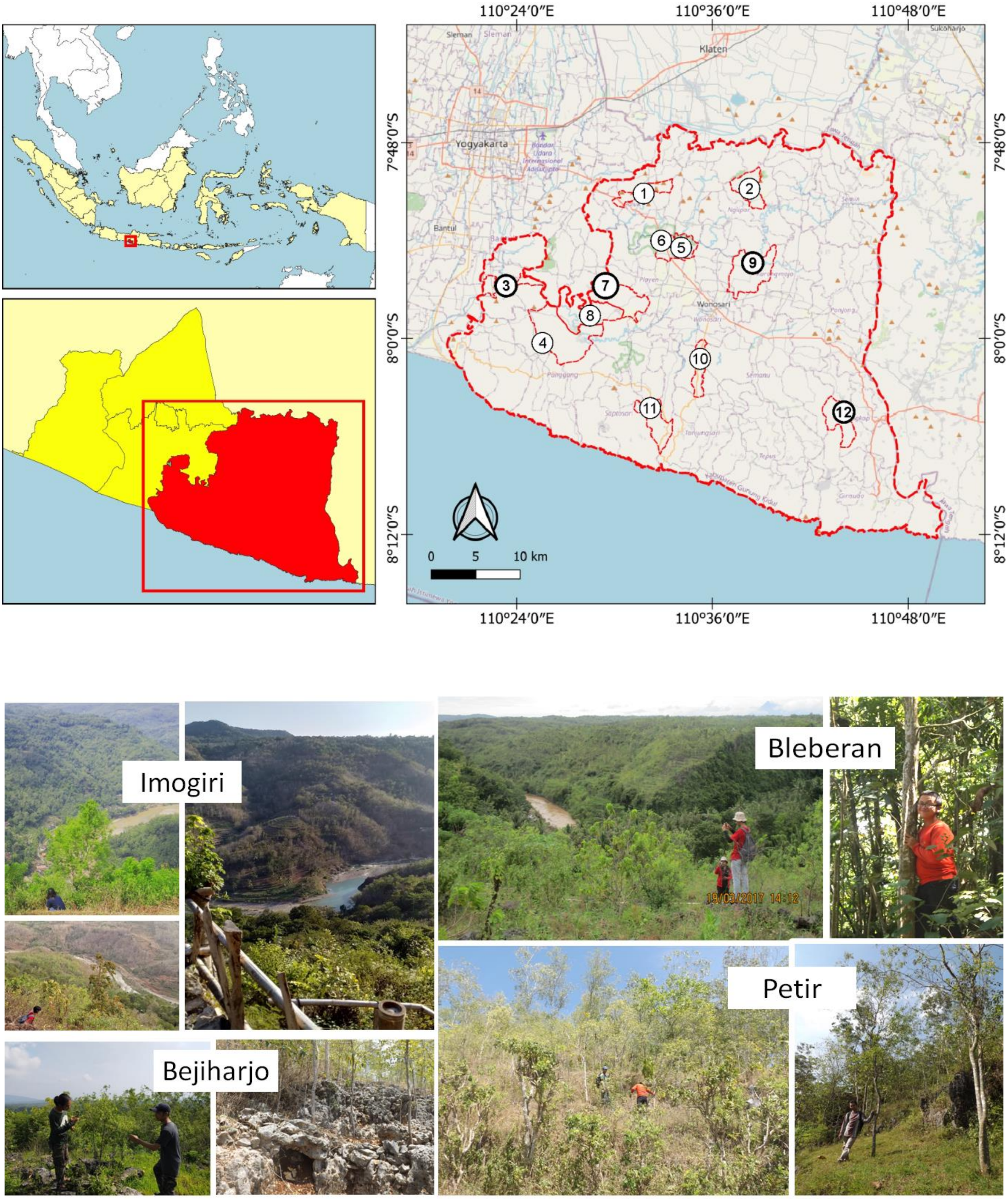

Figure 1. Landrace groups of sandalwood in Gunung Sewu, Java Island. The first sandalwood group in the fluvial landform mountainy areas in the Western Zone consists of the Nglanggeran (1) and Sriten (2) landraces in the North-Western part, and the Imogiri (3) and Watu Payung (4) in the South-Western ones. The second group in the Middle Zone consists of the Watusipat (5), Wanagama (6), Bleberan (7), and Banyusoco (8) in the basin area along the ancient Oya River; and the Bejiharjo (9), Mulo (10) and Tritis (11) landraces in the caves and ground-river areas. The third group in the hilly-karst areas in the Southern Zone consists of the Petir-Semugih (9), Botodayakan (10), and Tepus (11) landraces. Scions in this study were collected from the Imogiri (3), Bleberan (7), Bejiharjo (9) and Petir (12) landraces; while the grafting was prepared in Petir (12)

Bleberan Village (7°56′30.8” S; 110°29′23.8” E; 150–170 MASL), Playen District, is a part of the Wonosari Basin Formation in the Middle Zone of Gunung Sewu. Bleberan is a catchment area of the subterranean river, the Oya River. It represents a tropical lowland ecosystem under the intermediate of *Aw* and *Am* of the Schmidt and Fergusson climatic type; characterized by a lowland basin landscape that receives abundant rainfall. The Bleberan landrace covers 52.9 ha of hills, rivers, and falls. The occurrence of sandalwood along the riparian sides of the Oya River was first documented in the 1970s. Recent studies revealed the wide dispersion of the species from along the catchment area to the hills nearby, which is mostly associated with tropical lowland forest vegetation such as mahogany, teak, cajuputi and acacia (Ratnaningrum et al. 2021). This landrace is a priority for the conservation program since it contains more rale alleles which can be used for genetic infusion (Fathin and Ratnaningrum 2018; Ratnaningrum and Kurniawan 2019; Ratnaningrum et al. 2021).

Bejiharjo Village (7°55′20.7” S; 110°38′31.0” E; 150–180 MASL), Karangmojo District, is derived from the Sambipitu-Oyo Formation in the dry-lowland region of the Middle Zone of Gunung Sewu. It covers 9 ha of dry-rocky hills with caves and ground-rivers below; it represents a dryland ecosystem under the strong *Aw* of the Schmidt and Fergusson climatic type. The recent sandalwood landrace is a remnant of plantations established in the 1970s using seeds from Nglipar, an older landrace. This landrace exists in very small fragmented groups; however it is a priority in the government conservation program, since sandals of the Karangmojo Group are among those with higher level of santalol (Haryjanto et al. 2017; Ratnaningrum et al. 2021).

Petir Village (8°044′31.0” S; 110°44′05.6” E; 70-100 MASL), Rongkop District, is a part of Wonosari-Punung Karst Formation in the Southern Zone of Gunung Sewu. This site is now existed as the hilly karst landscapes with open dry-rocky hills, characterizing the dry rocky-limestone ecosystems under the *Aw* of the Schmidt and Fergusson climatic type. Sandalwood landrace was first documented in 1960’s, recently covering 78 ha of plants grown on karst hilly areas, in association with dry rocky-limestone vegetation including acacia and cajuputi (Ratnaningrum et al. 2015; 2017a). This largest landrace is of importance since it provides the most abundant seeds for rehabilitation programs in Gunung Sewu (Pratiwi 2019; Sawiyati 2019).

Procedures

Scions and rootstocks preparation

Scions were picked from the 27 genotypes which were previously selected based on the contents of rare alleles (Ratnaningrum et al. 2015, 2017a, 2021; Putri et al. 2019; Pratiwi 2019), the reproductive ability (Ratnaningrum et al. 2015, 2017b, 2018; Ratnaningrum and Kurniawan 2019; Sawiyati 2019), and/or the level of santalol (Haryjanto et al. 2017; Ratnaningrum et al. 2021). In each selected parent, the young, fresh and fleshy twigs from active terminal branches were picked, with a length ranging from 25 to 40 cm, and a diameter ranging from 5 to 10 mm (Page et al. 2012; Huang et al. 2019). These scions were packed in the ice box and taken to Petir to be grafted.

Rootstocks were selected from the actively growing semi-hardwood stems with a 7-10 mm diameter range (Page et al. 2020). The first rootstock type used in this study is the 8 months old seedlings of the red-big flower sandalwood variant which is planted in polybag with soil:manure:topsoil (2:2:1). The second rootstock type is the root-suckers naturally emerged from the horizontal roots, with a 7-10 mm diameter range (Page et al. 2012. 2021).

Grafting execution

The grafting was conducted at the end of the rainy season in February 2021 (2035 mm monthly rainfall, 28^{0}C to 30^{0}C, 90% to 96% relative humidity) using The Top Cleft Grafting method (Page et al. 2012, 2021). The top end of the rootstock was cut in a V shape. A scion was cut in the opposite direction with the base also forming a V shape. The scion was then inserted into the rootstock incision in such a way that both cambiums were jointed precisely. The joint connection is tied by a grafting tape and covered by a plastic bag to reduce evaporation. The cover is removed after the scion sprouts, while the tie is removed after the joint is completely fused, usually at 8 weeks post-grafted.

A completely randomized design was applied with 27 genotypes of scion, five replications each. Since the two rootstock types are grown in different environmental conditions, therefore they were analyzed in separated experimental units. The first experimental unit consisted of 27 genotypes of scion grafted onto Type 1 rootstock, five replications each, 135 units in total. This first experimental unit was placed in the greenhouse. The second experimental unit consisted of 27 genotypes of scion grafted onto Type 2 rootstock, five replications each, 135 units in total. The Type 2 rootstock is derived from root-suckers and therefore is not removed from the parental horizontal roots, which grow in the hilly area nearby.

RESULTS AND DISCUSSIONS

Survival assesments at eight weeks after grafting showed that Petir genotypes are the most surviving scions (100% in Type 2 and 75% in Type 1 rootstock), compared to any other genotypes (ranging from 55% to 65% in Imogiri, 54% to 58% in Bleberan, and 31% to 33% in Bejiharjo genotypes, respectively). On average, the Type 2 rootstock survived more grafts (57%) compared to those of Type 1 (49%) (Table 1; Figure 2a).

The best performances are achieved mostly by genotypes collected from Petir, followed by those from Imogiri. All four genotypes originating from Petir (Pt1, Pt2, Pt3 and Pt4) achieved the highest scores in most of the parameters observed. All four genotypes from Imogiri (Im1, Im2, Im3 and Im4) also showed great performances in several parameters observed.

The number of shoots and the height increment of grafting showed significant differences. The number of shoots are ranged from 18 to 26 shoots in Petir, 13 to 21 shoots in Imogiri, 13 to 15 shoots in Bleberan, and only 10 shoots in Bejiharjo genotypes, respectively (Table 1; Figure 2b). Whilst, the height increments are ranged from 5.1cm to 7cm in Petir, 2.67cm to 4.68cm in Imogiri, 2.37cm to 2.47cm in Bleberan, and only 1.14cm to 1.63cm in Bejiharjo genotypes, respectively (Table 1; Figure 2c). The diameter increment is insignificant, however Petir still achieved the biggest diameter (0.49cm to 0.86cm) in compared to those of Imogiri (0.28cm to 0.32cm), Bleberan (0.18cm to 0.22cm) and Bejiharjo (0.16cm to 0.29cm), respectively (Table 1; Figure 2d).

In average, the Type 2 rootstock achieved better performances (57% survival, 16 shoots, 3.17cm height increment, and 0.86cm diameter increment, respectively) in compared to those of Type 1 (49% survival, 13 shoots, 2.62cm height increment, and 0.49cm diameter increment, respectively) (Table 1; Figure 2a-d).

The success of sandalwood grafting was indicated by the complete connection of the scion and rootstock, followed by the emergence of new shoots from the scion, which indicated the success of the cambial nutrient transfer. The connected cambium tissues performed parenchymal cells (callus), which differentiate to form a new cambium attached to the original cambium, multiply in 1 to 7 days (Holbrook et al. 2002; Huang et al. 2019). The grafting compatibility was represented by the ability of the tissue to regenerate and rejoint the vessels of wounded tissues. Histologically, it was indicated by the high glucose content in leaves and a small gap in total sugar content between above and below graft union (Cholid et al. 2014). Usually, the top-cleft or wedge grafting method achieves the best performance since the internal pressure exerted through compression of the wood is higher compared to other methods (Bala et al. 2017). In this study, it took 8 weeks for scion to produce the new shoots. Similarly, apple graftings in Nepal produce more shoots 60 days after being grafted (Devkota et al. 2020). The top-cleft grafting of *Mangifera indica* in Ethiopia required only 17 days to produce new buds (Beshir et al. 2019). Grafting of *Camellia oleifera* in China was ready to flower after eight months (Zeng et al. 2022).

Table 1. The survival rate or grafting compatibility (%), height (cm) and diameter (cm) increment, and the number of shoots resulted from 27 genotypes of scion grafted onto two rootstock types

Landraces	No. of genotype	Code of genotype	Superior characters	Survival (%)		Height increment (cm)		Diameter increment (cm)		Number of shoots	
				Rootstock Type 1	Rootstock Type 2	Rootstock Type 1	Rootstock Type 2	Rootstock Type 1	Rootstock Type 2	Rootstock Type 1	Rootstock Type 2
Imogiri	1	Im 1	Rare allele	40	80	4.00	6.00	0.25	0.03	16.00	24.00
	2	Im 2	Rare allele	60	100	2.17	3.40	0.17	0.20	13.00	25.00
	3	Im 3	Rare allele	60	20	3.33	5.00	0.17	1.00	11.00	23.00
	4	Im 4	Rare allele	60	60	1.17	4.33	0.53	0.07	11.00	13.00
Bejiharjo	5	P 1	Abundant fruits	40	20	8.50	0.00	0.85	0.30	7.00	6.00
	6	P 2	Abundant fruits	40	0	1.00	-	0.30	-	10.00	-
	7	P 3	Abundant fruits	20	40	0.50	1.00	0.00	0.10	8.00	7.00
	8	P 4	Rare allele	40	40	0.25	2.75	0.10	0.20	9.00	10.00
	9	P 5	High santalol	40	0	0.75	-	0.25	-	10.00	-
	10	P 6	High santalol	40	40	0.00	1.00	0.00	0.30	14.00	13.00
	11	P 7	High santalol	20	40	1.50	1.00	0.50	0.05	10.00	12.00
	12	P 8	High santalol	0	20	-	0.00	-	0.10	-	13.00
	13	P 9	High santalol	40	100	0.50	2.20	0.35	0.10	13.00	11.00
Bleberan	14	S 1	High crossing ability	60	60	3.33	1.00	0.33	0.10	15.00	13.00
	15	S 2	High crossing ability	60	60	1.37	2.33	0.23	0.33	14.00	13.00
	16	S 3	High crossing ability	60	60	1.33	5.50	0.13	0.40	15.00	13.00
	17	S 4	Rare allele	60	60	3.17	3.00	0.17	0.13	15.00	13.00
	18	S 5	Rare allele	40	60	2.25	2.83	0.20	0.20	15.00	13.00
	19	S 6	Rare allele	0	60	-	2.50	-	0.43	-	14.00
	20	S 7	Rare allele	60	60	3.17	1.83	0.17	0.13	15.00	13.00
	21	S 8	Rare allele	20	60	4.00	2.67	0.20	0.17	16.00	14.00
	22	S 9	Abundant fruits	100	40	1.00	1.50	0.08	0.30	12.00	14.00
	23	S 10	Abundant fruits	80	60	1.75	1.50	0.10	0.03	14.00	13.00
Petir	24	Pt 1	Abundant fruits	80	100	5.75	7.40	0.70	1.00	18.00	26.00
	25	Pt 2	Abundant fruits	60	100	4.30	6.75	0.40	0.65	21.00	21.00
	26	Pt 3	High santalol	60	100	5.00	7.20	0.35	1.00	12.00	29.00
	27	Pt 4	High santalol	100	100	5.33	6.67	0.50	0.80	19.00	27.00
Average				**49.63**	**57.04**	**2.62**	**3.17**	**0.49**	**0.86**	**13.32**	**15.72**
F stat.						0.997ns	1.629*	0.953ns	0.812ns	0.946ns	2.914*
P-value						0.475ns	0.064*	0.525ns	0.602ns	0.534ns	0.001*

Note: *F* ratios and *P* values are resulted from variance analysis among genotypes. Asterix (*) represents significantly differences in P < 0.05. The grey shade column represents the best five genotypes in each parameter observed

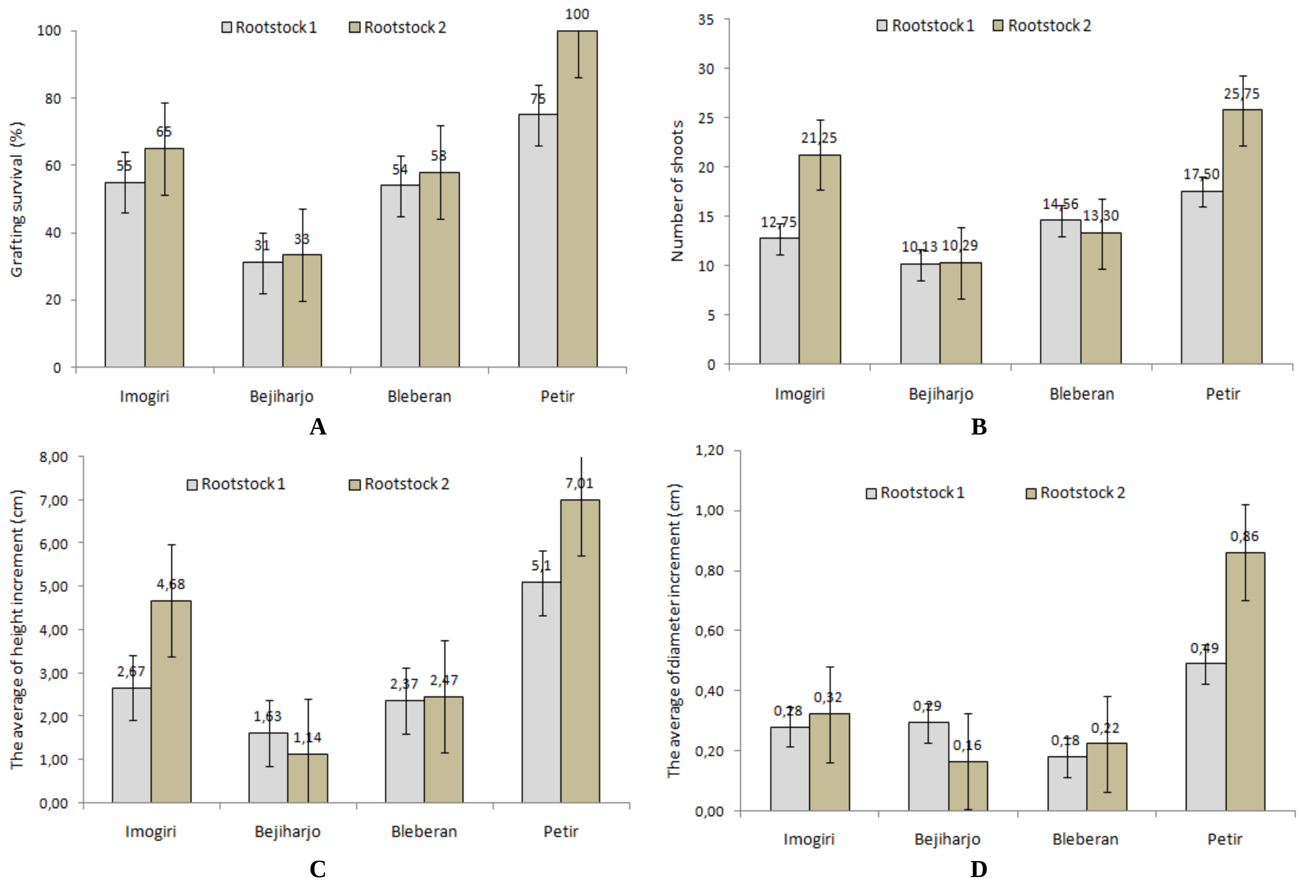

Figure 2. A. The survival rate or grafting compatibility (%). B. The number of shoots, C. The height (cm), D. The diameter (cm) increment resulted from 27 genotypes of scion grafted onto two rootstock types

This grafting success was affected more by genetic factors which control the rootstock-scion compatibility, the balance between carbohydrates and nitrogen (C/N ratio), auxin activity, the presence of cofactors that accelerate the healing process (Huang et al. 2019), the quantity of cambium, and the nutrient and hormone transfers from rootstock to scion (Holbrook et al. 2002). Grafting compatibility is controlled by the abundance of antioxidant gene transcripts, as was observed in the pear graftings in Denmark (Irisarri et al. 2014). SOD and CAT enzymes controlled wounding responses, oxidative stress protection, and protection of tissue damage during graft connection development. The incompatible response might be an active process of rejection due to the less efficient antioxidant system and the production of inappropriate cell types (Irisarri et al. 2014). Furthermore, the healing process involves traumatic responses, physiological and biochemical processes, cell and tissue differentiation, signal exchange between scion and rootstock, and the reconnection of vascular bundles (Huang et al. 2019). Grafting failure was caused more by the physiologic condition of scions and less favorable environmental conditions at the time of grafting. Accordingly, such failures were due to the unhealthy rootstocks, physiologically immature scions, mechanical damage to the cambial region during execution, loose tie which caused water absorption and fungal attack, and rootstock-scion incompatibility (Munjuga et al. 2013).

Accordingly, the age and size of rootstock and scion are important since it determines the availability of food storage, hormones and cofactors, and ensure their transfers (Page et al. 2012, 2020, 2021; Pullaiah et al. 2021). The top-cleft grafting of *Annona muricata* depends on the length of scion used as well as the point at which they are attached to the rootstocks. The 10-15 cm length of scion inserted at the upper part of the 15 cm rootstock gave the best success and growth (Yakubu et al. 2022). A certain size of rootstocks (15cm to 20cm length) and scions (15 cm length) were also crucial for the success of *Allanblackia stuhlmannii* graftings in Tanzania (Munjuga et al. 2013).

The age of both rootstocks and scion donors are important for the grafting success, and are considered species-specific. Both rootstock types in this study were selected from the 8 months old seedlings with actively growing semi-hardwood stems, with a 7-10 mm diameter range (Figure 3). For *Santalum* groups, 12 months is considered the oldest age for rootstock (Page et al. 2012, 2020; Huang et al. 2019; Pullaiah et al. 2021). An over 1-year rootstock performed poor survival and was lesscompatible due to the connection failure and prolonged healing period (Huang et al. 2019). The 1-month-old rootstocks achieved the best success in the top-cleft grafting of *Carica papaya* in Taiwan (Nguyen et al. 2018). The best compatibility in *Jatropha curcas* was performed by two months old rootstock grafted by the top-cleft method (Cholid et al. 2014). In Malawi, the best *Anacardium occidentale* scions should be collected from 12 to 20-year-old trees. Scions collected from the younger trees were unable to cope with weather stresses (Chipojola et al. 2013). In *Abies fraseri,* scions should be collected from the upper crown from no older than a 3-year-old tree (Hinesley et al. 2018). However in *Pinus engelmannii* graftings, the best scions were those obtained from trees aged between 20 and 60 years (middle-aged trees). The grafting survival decrease with the increase of the total area and density of resin channels in scion (Pérez-Luna et al. 2019). In line with this, the branch type is also important in determining the developmental patterns of grafting. *Araucaria angustifolia* grafted with plagiotropic primary branches resulted in conversion to the trunk, represented by the vertical growth, organization of trunk, and persistent branches with defined whorls, in a similar developmental pattern to those grafted with trunk grafts (Constantino et al. 2020).

The better survival and performance of Type 2 rootstock in this study was due to better adaptability and microclimate condition. A greenhouse provides a more stable environment for the Type 1 rootstocks, however the nutrient sources were limited and the root development was inhibited in the polybags. Type 2 rootstock was derived from root-suckers which were still attached to their parents in their natural habitat, and therefore were more adaptive, less exposed to environmental stresses, and received more abundant rainfall and nutrients. In addition, using root-suckers for rootstocks gives more advantages in genetic base enrichment by adding some new genotypes to the population. Many studies revealed that the root-suckers -- the genotypically identical shoots that emerged from parental horizontal roots -- caused crucial problems in sandalwood mating systems, since the mature root-suckers will mate with each other and increase the geitonogamy in a population (Warburton et al. 2000; Lhuillier et al. 2006; Rao et al. 2007; Dani et al. 2011; Sumardi and Fiani 2015; Ratnaningrum et al. 2015; 2017a; 2021; Ratnaningrum and Kurniawan 2019; Sandeep et al. 2019). Therefore, replacing the apical shoots of root-suckers using different genotypes will increase genetic diversity in the population, avoiding the probability of inbreeding.

Figure 3. The performances of scions from Imogiri, Bleberan, Bejiharjo and Petir landraces grafted onto Type 1 (above) and Type 2 (below) rootstocks

The scions and rootstocks used in this study are at the same size and age; hence the variation that occurred in survival and performances were due to the genetic differences. Among the 27 genotypes tested for scion, the best performances are performed by genotypes collected from Petir, followed by those from Imogiri. Both landraces are the highest in genetic diversity, which are represented in the higher value of heterozygosity (Ho ranged from 0.5 to 0.7; Ratnaningrum et al. 2015, 2017a; Pratiwi 2019; Putri et al. 2019). Contrastly, the Bejiharjo landrace undergoes a low genetic base which leads to inbreeding, resulting in some level of inbreeding depression which might be expressed in the grafting incompatibility (Ratnaningrum et al. 2015, 2017a, 2021). A similar case was also observed with graftings using 39 genotypes of *Santalum austrocaledonicum* in Vanuatu, which expressed different scion-rootstock compatibility due to genetic differences (Page et al. 2020).

Grafting of *Castanea sativa* in Turkey emphasizes the importance of selected genotypes on graft compatibility (Kulaç et al. 2021). Grafting improves tolerance to low phosphorus (P) stress in the selected genotypes of *Camellia oleifera* in China. The P deficiency is tolerated by maximizing the cost-effectiveness of P remobilization to photosynthetic organs. The more vigorous genotypes with higher shoot dry weights can improve tolerance to the low-P supply, which tends to be a result of their greater ability to take up P and translocate it to the shoots (Zeng et al. 2022). Grafted *Abies fraseri* scions to disease-resistant rootstocks of *Abies* species is recommended to ensure the success of graftings, particularly in the more humid environments when Phytophthora root rots were responsible for the grafting mortality (Hinesley et al. 2018). Genotypically, grafting compatibility is controlled by the abundance of antioxidant gene transcripts, as was observed in the pear graftings in Denmark (Irisarri et al. 2014). SOD and CAT enzymes controlled wounding responses, oxidative stress protection, and protection of tissue damage during the graft connection development. The incompatible response might be an active process of rejection due to the less efficient antioxidant system and the production of inappropriate cell types (Irisarri et al. 2014). The best result was achieved in the top-cleft grafting of *Handroanthus* spp. scions which were grafted onto the same species (83% success), while the success was somehow lower while rootstocks were of different species (27% to 55% success). Grafting of the same species guarantees a well-established vascular connection between parts (Simões et al. 2021).

The grafting techniques are also crucial for grafting success. Previous studies revealed that top-cleft grafting techniques are effective for sandalwood. In India and Australia, the top-cleft grafting on 12-month-old rootstock gave 60% success (Page et al. 2012, 2020, 2021; Pullaiah et al. 2021). In Vanuatu, the top-cleft grafting of *S. austrocaledonicum* using actively growing semi-hardwood stems gained 60% to 90% survival (Page et al. 2020). This top-cleft techniques are also common in *Agathis loranthifolia* with 70.83% success (Harimurti 2008), and in *Intsia bijuga* with 20.67% success (Sukendro et al. 2010). The top-cleft grafting is also considered the most effective method for the success of *Allanblackia stuhlmannii* in Tanzania (19%; Munjuga et al. 2013), *Vitex payos* in Kenya (58%; Bala et al. 2017), *Carica papaya* in Taiwan (80%; Nguyen et al. 2018), *Juglans regia* in India (46%; Singh et al. 2019), *Mangifera indica* in Ethiopia (100%; Beshir et al. 2019), and *Handroanthus* spp. in Brazil (83.3%; Simões et al. 2021). However, for some other species, different grafting methods were also promising. In Turkey, the side graft of *Castanea sativa* performed high compatibility (74% success) while chip budding was the lowest (29%) (Kulaç et al. 2021). Contrastly, *Pistacia lentiscus* and *P. atlantica* graftings in Turkey gained more success with the chip-budding method (Parlak 2018). In China, among three grafting techniques (oblique, top-cleft and skin graftings) applied for *Pterocarpus santalinus*, the oblique grafting performed the highest compatibility (80%). However, this technique is not applicable for rootstocks having smaller stem diameters (Huang et al. 2019), and therefore top-cleft grafting is more recommended for sandalwood. In addition, the grafting techniques and the skill of propagators are also important (Huang et al. 2019; Pullaiah et al. 2021; Page et al. 2012, 2021).

The skill of the propagators also determines the success of grafting. In *S. austrocaledonicum*, a 60% to 90% success was achieved with the trained propagators (Page et al. 2020). A similar case was also reported in this study, in which most connection failure experienced in the preliminary trial (only 15% survival rate) was due to the inexpert propagators. Having trained propagators has increased survival from 60% to 100%.

The climate condition plays an important role in grafting success. The mild, humid environment is preferred for the success of grafting in most subtropical and tropical regions. In India, winter is considered the best time for sandalwood grafting (Pullaiah et al. 2021), while in China, grafting of *Pterocarpus santalinus* was best conducted in the early spring (Huang et al. 2019). In India, the best result was achieved when the grafting of *Juglans regia* was conducted during the wet season in early February (Singh et al. 2019). The best survival of apple grafting (92.5%) in Nepal was achieved when it was conducted during the wet season in early March (Devkota et al. 2020). The best result of *Pistacia lentiscus* and *P. atlantica* graftings in Turkey was obtained when it was conducted in the early spring during February to March (Parlak 2018). Similarly, grafting of *Mangifera indica* in Ethiopia gave the best result (100%) when it was conducted during more humid weather in March and June (Beshir et al. 2019).

However, more moist conditions might increase the fungal attack which reduces survival to only 20% (Pullaiah et al. 2021). The fungal attack was also observed in this study which was conducted during the peak of the rainy season in February 2021. The fungal attack which first occurred on the rootstock, followed by the dried scions, was responsible for a large portion of the failure. A similar result was reported in India, when the fungal attacks increased the mortality rate of the sandalwood graftings (Pullaiah et al. 2021). The fungal attack reduced the survival of the grafted *Intsia bijuga* (21.67%; Sukendro et al. 2010) and *Tectona grandis* (35.53%; Santoso and

Wardani 2006; 20.27%; Indriyatno and Na'iem 2004). In addition, the low survival rate was also caused by the imperfect rootstock-scion connection due to the different sizes of both parts, and the lack of nutrient storage in the small-sized materials (Indriyatno and Na'iem 2004; Page et al. 2020). The grafted *Agathis loranthifolia* achieved higher survival (70.83%) when the fungicides were applied and the scions were picked during the dormant phase (Harimurti 2008). Grafting rots due to the excess humidity were reported in the peak of the rainy season from April to June, which contributed to the mass failure of *Vitex payos* in Kenya (Bala et al. 2017). Accordingly, grafting *Abies fraseri* scions to disease-resistant rootstocks of *Abies* species is recommended to ensure the success of graftings, particularly in the more humid environments when Phytophthora root rots were responsible for the grafting mortality (Hinesley et al. 2018).

Drier conditions also have a negative impact on graftings due to heat shock (Huang et al. 2019). In Malawi, a higher temperature at the end of the dry season in October was more suitable for production of new shoots in the *Anacardium occidentale* graftings; when it was followed by the onset of rains in November to continue the grafting development (Chipojola et al. 2013). A mild summer is more suitable than autumn for cleft grafting of *Carica papaya* in Taiwan (Nguyen et al. 2018). In the arid regions of Kenya, scions collected during the dormant phase before October gave the best grafting results. October, the peak of dry winter, was also considered the best season since it provides the best environmental condition for the growth of graftings. Plants grafted at the peak of summer from December to March gave poor survival due to a heat shock (Bala et al. 2017).

In conclusion, Petir genotypes are the most surviving scions (100% in Type 2 and 75% in Type 1 rootstock), compared to any other genotypes (ranging from 55% to 65% in Imogiri, 54% to 58% in Bleberan, and 31% to 33% in Bejiharjo genotypes, respectively). On average, the Type 2 rootstock survived more grafts (57%) compared to those of Type 1 (49%). All four genotypes originating from Petir (Pt1, Pt2, Pt3 and Pt4) achieved the highest scores in most of the parameters observed. The number of shoots and the height increment of grafting showed significant differences. The number of shoots ranged from 18 to 26 shoots in Petir, 13 to 21 shoots in Imogiri, 13 to 15 shoots in Bleberan, and only 10 shoots in Bejiharjo genotypes, respectively. Whilst, the height increments are ranged from 5.1cm to 7cm in Petir, 2.67cm to 4.68cm in Imogiri, 2.37cm to 2.47cm in Bleberan, and only 1.14cm to 1.63cm in Bejiharjo genotypes, respectively. The diameter increment is insignificant, however Petir still achieved the biggest diameter (0.49cm to 0.86cm) in compared to those of Imogiri (0.28cm to 0.32cm), Bleberan (0.18cm to 0.22cm) and Bejiharjo (0.16cm to 0.29cm), respectively. On average, the Type 2 rootstock achieved better performances (57% survival, 16 shoots, 3.17cm height increments, and 0.86cm diameter increment, respectively) compared to those of Type 1 (49% survival, 13 shoots, 2.62cm height increments, and 0.49cm diameter increment, respectively). Mass propagation by the top-cleft grafting techniques is considered effective in conserving the superior genotypes of sandalwood and providing a copy of those genotypes for materials of the crossing units and hedge orchards. The use of Petir and Imogiri genotypes as the scions, and the red-big flower variant root-suckers as the rootstocks, are highly recommended for the best grafting success.

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