Genetic diversity of *Dyera polyphylla* (Miq.) Steenis populations used in tropical peatland restoration in Indonesia

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SUMMARY

Dyera polyphylla is a native tree species of peat swamp forests in Southeast Asia. Where it has been used in peatland restoration, the trees are of uncertain genetic origin. We analysed the genetic diversity of seven populations of *D. polyphylla* (9–20 individual trees *per* population) from both natural forests and plantations on peatland farms in the Indonesian provinces of Jambi and Central Kalimantan. Using six selected primers, analysis of amplified fragment length polymorphism (AFLP) indicated that 86.5–96.8 % of loci tested (280 in total) were polymorphic, with an estimated heterozygosity *H* ranging from 0.29 to 0.38. The highest genetic variation was within populations, rather than among them. Cluster analysis based on Nei's distance matrix indicated that the sampled *D. polyphylla* populations from Jambi and Central Kalimantan were genetically distinct. STRUCTURE analysis indicated that the wild population at Senyerang (Jambi) was the most distinct. This site and Tumbang Nusa (Central Kalimantan) deserve *in situ* protection and are recommended as seed sources for peatland restoration in their respective provinces. In the absence of knowledge about specific traits, it is important to retain the high genetic diversity of existing wild and planted populations of *D. polyphylla* revealed by our work when selecting seed sources for future peat swamp forest rehabilitation programmes.

KEY WORDS: AFLP, agroforestry, Kalimantan, Sumatra, paludiculture

INTRODUCTION

Peatlands are common on the three main Indonesian islands of Sumatra, Borneo (Kalimantan) and Papua, covering a combined area of 14,833,100 ha. This most recent estimate of peatland area is based on a meta-analysis of global peatland distribution by the PEATMAP project (Xu *et al*. 2018), and is slightly lower than estimates derived from the official national peatland map published by the Ministry of Agriculture of Indonesia in 2011, e.g. 14,905,475 ha (Ritung *et al*. 2011). Owing to deforestation, massive drainage, spontaneous settlements and uncontrolled fire, the area of pristine peat swamp forest in Indonesia has been decreasing rapidly. Miettinen *et al*. (2016) reported that, in 2015, the area of degraded peat swamp forest in Sumatra and Kalimantan was 996,050 ha (6.4 % of total study area); while managed land, particularly industrial plantations and smallholdings, had increased to 7.8 Mha (about 50 % of study area). The extensive fires of 2015 caused further peatland degradation, but also triggered the creation of a new national agency in charge of peatland restoration. Peatland restoration is aligned with the national development agenda, as well as with global agendas such as the Bonn Challenge, the Aichi Targets of the Convention on Biological Diversity (CBD), adaptation and mitigation measures in the context of climate change, and the sustainable development goals (SDG). The Government of Indonesia has set a target of two million ha of degraded peatland restoration by 2019 (Indonesian President's Regulation 1/2016), while the goal of the Bonn Challenge is to restore 150 million ha of the world's deforested and degraded lands by 2020 and 350 million ha by 2030 (Minnemeyer *et al*. 2011).

Restoration of peatlands requires, first of all, that ongoing degradation is halted. Where local communities live in peatland areas, economically attractive land use that is compatible with undrained peatland forest conditions is needed (van Noordwijk *et al*. 2014). Native tree species are preferred for restoration and their use has increased (Kettle 2012, Thomas *et al*. 2014), because they are adapted to the conditions on undrained and rewetted sites. However, lack of clarity on the origin and genetic diversity of the planting stock used in restoration is a cause of great concern (Thomas *et al*. 2014, Lander & Boshier

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2014). The peatland species *Dyera polyphylla* (Miq.) Steenis belongs to the *Apocynaceae* family and is a source of latex. Its natural distribution is in the Malay Peninsula, the east coast of Sumatra and Kalimantan (Williams 1963, Soepadmo *et al.* 2002). No data on genetic differentiation between the Sumatran and Bornean populations exist, but they may have separated at the end of the last glaciation 10,000 years ago, as has been documented for other species (Raes *et al*. 2014). *D. polyphylla* (locally known as jelutong) produces a light and brightly coloured timber that can be used for pencils, light construction and furniture. The latex and resin have economic value, as they are used in the industrial production of tubes, pipes and varnish (Boer 1997, Soepadmo *et al.* 2002). *D. polyphylla* latex tapped from wild populations was a relevant part of regional economic growth in the 1950s and 1960s (Williams 1963). The upward trend of *D. polyphylla* latex production in Indonesia continued into the 21st century. In 1996–2006, latex production was 600 t *per* year while the latest data, for 2011–2012, show latex production reaching 800 t *per* year (Tata *et al*. 2015).

A decline in the density of wild *D. polyphylla* populations was recently documented for the Tanjung Jabung Barat (abbreviated as Tanjabar) and Tanjung Jabung Timur (abbreviated as Tanjabtim) districts of Jambi (Tata *et al*. 2016) on Sumatra's east coast, other parts of Jambi (Siregar *et al.* 2016) and the Kapuas district of Central Kalimantan (Kalima *et al*. 1998). This reduced the supply of latex and existing trade channels declined. A government regulation in 2008 which taxed all *D. polyphylla* latex, regardless of whether it was sourced from natural forest or managed stands, led to further decline of the *D. polyphylla* latex trade (Tata *et al*. 2015, 2016). Even so, *D. polyphylla* has been promoted as one of the few economically attractive native tree species for peatland restoration in Indonesia (Giesen 2015, Tata & Susmianto 2016) and it may regain its place in restored peatland economies if the regulation mentioned above is revised and trade channels are restored. In Tanjabar (Jambi), for example, *D. polyphylla* has been planted as part of a rehabilitation programme for the Bram Itam peatland forest reserve (Mulia *et al*. 2014, Tata *et al.* 2016).

In view of current planting programmes and their expected expansion, the choice of seed sources needs attention. As most efforts so far have been at local scale, relying on locally derived seed sources, the genetic diversity of currently planted populations may resemble that in natural populations; but little is known about possible exchanges of seed between Sumatra and Kalimantan. No explicit trait-based selection has been documented for the species. Allozyme variation in Central Kalimantan populations of *D. polyphylla* was reported by Wahyudiningsih *et al.* (2014). Beyond allozyme variation, amplified fragment length polymorphism (AFLP; Vos *et al*. 1995) has been used to characterise the genetic diversity of tree populations at marker level (Bonin *et al*. 2007, Muchugi *et al*. 2008, Mutegi *et al.* 2016). Despite its limitations compared with newer DNA fingerprinting methods (Scotti *et al.* 2016, Andrews & Luikart 2014, Benesttan *et al*. 2016), the AFLP method can provide insights into research questions which require comparisons across populations.

The research reported here aimed to explore the genetic variability and population structure of *D. polyphylla* in peatland areas along Sumatra's east coast (Jambi province) and in Central Kalimantan, using AFLP markers. We set out to compare diversity in planted *versus* natural populations and possible genetic exchange between Sumatra and Kalimantan. We expect the results to have implications for current peatland restoration efforts.

METHODS

Study area

This research was conducted in three districts of two provinces, e.g. Tanjabar and Tanjabtim districts of Jambi province, and Pulang Pisau district of Central Kalimantan province. The seven sites where samples were collected are shown in Figure 1 and listed in Table 1.

Procedures

Plant material

Leaf samples were collected from 9–20 individual trees *per* population of wild (natural forest) or planted *D. polyphylla* trees at seven sites (Table 1). The trees at each site (population) were chosen randomly with a minimum distance of 100 m between individuals. The age of *D. polyphylla* trees in the planted populations varied between 6 and 20 years (Table 1). The stem diameter at breast height (dbh) of the planted trees sampled ranged from 5 to 33 cm, while stem dbh for the wild populations ranged from 13 to 61 cm. The planted trees in Jambi and Central Kalimantan had not been tapped. The wild populations in Jambi, on the other hand, had been tapped for commercial use. Only young leaves without obvious deformities or damage were collected. Identification of the plant materials was confirmed by the herbarium of the Forest Research and Development Centre in Bogor, Indonesia.

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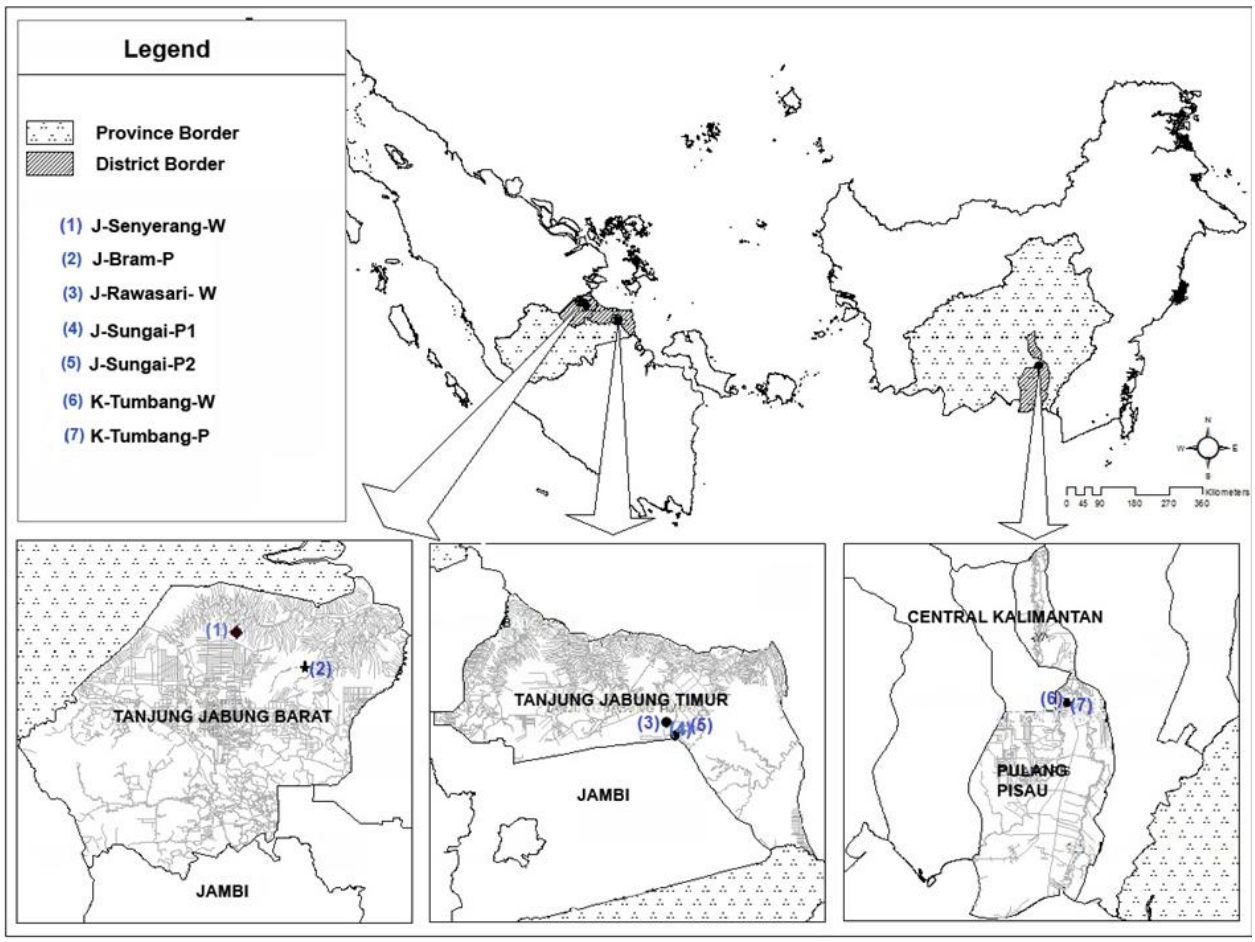

Figure 1. Locations of the study areas in the provinces of Jambi (on the island of Sumatra) and Central Kalimantan (on Borneo), with natural plus man-made drainage indicated.

Table 1. Locations of leaf sample collections from the seven *D. polyphylla* populations. The population code prefix indicates the province (J=Jambi, K=Central Kalimantan) and the suffix distinguishes wild (W) from planted (P) populations (two at J-Sungai). Sites 1–5 are described in more detail by Tata *et al.* (2016).

Site No.	Region	Site / population	Population code	Latitude / longitude	Type of population*	Number of samples (N)
1.	Jambi	Senyerang	J-Senyerang-W	00° 50' 21.60" S 103° 09' 55.20" E	Secondary peat swamp forest (wild)	9
2.		Bram Itam	J-Bram-P	00° 51' 15.55" S 103° 11' 46.26" E	Planted as forest rehabilitation (6 years)	20
3.		Rawasari	J-Rawasari-W	01° 15' 44.04" S 104° 02' 41.54" E	Secondary peat swamp forest (wild)	12
4.		Sungai Aur	J-Sungai-P1	01° 17' 47.94" S 104° 04' 44.59" E	Planted on peatland (20 years)	15
5.		Sungai Aur	J-Sungai-P2	01° 17' 46.01" S 104° 04' 44.54" E	Planted on mineral soil (15 years)	15
6.	Central Kalimantan	Tumbang Nusa	K-Tumbang-P	02° 21' 04.56" S 114° 05' 56.76" E	Planted on peatland (7 years)	15
7.		Tumbang Nusa	K-Tumbang-W	02° 21' 16.50" S 114° 05' 33.96" E	Secondary peat swamp forest (wild)	14

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The leaves were collected in the afternoon and were usually kept fresh overnight before transfer, the next day, to the Biotechnology Laboratory at *Riset Perkebunan Nusantara* (Nusantara Estate Crop Research Centre) in Bogor. Some leaves that were collected from remote areas were stored in sealed envelopes containing silica gel.

DNA extraction

Total genomic DNA was extracted from both fresh and silica-gel dried leaves following the protocol of the DNeasy® Plant Handbook by Qiagen® (Hilden, Germany). When the Qiagen® protocol did not work properly, Dellaporta's DNA extraction method (Dellaporta *et al.* 1983) was used. The leaves were cleaned in running tap water and dried using paper tissues. Leaf material (1 g) was then quickly frozen with liquid N_2 and ground into powder using a mortar and pestle. Fresh leaves usually produce better-quality DNA. The quality of genomic DNA was examined by agarose gel electrophoresis and spectrophotometry. The DNA concentration was quantified with a NanoDrop 1000 spectrophotometer (Thermo Scientific, Wilmington, USA). The concentration of the DNA stock was 50–100 ng μl^{-1} in TE (Tris-EDTA, pH 8) buffer.

AFLP analysis

The AFLP reaction was performed following Invitrogen® protocols for the AFLP analysis system (California, USA). Each genomic DNA sample (200 ng) was digested with two restriction enzymes *Eco*RI/*Mse*I. Selective amplification was conducted using 22 combinations of two AFLP primers specific for *Eco*RI and *Mse*I primer adaptors on a test panel of representative *D. polyphylla* samples. The primer combinations that gave the most reliable amplifications and polymorphisms in repeated trials were chosen for the complete set of sample analyses.

All PCR reactions were performed in the GeneAmp PCR System 9700 (Applied Biosystem, CA, USA). The PCR amplification products were visualised on 6 % polyacrilamide gel using $AgNO_3$ as a loading dye. The electrophoresis was performed in a Sequi-Gen GT Nucleic Acid Electrophoresis Cell (Biorad, USA). The pre-electrophoresis was run at 75 watts for 30 minutes (± 2000 V, 100 mA) until the temperature of the gel reached 50 °C. The electrophoresis was then continued at 65 watts for one hour. The presence or absence of bands was scored manually. The analysis was conducted in the Common Laboratory of SEAMEO BIOTROP, Bogor, Indonesia.

Data analysis

The presence or absence of unequivocally scorable bands was converted into a binary character matrix, scoring 1 for presence and 0 for absence of a band at a particular position within the genome. Nei's unbiased heterozygosity diversity estimate (Nei 1978) was generated using Tools for Population Genetic Analysis (TPFGA) version 1.3 software (Miller 1997). In this analysis, the allele frequencies are estimated from the frequency of the null allele and Hardy Weinberg equilibrium is assumed. The genetic distance (Nei 1978) was derived using GenAlEx (Genetic Analysis in Excel) 6.5 software (Peakall & Smouse 2012). Analysis of molecular variance (AMOVA) (Excoffier *et al*. 1992) based on Euclidean distances between individuals as well as genetic differentiation among populations (F_{ST}) was computed using GenAlEx 6.5 allowing 1000 permutations. The dendogram and Principal Coordinate Analysis (PCoA) showing clustering of populations were generated using TFPGA 1.3 and GenAlex 6.5, respectively. The clustering was validated by computing 1000 bootstraps. Another cluster analysis, STRUCTURE (Pritchard *et al.* 2000), was used to understand the relationship among populations of 100 individuals and 252 loci. For this analysis, all runs were performed with a burn-in period of 50,000 iterations and 50,000 repeats after burn-in. The algorithm employed by STRUCTURE HARVESTER was used to determine the number of *K* groups that best fitted the dataset and to visualise the output (Earl & vonHoldt 2012). STRUCTURE 2.3.4 software and STRUCTURE HARVESTER Web v0.6.94 were used for the analysis.

RESULTS

Marker development and genetic diversity

The 22 primer combinations of *Eco*RI and *Mse*I that were tested resulted in six combinations of good amplification, namely: E-ACC/M-CAA, E-ACC/M-CAC, E-ACC/M-CTA, E-ACG/M-CAA, E-AGC/M-CTA and E-AGG/M-CTC. These were used for selective amplification of the full set of individuals. A total of 280 polymorphic markers were scored across the seven populations. Estimates of Nei's unbiased genetic diversity (Table 2) showed high diversity across all seven of the *D. polyphylla* populations studied. The percentage of polymorphic loci ranged from 86.5 to 96.8 % (mean PPL = 92.3 %) while average heterozygosity ranged from $H = 0.29$

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Table 2. Mean diversity estimate (*H*) of 7 *Dyera polyphylla* population generated from 280 AFLP markers. The population codes are explained in Table 1.

Region	Population code	N	Percentage Polymorphic Loci (%)	Average Heterozygosity (*H*)
Jambi	J-Senyerang-W	9	86.5	0.38
	J-Bram-P	20	96.8	0.35
	J-Rawasari-W	12	86.5	0.29
	J-Sungai-P1	15	87.7	0.30
	J-Sungai-P2	15	96.8	0.34
Central Kalimantan	K-Tumbang-W	15	96.8	0.33
	K-Tumbang-P	14	95.2	0.35
Mean			92.3	0.33

to $H = 0.38$ (mean $H = 0.33$). There was no indication that planted populations had reduced genetic variability. The wild population at J-Senyerang-W had the highest diversity estimate ($H = 0.38$), while another wild population in Jambi (J-Rawasari-W) had the lowest level of heterozygosity ($H = 0.29$).

Analysis of molecular variance

An analysis of molecular variance (AMOVA) for the seven populations of *D. polyphylla* showed that the greatest variation was found within populations (91 %), with only 9 % of the variation among populations (9 %) (Table 3). This means that genetic variation is maintained within populations rather than among populations. Genetic differentiation among the populations was low ($F_{ST} = 0.094$).

Genetic distance and cluster analysis

The value of pairwise genetic distances of *D. polyphylla* is shown in Table 4. The largest genetic distance (0.251) was found between the populations at J-Sungai-P1 and J-Senyerang-W, although both were located in the same province. The populations at J-Sungai-P2 and J-Rawasari-W had the lowest genetic distance, suggesting that the wild population at Rawasari (or a closely related population) was used as the seed source for the planted population at J-Sungai-P2.

A phenogram based on Nei's genetic distances for the seven populations is shown in Figure 2. The populations were separated into three groups. Populations from Tanjabtim (Jambi), which consisted of J-Rawasari-W, J-Sungai-P1, and J-Sungai-P2, were grouped into one cluster, while J-Bram-P (Tanjabar, Jambi) was grouped with populations from Central Kalimantan (K-Tumbang-W and K-Tumbang-P) suggesting that seed sources from Kalimantan had been used at the Jambi site. The population from Senyerang, upstream from the Bram Itam site, is the most genetically distinct from all others.

In a principal coordinates analysis (PCoA) of the seven *D. polyphylla* populations (Figure 3) the first two axes explained 38.8 % and 20.7 % of the total variation, respectively. The wild population at K-Tumbang-W (Kalimantan) and the planted population at J-Bram-P (Jambi) were well distributed on both axes, while the two wild populations at J-Senyerang-W and J-Rawasari-W in Jambi were separated on Axis 1.

The STRUCTURE HARVESTER analysis that was used to compute the true *K* (Figure 4) revealed two major clusters. The phylogenetic tree shown in Figure 2 also displayed two main branches.

The STRUCTURE bar plot for the seven *D. polyphylla* populations in shown in Figure 5. It was obtained for $K = 2$. The bar-plot shows that individuals from Rawasari and Sungai Aur (Jambi) are closely related and mostly in one cluster. The wild population from Senyerang (J-Senyerang-W; individual number 92-100 in Appendix) appears to be distinct, with all individuals in the second cluster, which agrees with our earlier analysis. The other three populations show slight overlap in both clusters.

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Table 3. Analysis of molecular variance (AMOVA) for the seven populations of *Dyera polyphylla*. F_{ST} = genetic differentiation among populations.

Source	Degrees of freedom	Mean square	Variation (%)	F_{ST}	*P*-value
Among populations	6	112.152	9	0.094	0.001
Within populations	92	45.816	91		
Totals	98		100		

Table 4. Genetic distances between the seven populations of *Dyera polyphylla*. The population codes are explained in Table 1.

Population	K-Tumbang-P	K-Tumbang-W	J-Rawasari-W	J-Sungai-P2	J-Sungai-P1	J-Bram-P	J-Senyerang-W
K-Tumbang-P	***						
K-Tumbang-W	0.060	***					
J-Rawasari-W	0.084	0.089	***				
J-Sungai-P2	0.068	0.074	**0.049**	***			
J-Sungai-P1	0.100	0.105	0.051	0.053	***		
J-Bram-P	0.087	0.069	0.103	0.078	0.098	***	
J-Senyerang-W	0.177	0.166	0.239	0.203	**0.251**	0.147	***

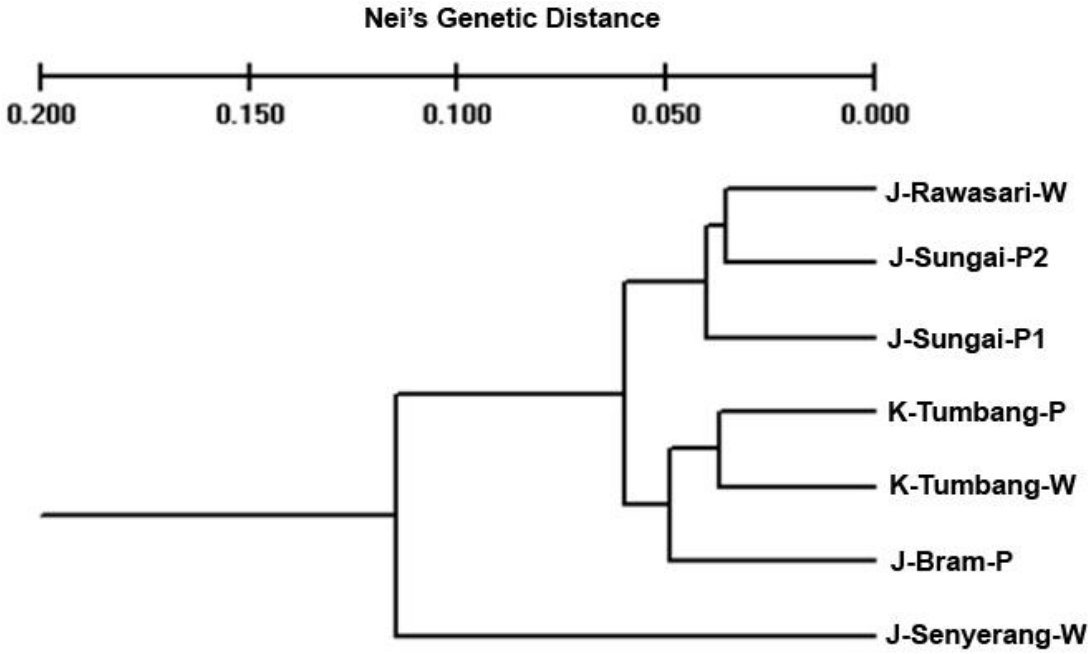

Figure 2. Phenogram based on Nei's genetic distance generated from 280 AFLP markers for 100 *Dyera polyphylla* individuals sampled from seven populations. Validation within 1000 bootstraps. The population codes are explained in Table 1. Distances are expressed on a dimensionless 0–1 scale from zero to maximum dissimilarity in terms of the criteria used.

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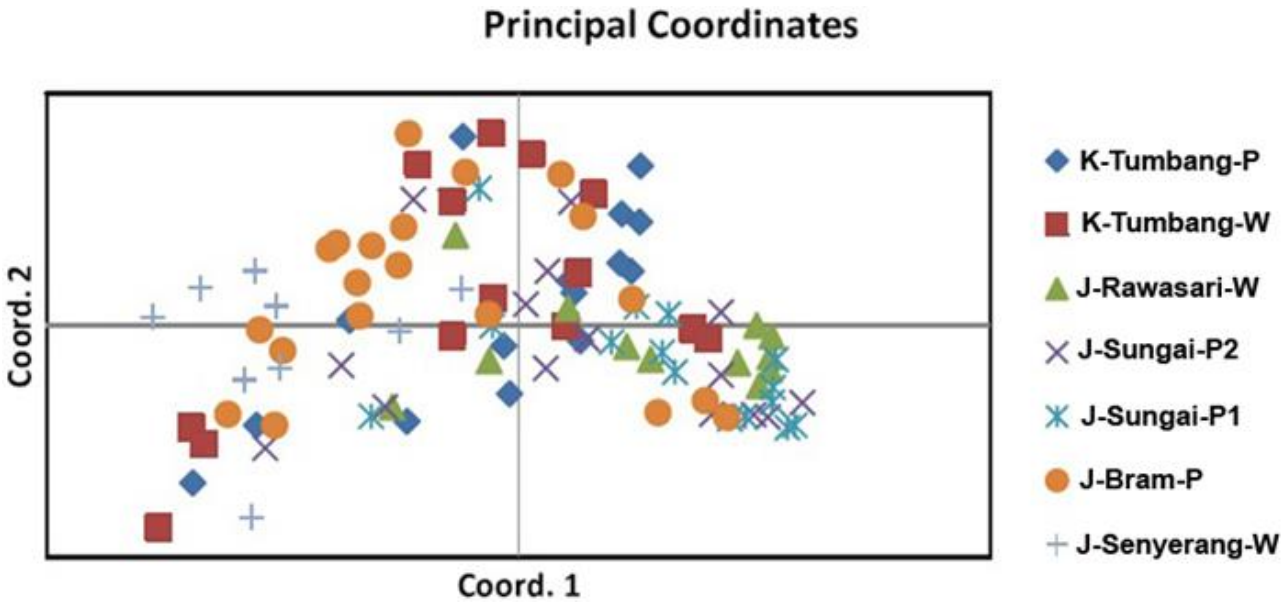

Figure 3. Principal coordinates analysis (PCoA) of the seven *Dyera polyphylla* populations. The population codes are explained in Table 1.

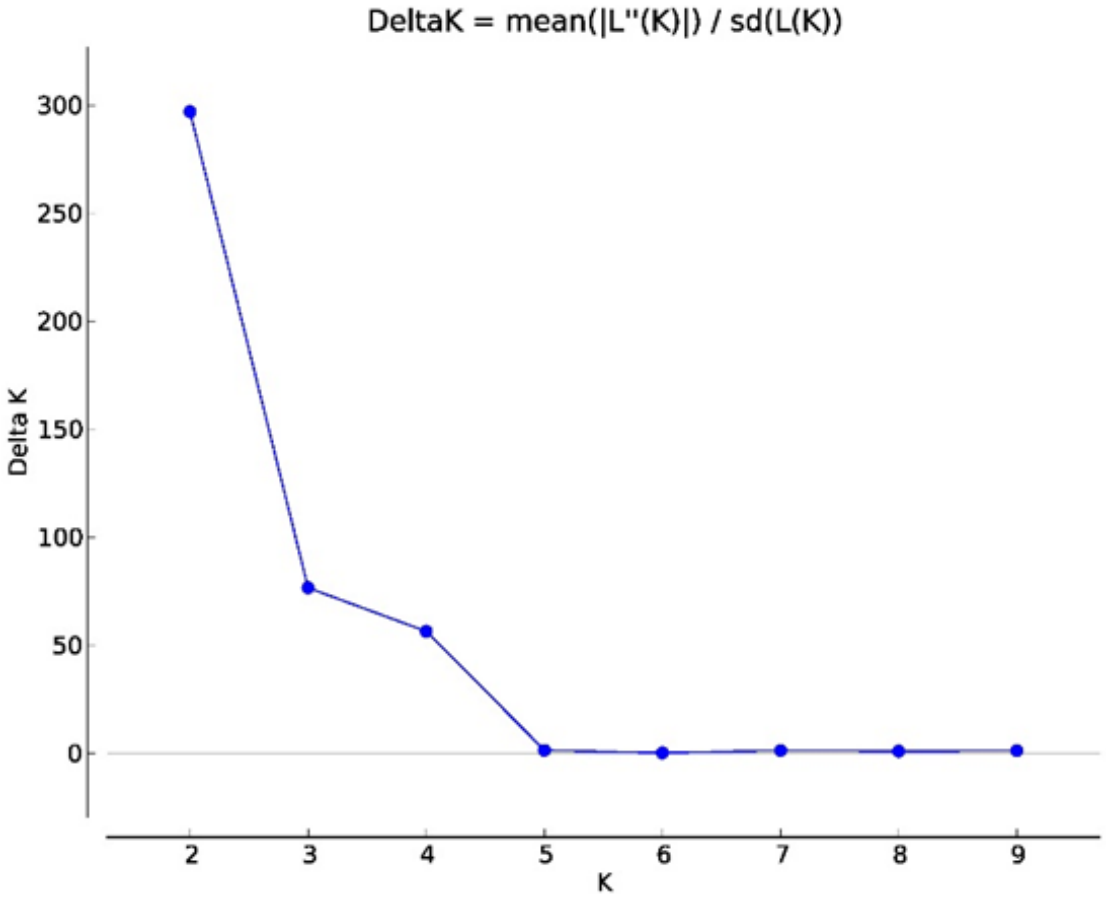

Figure 4. Number of *K* groups (true *K*) derived from 252 loci of 100 *Dyera polyphylla* individuals.

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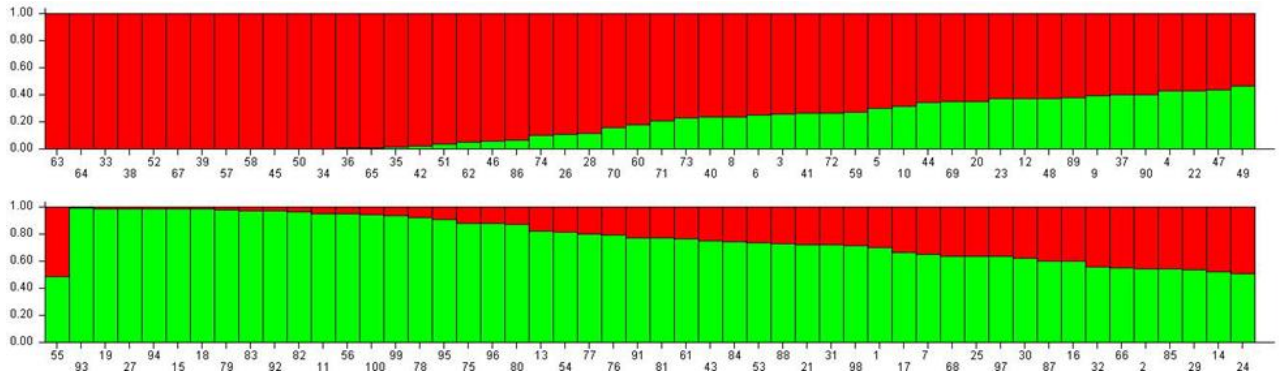

Figure 5. Inferred population structure of *Dyera polyphylla* based on 100 individuals and 252 loci. A key to the individual samples used in this analysis is provided in the Appendix.

DISCUSSION

Genetic diversity of *Dyera polyphylla* populations

Our results indicated (1) that there was no loss of genetic diversity when planted populations were compared to wild ones, (2) relatively low genetic variation among populations and (3) sufficient difference in signature between the Kalimantan and Sumatra populations to suggest that *D. polyphylla* seed sourced from Kalimantan was used to plant one of the Sumatran sites. No records of seed sources could be found to corroborate this finding.

The seven populations tested showed a high level of heterozygosity ($H = 0.29–0.38$). Similarly high levels of diversity were revealed by Wahyudiningsih *et al*. (2014), in five populations of *Dyera lowii* Hook.f. (synonym for *D. polyphylla*) from Central Kalimantan, and in the *Gonystylus bancanus* (Widyatmoko & Aprianto 2013) that occurs in the same ecosystem. Long-lived outcrossing tree species display high levels of diversity, which is believed to counter inbreeding (Hamrick *et al*. 1992, Muchugi *et al*. 2008). The genetic diversity of a species is related to its breeding system, pollination type (Hamrick & Godt 1996, Mijnsbrugge 2014), life history (Hamrick & Godt 1996, Chen *et al*. 2015), population size, distribution and selection pressure (Amos & Harwood 1998, Broadhurst & Boshier 2014). *D. polyphylla* is entomogamous, pollinated by e.g. insects (Willemstein 1987). Cross pollination within populations is likely within a distance range of 5–30 m (Barluenga *et al*. 2011), which is a common inter-tree distance at normal stand densities of 60 trees ha^{-1} (Tata *et al*. 2016). The seed of *D. polyphylla* is abundant and has wings, facilitating its dispersal by wind (Middleton 2007). Thus, seed dispersal distances may exceed dominant pollination distances. These factors may have led to the high diversity revealed within the seven *D. polyphylla* populations studied here. The high genetic diversity will ensure that seeds collected from these populations capture significant species diversity from within the peatland ecosystem. This is quite important in habitat restoration utilising long-lived species such as *D. polyphylla.*

The AMOVA indicated that most of the genetic variation of *D. polyphylla* is found within (91 %) rather than among populations (9 %), which means that many alleles are common among the populations and there are few rare alleles. Unless there are genetic barriers, most tropical tree species show low genetic variation partitioning among regions and populations (Muchugi *et al*. 2008, Widyatmoko & Aprianto 2013, Nurtjahjaningsih *et al*. 2015). The low genetic differentiation ($F_{ST} = 0.094$) further indicates the relative genetic homogeniety of these populations, which is in agreement with the observed genetic structuring.

The results of Principal Coordinates Analysis (PCoA) and STRUCTURE analysis showed that the clustering pattern is not associated with geographical distances, and are in agreement with the AMOVA results that show less genetic variation partitioning among the *D. polyphylla* populations. Genetic similarity among populations and among regions is usually related to absence of genetic or breeding barriers (Sreekanth *et al*. 2012). Separation of islands by water masses (geographical barriers) may result in high genetic differentiation. However, this was not observed in the populations studied. The common history of Sumatra and Kalimantan on the Sundaland plate may imply that these populations separated only after the last glacial period, some 10,000 years ago (Wurster & Bird 2016). The phenogram, PCoA and

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STRUCTURE analysis showed that there is a clear genetic distinction between the three wild populations (J-Senyerang-W, J-Rawasari-W, K-Tumbang-W). STRUCTURE analysis showed that the J-Senyerang-W population is quite distinct, implying that there is minimal gene flow from this population to the other two. The Senyerang population (in Tanjabar district) was located in the peat swamp along the Senyerang river, while the two populations in Tanjabtim district (Rawasari, Sungai) were found along the larger Batang Hari river. The habitat of *D. polyphylla* in Senyerang was a fragmented secondary peat swamp forest surrounded by complex agroforests, e.g. mixtures of rubber tree (*Hevea brassiliensis* Mull.Arg), coconut (*Cocos nucifera* L.), areca-nut (*Areca cathecu* Burm.f) and planted *D. polyphylla*, a plantation forest and smallholder oil palm plantations. Thus, the situation may have limited gene flow from the Senyerang population to the other two. It is important to establish whether this genetic distinction confers any adaptational advantage or disavantage to the J-Senyerang-W population. If there is an advantage, effort should be devoted to conserving its genetic identity.

The population of planted *D. polyphylla* at Bram Itam (J-Bram-P) resulted from peatland restoration initiated by the Forest District office of Tanjabar Jambi in 2005. It is interesting to note the genetic similarity of trees at Bram Itam (in Jambi) with the populations at Tumbang Nusa in Central Kalimantan (K-Tumbang-W and K-Tumbang-P). However, the PCoA and STRUCTURE clustering indicated that a few individuals may also have come from Senyerang (J-Senyerang-W). A remnant peat swamp forest was still present near the J-Bram-P restoration site in 2005. *D. polyphylla* seeds from a local seed supplier were insufficient for the restoration programme and seed had to be sourced from farther afield. According to a local forestry official, seedlings used for the reforestation programme at Bram Itam Peat Forest Reserve came from various seedling vendors without knowledge of their origin (Liyanto, Forest District Agency Tanjung Jabung Barat, Jambi; personal communication 2014). The seeds or seedlings may have been collected from Central Kalimantan province, which is known as a prominent *D. polyphylla* seedling source. Tree seed distribution in Indonesia has been documented by Roshetko *et al*. (2008); most of the seed is collected at a limited number of locations that are not selected for superior quality of provenances, but rather depend on the development of trade channel routes. Despite this, the planted populations assessed here showed high genetic diversity. Deliberate efforts to retain genetic diversity are a generic safeguard, whether the material planted is derived from seed, by vegetative propagation (Thomas *et al*. 2014, Zahawi & Holl 2014), or from wildings (Giasoddhin *et al*. 2014).

Implications for peatland restoration

The rehabilitation of peat swamp forests using native peatland tree species, also known as paludiculture (Wichtmann *et al*. 2016), as well as hydrological restoration, started some years ago in Indonesia (Bonn *et al*. 2016, Saito *et al*. 2016, Tata & Susmianto 2016), before the presidential regulation was launched in 2016. Our study included one site (J Bram-P) with successful peatland rehabilitation using *D. polyphylla*, planted as part of a peat swamp forest rehabilitation programme in 2005 by the Tanjabar Forest District office. Although the origin of the seedlings is unknown, this population has high genetic diversity ($H = 0.35$) and PPL = 96.81 %. Indeed, all of the populations that we studied showed high genetic diversity, which is an important factor in determining adaptability and survival of species facing habitat change and climate change (Ehlers *et al*. 2008, Dawson *et al*. 2011, Loo *et al*. 2015).

Seeds for peatland restoration programmes should come from local populations with high genetic variability (Broadhurst & Boshier 2014, Thomas *et al*. 2014). The use of seeds collected from a local population or close to the restoration site is expected to prevent any negative impact on intraspecific hybridisation that results in the suppression of outbreeding, and to help maintain biotic interaction with pollinators and pathogens (Broadhurst & Boshier 2014). The wild *D. polyphylla* populations in Senyerang, Rawa Sari and Tumbang Nusa (J-Senyerang-W, J-Rawasari-W, K-Tumbang-W) and a planted *D. polyphylla* population (J-Sungai-P1) have been used as mother trees and seed sources for seedlings grown in nurseries in the two provinces. For peatland restoration in Jambi, it is suggested that seed from Senyerang (J-Senyerang-W) and Sungai Aur (J-Sungai-P1) should be used; while for peatland restoration in Central Kalimantan, seed provenanced from the wild population at K-Tumbang-W is suggested because it has a high diversity estimate ($H = 0.35$). It has previously been recommended that the *D. polyphylla* population in Selat Nusa (Central Kalimantan), which has high allozyme variability ($He = 0.72$), should be conserved (Wahyudiningsih *et al*. 2014); this population can also be used as a seed source for restoration in Central Kalimantan.

Seed from the wild population at Rawa Sari (J-Rawasari-P) has been used for peatland rehabilitation in Sumatra. This may lead to loss of genetic diversity in planted stock because the Rawa

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Sari population displays only moderate genetic diversity ($H = 0.29$). The wild population in Rawasari is a fragmented secondary forest which is isolated owing to deforestation and uncontrolled fire in the surrounding areas. At this location, a strategy to improve gene flow through agroforestry and creation of a multifunctional landscape, as at Senyerang (J-Senyerang-W), is recommended. Various tree species in agroforestry systems can perform pivotal functions in conservation (Dawson *et al.* 2009, Lander & Boshier 2014).

Maintaining the high genetic diversity of *D. polyphylla* is a priority in the conservation and restoration of tropical peatlands. Considering that large degraded peatlands in Indonesia need to be restored, seed supplies should provide as much genetic diversity as possible. Using seed from small populations and those with low genetic variability will reduce genetic diversity (Broadhurst & Boshier 2014, Mijnsbrugge 2014). Therefore, in restoration, appropriate seed sourcing strategies are necessary. These may include: (i) composite provenancing, *i.e.* collecting a mixture of seeds that attempts to emulate natural gene-flow dynamics; and (ii) admixture provenancing, which involves collecting seeds from large populations only, but from various environments, and mixing them before sowing or planting out, which generates new populations with a variety of genotypes of wide provenance (Broadhurst & Boshier 2014).

CONCLUSION

Dyera polyphylla populations on peatland in Jambi and Central Kalimantan provinces showed high genetic diversity ($H = 0.29$–0.38). In both provinces, genetic diversity was as high in planted populations as in wild ones. Maintaining the genetic entity of the species in this ecosystem is an important consideration when establishing new populations. In peatland restoration, a seed source with high genetic diversity should be used, because the populations thus established may act as future seed sources.

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Appendix: Key to the individual samples used in the STRUCTURE analysis presented in Figure 5.

Number	Code of Individual
1	K-Tumbang-P.1
2	K-Tumbang-P.2
3	K-Tumbang-P.3
4	K-Tumbang-P.4
5	K-Tumbang-P.5
6	K-Tumbang-P.6
7	K-Tumbang-P.7
8	K-Tumbang-P.8
9	K-Tumbang-P.9
10	K-Tumbang-P.10
11	K-Tumbang-P.11
12	K-Tumbang-P.12
13	K-Tumbang-P.13
14	K-Tumbang-P.14
15	K-Tumbang-P.15
16	K-Tumbang-W.1
17	K-Tumbang-W.2
18	K-Tumbang-W.3
19	K-Tumbang-W.4
20	K-Tumbang-W.5
21	K-Tumbang-W.6
22	K-Tumbang-W.7
23	K-Tumbang-W.8
24	K-Tumbang-W.9
25	K-Tumbang-W.10
26	K-Tumbang-W.11
27	K-Tumbang-W.12
28	K-Tumbang-W.13
29	K-Tumbang-W.14
30	J-Rawasari-W.1
31	J-Rawasari-W.2
32	J-Rawasari-W.3
33	J-Rawasari-W.4
34	J-Rawasari-W.5
35	J-Rawasari-W.6

Number	Code of Individual
36	J-Rawasari-W.7
37	J-Rawasari-W.8
38	J-Rawasari-W.9
39	J-Rawasari-W.10
40	J-Rawasari-W.11
41	J-Rawasari-W.12
42	J-Sungai-P2.1
43	J-Sungai-P2.2
44	J-Sungai-P2.3
45	J-Sungai-P2.4
46	J-Sungai-P2.5
47	J-Sungai-P2.6
48	J-Sungai-P2.7
49	J-Sungai-P2.8
50	J-Sungai-P2.9
51	J-Sungai-P2.10
52	J-Sungai-P2.11
53	J-Sungai-P2.12
54	J-Sungai-P2.13
55	J-Sungai-P2.14
56	J-Sungai-P2.15
57	J-Sungai-P1.1
58	J-Sungai-P1.2
59	J-Sungai-P1.3
60	J-Sungai-P1.4
61	J-Sungai-P1.5
62	J-Sungai-P1.6
63	J-Sungai-P1.7
64	J-Sungai-P1.8
65	J-Sungai-P1.9
66	J-Sungai-P1.10
67	J-Sungai-P1.11
68	J-Sungai-P1.12
69	J-Sungai-P1.13
70	J-Sungai-P1.14
71	J-Sungai-P1.15

Number	Code of Individual
72	J-Bram-P.1
73	J-Bram-P.2
74	J-Bram-P.3
75	J-Bram-P.4
76	J-Bram-P.5
77	J-Bram-P.6
78	J-Bram-P.7
79	J-Bram-P.8
80	J-Bram-P.9
81	J-Bram-P.10
82	J-Bram-P.11
83	J-Bram-P.12
84	J-Bram-P.13
85	J-Bram-P.14
86	J-Bram-P.15
87	J-Bram-P.16
88	J-Bram-P.17
89	J-Bram-P.18
90	J-Bram-P.19
91	J-Bram-P.20
92	J-Senyerang.1
93	J-Senyerang.2
94	J-Senyerang.3
95	J-Senyerang.4
96	J-Senyerang.5
97	J-Senyerang.6
98	J-Senyerang.7
99	J-Senyerang.8
100	J-Senyerang.9

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