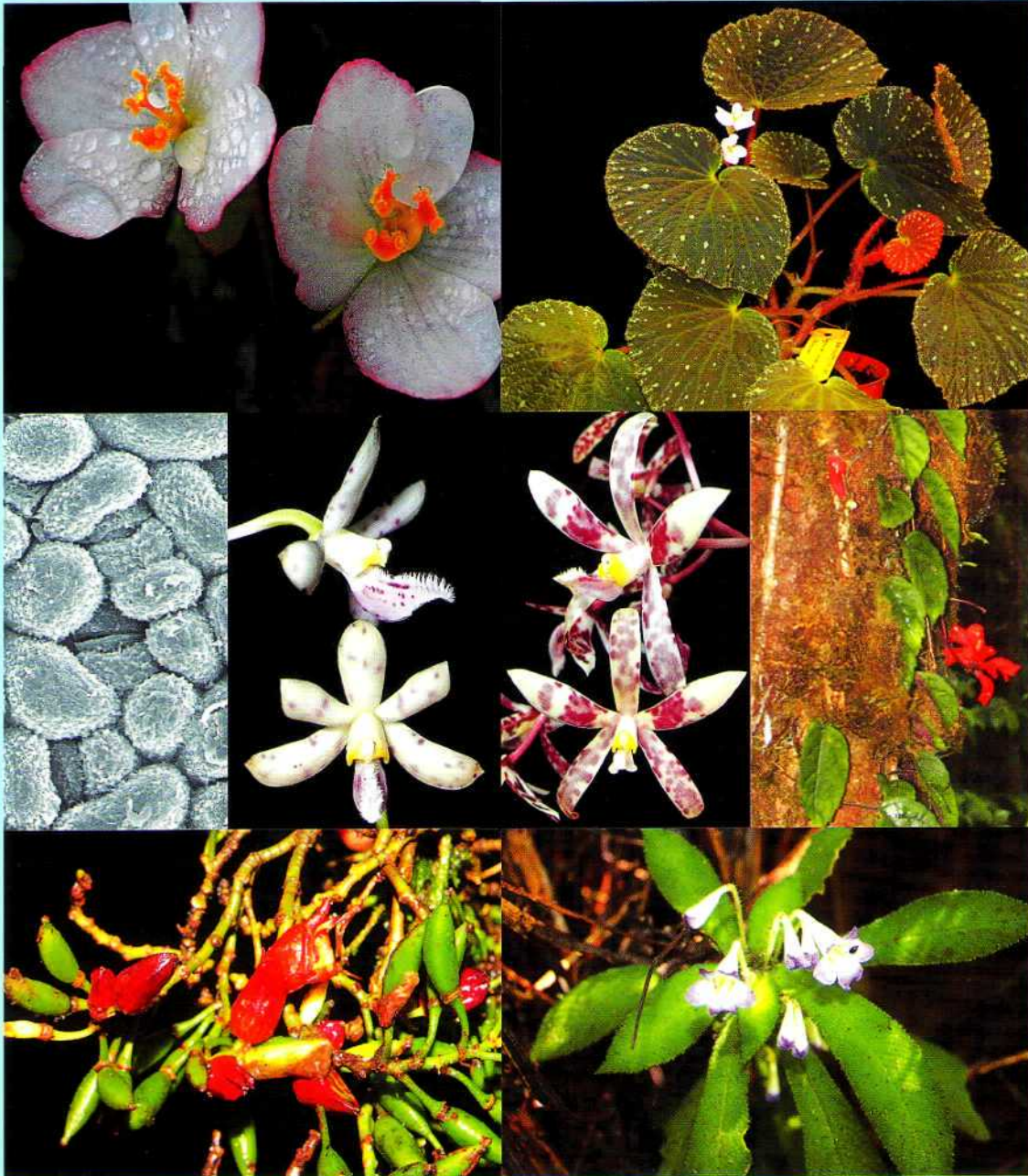




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HERBARIUM BOGORIENSE, BOTANY DIVISION,
RESEARCH CENTER FOR BIOLOGY- INDONESIAN INSTITUTE OF SCIENCES
CIBINONG SCIENCE CENTER, JLN. RAYA JAKARTA - BOGOR KM 46,
CIBINONG 16911, P.O. Box 25 Cibinong
INDONESIA
PHONE (+62) 21 8765066; Fax (+62) 21 8765062
E-MAIL: reinwardtia@mail.lipi.go.id

1	1
2	3 3 4
4	4

Cover images: 1. *Begonia holosericeoides* (female flower and habit) (Begoniaceae; Ardi *et al.*); 2. Abaxial cuticles of *Alseodaphne rhododendropsis* (Lauraceae; Nishida & van der Werff); 3. *Dipodium puspitae*, *Dipodium purpureum* (Orchidaceae; O'Byrne); 4. *Agalmyla exannulata*, *Cyrtandra coccinea* var. *celebica*, *Codonoboea kjellbergii* (Gesneriaceae; Kartonegoro & Potter).

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PHYLOGEOGRAPHIC STRUCTURE OF THE COMMERCIALLY IMPORTANT TROPICAL TREE SPECIES, *DRYOBALANOPS AROMATICA* GAERTN. F. (DIPTEROCARPACEAE) REVEALED BY MICROSATELLITE MARKERS

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FIFI GUS DWIYANTI

United Graduate School of Agricultural Sciences, Ehime University, 3-5-7 Tarumi, Matsuyama, Ehime 790-8566, Japan. E-mail: fifigusdwiyanti@yahoo.com

KOICHI KAMIYA

Forest Genetics Laboratory, Faculty of Agriculture, Ehime University, 3-5-7 Tarumi, Matsuyama, Ehime 790-8566, Japan. E-mail: kkamiya@agr.ehime-u.ac.jp

KO HARADA

Forest Genetics Laboratory, Faculty of Agriculture, Ehime University! 3-5-7 Tarumi, Matsuyama. Ehime 790-8566, Japan. E-mail: kharada@agr.ehime-u.ac.jp

ABSTRACT

DWIYANTI, F. G., KAMIYA, K. & HARADA, K. 2014. Phylogeographic structure of the commercially important tropical tree species *Dryobalanops aromatica* Gaertn. F. (Dipterocarpaceae) revealed by microsatellite markers. *Reinwardtia* 14(1): 43 - 51. — *Dryobalanops aromatica* Gaertn. F. (Kapur) is an economically important timber species in Southeast Asia that can serve as a good model for studying the impact of the Pleistocene glaciations on the genetic diversity and distribution of species in tropical regions. Seven polymorphic microsatellite markers were analyzed in five natural populations of *D. aromatica* ($N = 120$ individuals): Gunung Panti in Malay Peninsula, Lingga Island in Lingga Archipelago, Lambir Hills National Park, Limbang and Similajau National Park in Borneo. The level of gene diversity (H_E) for the five populations was relatively high with a range from 0.571 (Similajau) to 0.729 (Gunung Panti). The high genetic diversity in the present study could be attributed to the larger refugia population sizes of *D. aromatica* than that of other species. The population genetic structure revealed two distinct groups: the Malay Peninsula-Lingga Archipelago and Borneo. This pattern suggests that populations in each geographical area might be the consequence of post-glacial expansion from one or two refugia, but that gene flow between different glacial refugia was fairly restricted.

keywords: *Dryobalanops aromatica*, microsatellite, phylogeography, genetic diversity, genetic structure.

ABSTRAK

DWIYANTI, F. G., KAMIYA, K. & HARADA, K. 2014. Struktur filogeografi pohon komersial penting *Dryobalanops aromatica* Gaertn. F. (Dipterocarpaceae) dengan marka mikrosatelit. *Reinwardtia* 14(1): 43 - 51. — *Dryobalanops aromatica* Gaertn. F. (Kapur) merupakan jenis pohon penghasil kayu yang bernilai ekonomi penting di Asia Tenggara, yang mana dapat dijadikan model yang baik untuk mempelajari dampak Pleistosen glasiasi pada keragaman genetik dan distribusi spesies di daerah tropik. Tujuh penanda mikrosatelit dianalisis pada lima populasi alami *D. aromatica* ($N = 120$ individu): Gunung Panti di Semenanjung Malaysia, Pulau Lingga di Kepulauan Lingga, Taman Nasional Bukit Lambir, Limbang and Taman Nasional Similajau di Borneo. Tingkat keragaman genetik (H_E) untuk kelima populasi relatif tinggi, dengan selang dari 0.571 (Similajau) hingga 0.729 (Gunung Panti). Keragaman genetik yang tinggi pada studi ini dapat dihubungkan dengan ukuran populasi refugia yang lebih besar pada *D. aromatica* daripada spesies lain. Struktur genetika populasi menunjukkan dua kelompok yang berbeda: Semenanjung Malaysia-Kepulauan Lingga dan Borneo. Pola ini menunjukkan bahwa populasi pada masing-masing area geografik mungkin merupakan konsekuensi dari ekspansi postglasial dari satu atau dua refugia, namun aliran gen antara refugia yang satu dengan yang lainnya cukup terbatas.

Kata kunci: *Dryobalanops aromatica*, mikrosatelit, filogeografi, keragaman genetik, struktur genetik.

INTRODUCTION

The geographic area containing the Malay Peninsula, Sumatra, Java and Borneo is known as Sundaland and represents a globally important hot

spot of biodiversity (Sodhi *et al.*, 2004). It is renowned for its rich variety of plant species especially in lowland rainforests (Myers *et al.*, 2000; Mittermeier *et al.*, 2004; Sodhi *et al.*, 2004 and Ohtani *et al.*, 2013). The Pleistocene glacial

periods have been regarded as major factors influencing the geographical distribution, demographic dynamics, and pattern of genetic diversity of species (Comes & Kadereit, 1998; Haffer & Prance, 2001; Hewitt, 2004; Soltis *et al.*, 2006; Stewart *et al.*, 2010; Ramirez-Barahona & Eguiarte, 2013). However, little is known about the impact of Pleistocene glaciations on the genetic diversity and distribution of species in tropical and subtropical regions, especially in Sundaland area, even though the impact of glaciations in temperate zones has been the main focus of many phylogeographic studies (Cruzan & Templeton, 2000; Hewitt, 2000; Emerson & Hewitt, 2005).

Dryobalanops aromatica Gaertn. F., locally known as Kapur, can function as an ideal model species for studying the impact of glaciations in tropical regions, as the distribution of this species covers almost all of Sundaland. The species occurs naturally in the lowland mixed dipterocarp forests of Malaya, Sumatra, the Riau Archipelago and Borneo (Wood & Meijer, 1964; Ashton, 1964; Ashton, 1968; Symington, 2004), and is particularly abundant on deep humid yellow sandy soils with a propensity for ridges, at an altitudes below 400 m (Ashton, 2004). In the Malay Peninsula, the species is confined to the eastern side south of 5°N latitude *e.g.*, Johor, Pahang, Selangor and Terengganu (Symington, 2004; Chua *et al.*, 2010). In Sumatra, the species has been recorded from North West Sumatra (Angkola, Sibolga, Kelasan and Upper Singkil), East Sumatra (Bengkalis and Siak), Mursala, Lingga and Singkep Island (Ashton, 1982), while in Borneo it occurs in Sabah (Beaufort, Beluran, Kinabatangan, Labuan, Labuk Sugut, Papar, Penampang and Sipitang districts), Sarawak (Bintulu, Kapit, Lawas, Limbang, Marudi, Miri, Mukah and Tatau districts) and Brunei (Ashton, 2004; Chua *et al.*, 2010). The timber and the camphor harvested from this tree also give it economic value. The timber of the species is a moderately heavy and durable construction timber, while the camphor obtained from the wood attracted early Arab traders, at one time being worth more than its weight in gold in the Middle East and is used for incense and perfume (Ashton, 2004). However, the species has since 1998 been classified as 'critically endangered' (CR A1cd+2cd, B1+2c D c2.3) by the IUCN Red List of Threatened Species due to logging and camphor exploitation. Studies associated with this species are therefore of interest on several levels.

One of the methods available for inferring genetic diversification and biogeographical history

over the past several million years is analysis of molecular data of extant species based on nuclear microsatellites. Microsatellites as a class feature a variable number of tandem repeats with a repeat unit of new nucleotides and have been used as genetic markers. Because of their high mutation rates, microsatellite markers are especially useful in detecting recent evolutionary events such as expansion and migration after the last glacial maximum (LGM) about 20,000 years ago (Jeffreys *et al.*, 1985).

Phylogeographical studies using microsatellite on tropical tree species from Sundaland area are very scarce and limited, instead many studies using nuclear genes and chloroplast intergenic spacers or introns, such as in *Shorea curtisii* (Kamiya *et al.*, 2012), *Shorea parvifolia* (Iwanaga *et al.*, 2012), and *Shorea leprosula* (Ohtani *et al.*, 2013). Those studies detected two major genetically different groups of Sundaland populations: Sumatra-Malay and Borneo and suggested the presence of a scarcely forested land bridge on the Sunda Shelf during glacial periods in the Pleistocene and predominance of tropical lowland rainforest at least in Sumatra and eastern Borneo. Based on these results, we wanted to test whether this pattern also occurs in *D. aromatica* populations. Therefore, the objective of this study was to estimate the level of genetic diversity and to reveal phylogeographical relationships in five *D. aromatica* populations using microsatellite markers.

MATERIALS AND METHODS

Plant materials

Leaf tissue of adult trees or saplings was collected from five natural populations representing three geographical regions covering most of the natural distribution range of the species except for the Sumatra mainland: Gunung Panti (1.8344° N, 103.9005° E) in Malay Peninsula, Lingga Island (0.1607° S, 104.5855° E) in Lingga Archipelago, Lambir Hills National Park (4.1983° N, 114.0427° E), Limbang (4.7544° N, 115.0075° E) and Similajau National Park (3.5172° N, 113.3414° E) in Borneo (Fig. 1). A total of 120 individuals of *D. aromatica* was used in this study. Plant materials were dried in the field with silica gel and stored in a freezer at -80°C. They were subsequently used for DNA extraction.

Microsatellite genotyping

Silica gel-dried leaves were ground to a fine powder using a TissueLyser II (QIAGEN Japan, Tokyo). Total genomic DNA was extracted from

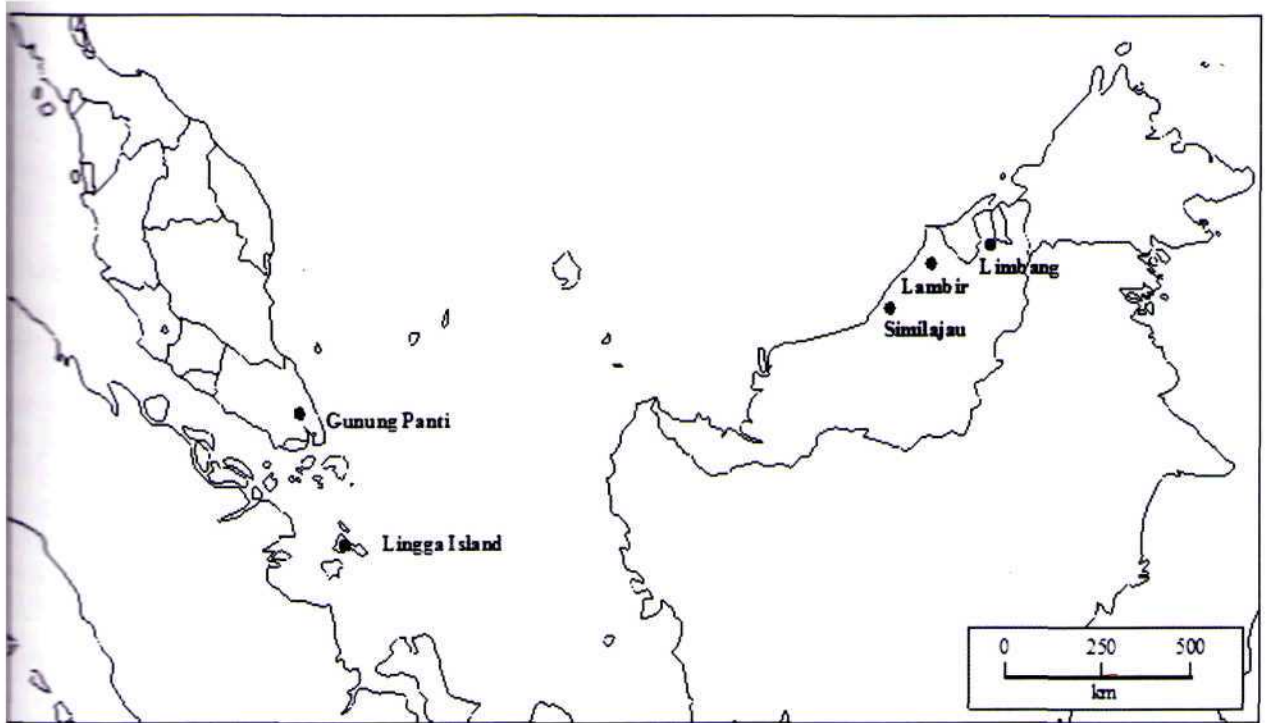
Fig. 1. Sampling location of *D. aromatica*

Table 1. Primer information for seven microsatellite loci used in this study

Locus	Primer sequence (5'-3')	Size (bp)	Annealing temperature (°C)
Dra187	F: TCTCTCTTATCCAACCTCTCTCA R: AGGGAACATAAAGCAGACATCAC	102-160	57
Dra266	F: AGACTTAATAATGGAGGACGAG R: CCACAATTAGCCACCATCTTAC	115-165	54
Dra426	F: CCAACGCTGCTCAAAGTTTCGTG R: GCTGGCTGGCATAATATAATCC	224-244	57
Dra428	F: CTATTGATGCCCTTATAGCTTT R: ACGAGCCTCTCTACTCTATAAT	265-303	57
Dra471	F: TCTCAGTCTCACAATCTATCCA R: TTTCTGTGTCATTTTAGCAACC	220-248	54
Dra519	F: TCAAGCCAGAAGAGATAGAGAC R: ATATTCCTTTTCATATTATTGGG	185-219	57
Dra569	F: GTAAAACCAATACACGTACATA R: ATGGAAGTCATTTTCATCTATTT	221-247	54

each sampled tree using the modified CTAB method (Doyle & Doyle, 1990). Seven microsatellite loci (Dra187, Dra428, Dra426, Dra519, Dra266, Dra471 and Dra569) developed for *D. aromatica* by Nanami *et al.* (2007) were used in this study. The forward primer of each marker was labeled with 6-FAM, VIC, NED, or PET phosphoramidite (Applied Biosystems Japan, Tokyo). Details of the markers used in this study are shown in Table 1.

A Type-it Microsatellite PCR kit (QIAGEN) was used to amplify microsatellite loci. Multiplex PCR amplification was performed in a volume of

5 μ l, containing 1 x Type-it Multiplex PCR Master mix, 0.2 (μ M) of forward and reverse primers and about 40 ng genomic DNA. An Applied Biosystems 2720 thermal cycler (Applied Biosystems) was used under the following conditions: initial denaturation at 95°C for 5 min, then 31 cycles of denaturation at 95°C for 30 s, annealing for 1 min 30 s and extension at 72°C for 30 s, followed by a final incubation at 60°C for 30 min. Annealing temperatures were 57°C for Dra187, Dra428, Dra426 and Dra519, and 54°C for Dra266, Dra471 and Dra569. Fragment sizes were determined using an ABI PRISM™ 310 Genetic Analyzer

Table 2. Genetic diversity of microsatellite loci in five populations of *D. aromatica*

Island name	Population	<i>N</i>	<i>N_a</i>	<i>N_e</i>	<i>H_o</i>	<i>H_E</i>	<i>F</i>
Malay Peninsula	Gunung Pant	20	6.86	4.27	0.521	0.729	0.289***
Lingga Archipelago Borneo	Lingga Island	13	7.14	3.72	0.681	0.689	0.007ns
	Similajau	32	5.29	2.62	0.616	0.571	-0.084***
	Limbang	27	8.43	3.52	0.503	0.575	0.192***
	Lambir	28	7.86	3.38	0.587	0.623	0.032***
Total		120					
Grand Mean		24	7.11	3.50	0.582	0.637	0.087

Number of samples (*N*), mean number of alleles per population (*N_a*), mean number of effective alleles (*N_e*), mean observed heterozygosity (*H_o*), Nei's mean expected heterozygosity (*H_E*), fixation index (*F*) with the significance level for deviation from the Hardy-Weinberg Equilibrium (HWE): *P* < 0.001 (***), not significant (ns).

Table 3. Pairwise *F_{ST}* values for five populations of *D. aromatica* with the significance level of population differentiation after Bonferroni correction

Population	Lambir	Limbang	Similajau	Gunung Pant	Lingga Island
Lambir	-				
Limbang	-0.01289 ns	-			
Similajau	0.09347***	0.12556***	-		
Gunung Pant	0.22536 ***	0.25598 ***	0.21946 ***	-	
Lingga Island	0.17874***	0.20128***	0.21273***	0.01111ns	-

P < 0.001 (***), not significant (ns).

(Applied Biosystems) and visualized using GeneMapper 3.0 software (Applied Biosystems).

Data analysis

Basic statistics of genetic diversity, including number of alleles per locus (*N_a*), observed heterozygosity (*H_o*), expected heterozygosity (*H_E*) and fixation index (*F*), were calculated using GenAlEx software version 6.41 (Peakall & Smouse, 2006). Deviations from Hardy-Weinberg (HW) equilibrium were tested for each locus in each population using GENEPOP 4.0.10 (Raymond & Rousset, 1995; Rousset, 2008). Pairwise *F_{ST}* was calculated to determine the level of population differentiation using the program ARLEQUIN Version 3.5.1.2 (Excoffier & Lischer, 2010).

An analysis of molecular variance (AMOVA) was carried out using ARLEQUIN version 3.5.1.2 (Excoffier & Lischer, 2010) to apportion variance

within populations, among populations within groups, and among groups. Populations were grouped into three island groups for the analysis, *i.e.* Malay Peninsula, Lingga Archipelago and Borneo (Table 2). Genetic distances between populations were estimated using the Nei genetic distance, *D* (Nei *et al.*, 1983), as implemented in GenAlEx version 6.41 (Peakall & Smouse, 2006). The resulting distance matrix was used to construct a neighbor-joining (NJ) phenogram using MEGA Version 3.1 (Kumar *et al.*, 2004).

STRUCTURE version 2.3.4 (Pritchard *et al.*, 2000) was used to estimate the number of genetically homogeneous populations (*K*) using a Bayesian model-based clustering method. A burn-in of 50,000 iterations was performed followed by 500,000 iterations of MCMC (Markov chain Monte Carlo) simulation. The model was run for a range of *K*-values from 1 to 7, with ten replications each. The best *K*-value supported by the data

was assessed according to the recommendations of Evanno *et al.* (2005), whereby the statistic AK was calculated based on the rate of change in the log likelihood of the data between successive K -values using STRUCTURE HARVESTER (Earl & von Holdt, 2012).

RESULTS

Genetic diversity and fixation index

The mean number of alleles per locus (N_a) across seven microsatellite loci ranged from 5.29 in Similajau to 8.43 in Limbang (Table 2). Observed heterozygosity (H_o) was highest in Lingga Island with a value of 0.681 and lowest in Limbang with a value of 0.503. Expected heterozygosity (H_E) ranged from 0.571 in Similajau to 0.729 in Gunung Panti with a mean value of 0.637 (Table 2).

The fixation index [F] ranged from $F = -0.084$ in the Similajau population to $F = 0.289$ in the Gunung Panti population. Significant departures from Hardy-Weinberg equilibrium were observed in all the populations, except the Lingga Island population. F was significantly negative in the Similajau population, but it was positive in the Gunung Panti population. The negative fixation index value for the Similajau population was significantly smaller than zero and showed an excess of heterozygotes, while the high fixation index value in Gunung Panti was significantly larger than zero and showed an excess of homozygotes (Table 2).

Genetic structure

Pairwise F_{ST} values (Table 3) ranged from -0.01289 (Limbang vs Lambir) to 0.21946 (Gunung Panti vs Similajau). Significant genetic differentiation was found in 8 out of 10 population pairs after a Bonferroni correction was applied. No genetic differentiations were observed between Lingga Island and Gunung Panti and between Limbang and Lambir.

The AMOVA revealed that 62.97% of the total molecular variance was within individuals (Table 4). 4.44% was attributed to among-populations differences within groups and 16.84% to among-groups differences. The remainder (15.75%) applied among individuals within populations. A NJ phenogram (Fig. 2) shows that relationships among the five populations agree well with geographic distribution.

The Structure analysis revealed the presence of distinct clustering in the five *D. aromatica* populations. The value of AK was highest when $K = 3$.

The populations can therefore be characterized by the following three clusters: the Limbang and Lambir populations mainly composed of cluster 1, the Similajau population mainly composed of cluster 2, and the Gunung Panti and Lingga Island populations mainly made up cluster 3 (Fig. 3).

DISCUSSION

Population genetic diversity

The levels of genetic diversity ($H_E = 0.571-0.729$) estimated for *D. aromatica* in this study were higher than for other dipterocarp species in Asian rain forests such as *Shorea javanica* (Rachmat *et al.*, 2012) and *S. leprosula* (Ohtani *et al.*, 2013), but comparable with *S. lumutensis* (Lee *et al.*, 2006), *Vateriopsis seychellarum* (Finger *et al.*, 2012), and *S. obtusa* (Senakun *et al.*, 2011). At face value, the genetic diversity value in Bornean populations was slightly lower than that of the Malay Peninsula and Lingga Archipelago. Similarly, the diversity value based on microsatellite markers ($H_E = 0.709$) reported by Lim *et al.* (2002) in *D. aromatica* in the Malay Peninsula region was higher than that reported by Harata *et al.* (2012) in Lambir, Borneo ($H_E = 0.589$). The high genetic diversity in the present study could be attributed to the larger refugia population sizes of *D. aromatica* than that of other species. High levels of genetic diversity may also be associated with population history, reproductive strategy and life history of the species, which have maintained a larger effective population size (Lee *et al.*, 2000 ; Lim *et al.*, 2002).

Three of five populations showed a significantly positive inbreeding coefficients (Table 2). The positive values could be attributed in part to the presence of null alleles, or inbreeding between relatives (biparental inbreeding), restricted seed and moderate pollen dispersal, or a Wahlund effect due to two or more breeding subunits inside a given population (Papi *et al.*, 2012). Lim *et al.* (2002) reported that the high fixation indices detected in *D. aromatica* populations in the Malay Peninsula, could be explained by a Wahlund effect. It is possible that all populations in the Peninsular Malaysia originated from one large population, which later sub-divided into several sub-populations. Since no evidence of Wahlund effect and no calculation of the null allele were in the present study, biparental inbreeding in *D. aromatica* could be regarded as a possible reason for the high fixation index in Gunung Panti population (Malay Peninsula).

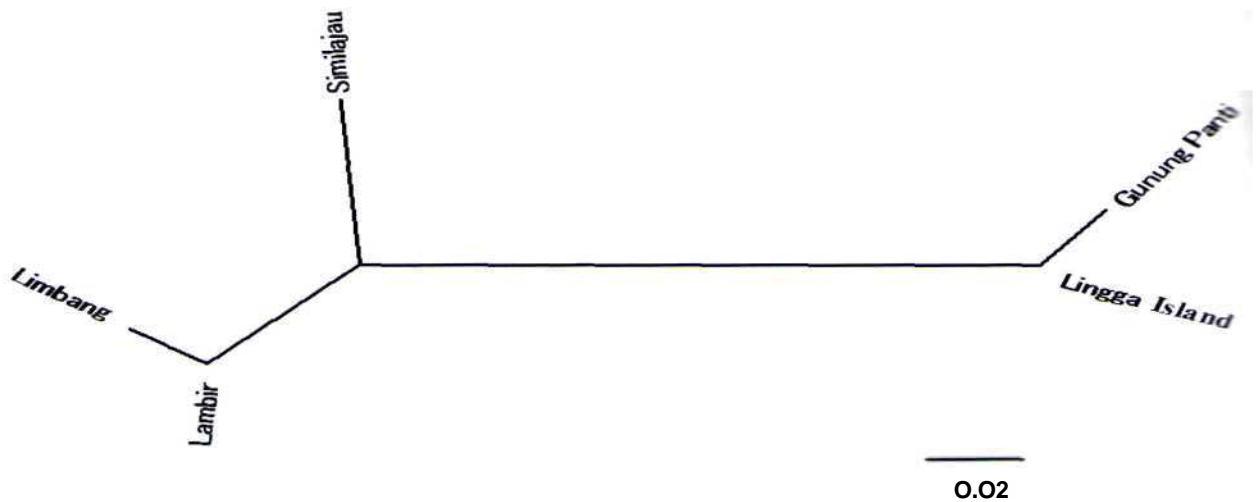


Fig. 2. Neighbor-joining (NJ) phenogram based on pairwise F_{ST} among the investigated *D. aromatica* populations

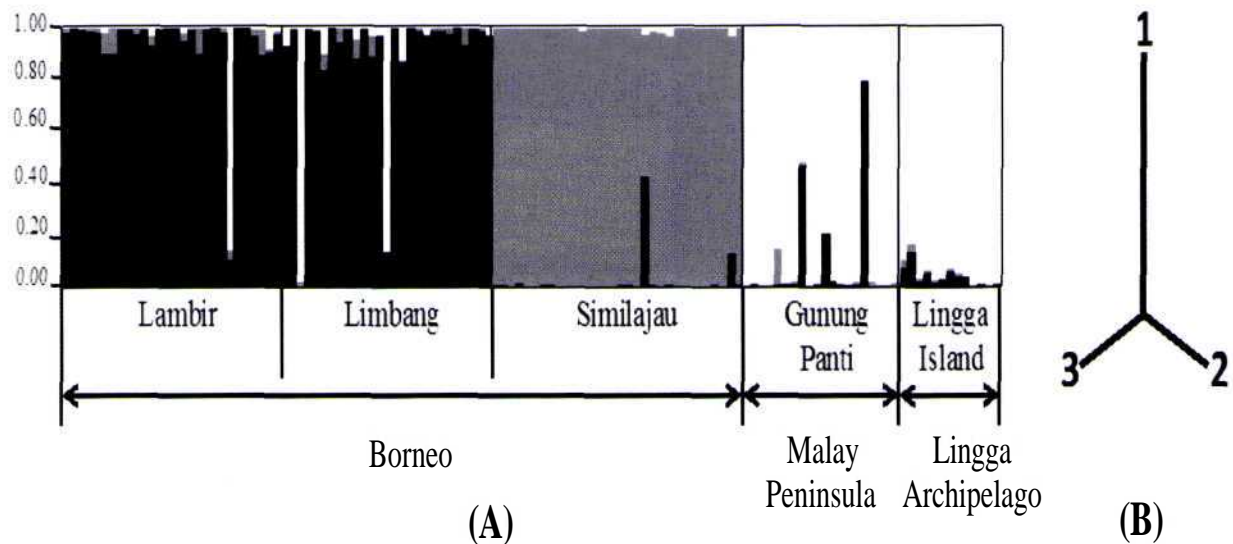


Fig. 3. Bayesian clustering analysis of five populations of *D. aromatica* using STRUCTURE ($K=3$). (A) Bar plot for each individual showing three clusters: cluster 1 composed of Lambir and Limbang (black), cluster 2 composed of Similajau (gray) and cluster 3 composed of Gunung Pantii and Lingga Island (white). (B) Tree Plot showing a representation of the genetic distance among those 3 clusters. "1" represents the black bars (cluster 1), "2" gray bars (cluster 2) and "3" white bars (cluster 3).

Phylogeographic structure

The phylogeographic structure of *D. aromatica* was estimated by calculating the level of population differentiation. It was found that the level of genetic differentiation increased with geographic distances. Significant pairwise values were mostly found for populations from different islands. For example, a low level of genetic differentiation was detected between the Malay Peninsula and Lingga Archipelago populations and also among populations within the Borneo region, while a high level of genetic differentiation was detected between the Malay Peninsula/Lingga Archipelago population and Borneo populations. At the Last Glacial maxi-

mum (LGM; approximately 0.02 MYA), Peninsular Malaysia, Sumatra, Java and Borneo Islands were connected by the exposed Sunda Shelf (Voris, 2000) and at this period, some studies suggested a savanna corridor across the Sunda shelf separated rainforest of Sumatra-Malay area and Borneo (Kaars, 1991; Kaars & Dam, 1995; Bird *et al.*, 2005). Thus, the present study suggests that populations in each geographical area might be the consequence of post-glacial expansion from one or two refugia, but that gene flow between different glacial refugia was fairly restricted. This suggestion is also supported by Iwanaga *et al.* (2012) who reported a very low

migration rate in *S. parvifolia* population after divergence of the Sumatra-Malay and Borneo imply that contacts of the Sumatra-Malay and Borneo population were limited. Therefore, when Sunda Shelf was exposed, the expanding savanna must have been strong but imperfect barrier to gene flow between Sumatra-Malay and Borneo.

The genetic differentiation patterns observed in the present study are also evident in the result of the STRUCTURE analysis and the neighbour-joining (NJ) phenogram. Both results show different patterns of *D. aromatica* genetic structure at the cluster level. STRUCTURE analysis divides the structure of *D. aromatica* populations into three clusters: Limbang-Lambir, Similajau and Gunung Panti-Lingga Island, while the NJ tree shows two distinct groups: the Malay Peninsula-Lingga Archipelago and Borneo populations. At the subcluster level however, both approaches show the same patterns: Lambir-Limbang, Similajau and Gunung Panti-Lingga Island (Fig. 2).

The clear distinction between the Malay Peninsula and Borneo populations observed in the present study was also found in *S. curtisii* by Kamiya *et al.* (2012), where it was reported that long-term population persistence with limited seed dispersal and low levels of gene flow may act as a driving force of divergence between the Malay Peninsula and Borneo populations. A Study of population structure in *S. parvifolia* (Iwanaga *et al.*, 2012) also suggests that the clear separation of the two groups was due to limited genomic exchanges between the two groups and that reproductive isolation has developed between them. In a study of phylogeography of *S. leprosula*, Ohtani *et al.* (2013) reported the presence of a longitudinal genetic cline both within the Malay/ Sumatra population group and the Borneo group, indicating that the genetic structures in Sumatra and the Malay Peninsula are not independent from each other due to long-term land connections between Sumatra and the Malay Peninsula across the shallow Strait of Malacca during glacial periods (current average depth about 25 m). Our result gives an additional support for the inference of non-forested land bridge at LGM between Sumatra-Malay Peninsula and Borneo.

CONCLUSION

The high genetic diversity in the present study could be attributed to the larger refugia population sizes of *D. aromatica* than that of other species. The phylogeographic structure revealed two distinct groups: the Malay Peninsula-Lingga

Archipelago and Borneo. This pattern suggests that populations in each geographical area might be the consequence of post-glacial expansion from one or two refugia, but that gene flow between different glacial refugia was fairly restricted. The present study gives an additional support for inference of non-forested land bridge at LGM between Sumatra-Malay Peninsula and Borneo.

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Address: Jin. Raya Jakarta-Bogor Km. 46 Cibinong 16911, P.O. Box 25 Cibinong

Telp. (+ 62) 21 8765066; Fax (+62) 21 8765062

E-mail: reinwardtia@mail.lipi.go.id

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MUHAMMAD EFFENDI, TATIK CHIKMAWATI & DEDY DARNAEDI. New cytotypes of <i>Pteris ensiformis</i> var. <i>victoria</i> from Indonesia.....	133
SUZANA SABRAN, REUBEN NILUS, JOAN T. PEREIRA & JOHN BAPTIST SUGAU. Contribution of the heart of Borneo (HoB) initiative towards botanical exploration in Sabah, Malaysia.....	137
WENNI SETYO LESTARI, BAYU ADJIE, TASSANAI JARUWATANAPHAN, YASUYUKI WATANO & MADE PHARMAWATI. Molecular phylogeny of maidenhair fern genus <i>Adiantum</i> (Pteridaceae) from Lesser Sunda Islands, Indonesia based on <i>Rbcl</i> and <i>Trnl-f</i>	143
ELIZABETH A. WIDJAJA & DANIEL POTTER. Floristic study of Mekongga Protected Forest: towards establishment of the Mekongga National Park.....	157
YESSI SANTIKA, EKA FATMAWATI TIHURUA & TEGUH TRIONO. Comparative leaves anatomy of <i>Pandanus</i> , <i>Freycinetia</i> and <i>Sararanga</i> (Pandanaceae) and their diagnostic value.....	163
SUHARDJONO PRAWIROATMODJO & KUSWATA KARTAWINATA. Floristic diversity and structural characteristics of mangrove forest of Raj a Ampat, West Papua, Indonesia.....	171
IAN M. TURNER. A new combination in <i>Orophea</i> (Annonaceae) for <i>Uvaria nitida</i> Roxb. ex G. Don.....	181
IVAN S AVINOV. Taxonomic revision of Asian genus <i>Glyptopetalum</i> Thwaites (Celastraceae R. Br.).....	183
YUSI ROSALINA, NISYAWATI ERWIN NURDIN, JATNA SUPRIATNA & KUSWATA KARTAWINATA. Floristic composition and structure of a peat swamp forest in the conservation area of the PT National Sago Prima, Selat Panjang, Riau, Indonesia.....	193
IMAN HID AY AT & JAMJAN MEEBOON. <i>Cercospora brunfelsiicola</i> (Fungi, Mycosphaerellaceae), a new tropical Cercosporoid fungus on <i>Brunfelsia uniflora</i>	211
MAX VAN BALGOOY & ELIZABETH A. WIDJAJA. Flora of Bali: a provisional checklist.....	219
EKA FATMAWATI TIHURUA & INA ERLINAWATI. Leaf anatomy of <i>Pandanus</i> spp. (Pandanaceae) from Sebangau and Bukit Baka-Bukit Raya National Park, Kalimantan, Indonesia.....	223
JULIA SANG & RUTH KIEW. Diversity of <i>Begonia</i> (Begoniaceae) in Borneo - How many species are there?.....	23 3
DIAN LATIFAH, ROBERT A. CONGDON & JOSEPH A. HOLTUM. A Physiological approach to conservation of four palm species: <i>Arenga australasica</i> , <i>Calamus australis</i> , <i>Hydriastele wendlandiana</i> sa <i>Alicuala ramsayi</i>	237

REINWARDTIA
Vol. 14. No. 1.2014
CONTENTS
Page

ABDULROKHMAN KARTONEGORO & DANIEL POTTER. The Gesneriaceae of Sulawesi VI: the species from Mekongga Mts. with a new species of <i>Cyrtandra</i> described.....	1
LIM CHUNG LU & RUTH KIEW. <i>Codonoboea</i> (Gesneriaceae) sections in Peninsular Malaysia.....	13
WISNU H. ARDI, YAYAN W. C. KUSUMA, CARL E. LEWIS, ROSNIATI A. RISNA, HARRY WIRIADINATA, MELISSA E. ABDO & DANIEL C. THOMAS. Studies on <i>Begonia</i> (Begoniaceae) of the Molucca Islands I: Two new species from Halmahera, Indonesia, and an updated description of <i>Begonia holosericea</i>	19
YUZAMMI, JOKO R. WITONO & WILBERT L. A. HETTERSCHIED. Conservation status of <i>Amorphophallus discophorus</i> Backer & Alderw. (Araceae) in Java, Indonesia.....	27
MOHAMMAD F. ROYYANI & JOENI S. RAHAJOE. Behind the sacred tree: local people and their natural resources sustainability.....	35
FIFI GUS DWIYANTI, KOICHI KAMIYA & KO HARADA. Phylogeographic structure of the commercially important tropical tree species, <i>Dryobalanops aromatica</i> Gaertn. F. (Dipterocarpaceae) revealed by microsatellite markers.....	43
SACHIKO NISHIDA & HENK VAN DER WERFF. Do cuticle characters support the recognition of <i>Alseodaphne</i> , <i>Nothaphoebe</i> and <i>Dehaasia</i> as distinct genera?.....	53
NURUL AMAL LATIFF, RAHAYU SUKMARIA SUKRI & FAIZAH METALI. <i>Nepenthes</i> diversity and abundance in five habitats in Brunei Damssalam.....	67
NURUL HAZLINA ZATNI & RAHAYU SUKMARIA SUKRI. The diversity and abundance of ground herbs in lowland mixed Dipterocarp forest and heath forest in Brunei Darussalam.....	73
MUHAMMAD AMIRUL AIMAN AHMAD JUHARI, NORATNI TALIP, CHE NURUL ATNI CHE AMRI & MOHAMAD RUZI ABDUL RAHMAN. Trichomes morphology of petals in some species of Acanthaceae.....	79
DIAN ROSLEINE, EIZI SUZUKI, ATIH SUNDAWIATI, WARDI SEPTIANA & DESY EKAWATI. The effect of land use history on natural forest rehabilitation at corridor area of Gunung Halimun Salak National Park, West Java, Indonesia.....	85
JULIUS KULIP. The Ethnobotany of the Dusun people in Tikolod village, Tambunan district, Sabah, Malaysia.....	101
PETER O'BYRNE. On the evolution of <i>Dipodium R. Br.</i>	123

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