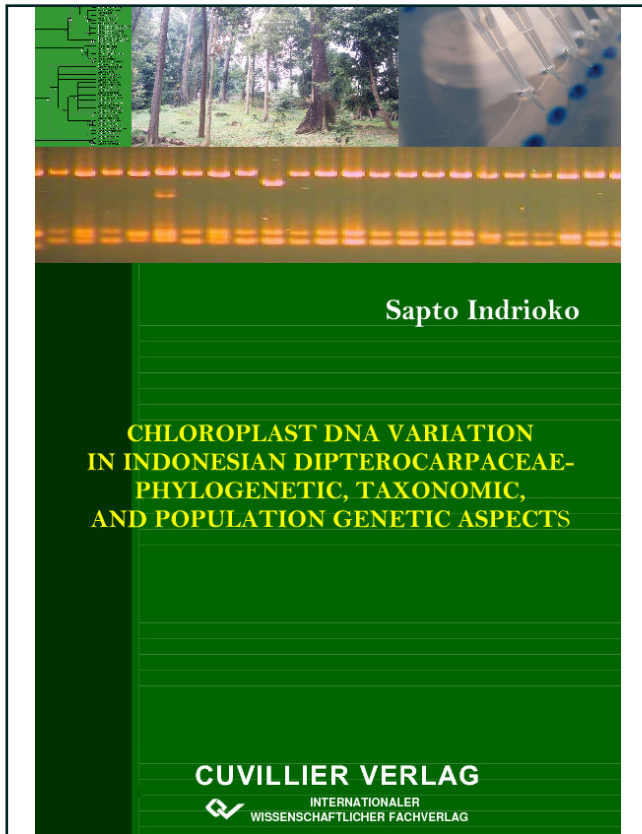




Sapto Indrioko (Autor)

Chloroplast DNA variation in Indonesian dipterocarpaceae-phylogenetic, taxonomic, and population genetic aspects



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1. INTRODUCTION

1.1. Family Dipterocarpaceae

1.1.1. Taxonomy

The placement of family Dipterocarpaceae has been adjusted several times. First, Dipterocarpaceae was grouped in the order Ochnales, then it was moved to the order Theales, and finally to the order Malvales (MAURY-LECHON and CURTET, 1998; APG; 2003).

ASHTON (1982), LONDOÑO (1995), MAGUIRE and ASHTON (1977), VERCOURT (1989) and VILLIERS (1991) described the taxonomical characters of Dipterocarpaceae as follows: **habitus** small or large resinous usually evergreen trees, usually buttressed; **leaves** alternate, simple, margin entire or sinuate, not crenate, terminating ± abruptly at the ± prominent geniculate petiole, penninerved, often with domatia in axils between nerves and midrib or along midrib and (rarely) nerves; tertiary nerves scalariform or reticulate; **stipules** paired, large or small, persistent or fugaceous, leaving small to amplexicaul scars; **inflorescence** paniculate, racemose, rarely cymose, ± regularly, rarely irregularly, branched, terminal or axillary; **bracts** and **bracteoles** paired, small or large, persistent or fugaceous; **flowers** secund or distichous, bisexual, actinomorphic, scented, nodding; **calyx** persistent, five-merous; two to five sepals usually greatly enlarging into wing-like lobes in fruit; **sepals** either free to base, imbricate in bud, remaining so or becoming valvate in fruit, or fused at base, forming a cup or tube ± enclosing the fruit, adnate to or free from it; **corolla** five-merous, contorted, base connate or free, usually partially or entirely unicellular hairy; **stamens** five to 110, one to three verticillate or irregular, hypogynous or subperigynous, centrifugal; **filaments** compressed or filiform, free or connate, frequently cohering with petals on falling; **anthers** erect, two-celled with (two to) four pollen sacs, introrse or laterally dehiscent; tapetal cells binucleate, pollen grains two-celled at anthesis; connective with short or prominent appendage; **ovary** superior or semi-inferior, three-, rarely two-locular; **style** ± thickened at base into a stylopodium, entire or trifid towards apex; **stigma** obscure or prominent, three- or six-lobed; ovules two (to three) in each loculus, axile, pendulous, or laterally anatropous, bitegmatic with ventral raphe and superior micropyle; **fruit** indehiscent, one-seeded; with woody pericarp and persistent ± aliform sepals; embryonic-sac development of **polygonum** type: endosperm of the nuclear type, embryo development normal, ripe seeds with or more usually without endosperm; cotyledons equal or more usually unequal and with one or more

or less enclosing the other, laminar or fleshy, entire or lobed, enclosing the radical; **germination** epigeal or hypogeal; pericarp splitting irregularly or along three sutures.

The family Dipterocarpaceae consists of three subfamilies: Dipterocarpoideae (13 genera, c. 470 spp.) from the Seychelles, Sri Lanka and India northeastwards to southern China and the Batan Islands, and southeastwards to New Guinea and D'Entrecasteaux Island; Monotoideae (three genera, c. 40 spp.) in Africa and South America; Pakaramoideae (one genus, one species) confined to South America (ASHTON, 1982; BANCROFT, 1935; MAURY-LECHON and CURTET, 1998). Based on the observation on Asian dipterocarp species, HALLÉ (1979) found three main architecture models of Dipterocarpaceae, i.e. Roux as the frequent model (*Anisoptera*, *Balanocarpus*, *Hopea*, *Shorea*, *Upuna*, *Vatica*), Rauh (*Dipterocarpus*, *Cotylelobium*), and Massart (*Shorea*, *Dipterocarpus*). Roux's model is characterized by continuous growth of the stem with plagiotrophic branches, while Massart's has rhythmic growth of the stem with plagiotrophic branches, and Rauh's also has rhythmic growth of the stem but with orthotrophic branches (HALLÉ *et al.*, 1978). An African dipterocarp, namely *Monotes kerstingii*, fits Troll's model which does not exist among Asiatic dipterocarps (HALLÉ and NG, 1981). The basic chromosom number of Dipterocarpoideae is $x=11$ in Tribe Dipterocarpeae and $x=7$ in Tribe Shoreae (ASHTON, 1982; JONG and KAUR, 1979; SOMEGO, 1978).

The natural distribution of Dipterocarpaceae in Indonesia comprises (see Figure 1):

- Kalimantan (including insular Malaysia and Brunei Darussalam), with a total of nine genera (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea*, *Vatica*, and *Upuna*), consisting of 267 (ASHTON, 1982) to 274 species (NEWMAN, *et al.*, 1996a, 1998a).
- Sumatra, with a total of eight genera (*Anisoptera*, *Cotylelobium*, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Parashorea*, *Shorea*, and *Vatica*), consisting of 106 (ASHTON, 1982) to 112 species and three sub species (NEWMAN, *et al.*, 1996b, 1998b).
- Java and Nusa Tenggara, with a total of five genera (*Shorea*, *Hopea*, *Dipterocarpus*, *Anisoptera*, and *Vatica*), consisting of 10 species (ASHTON, 1982; NEWMAN, *et al.*, 1998c).

- Sulawesi, with a total of four genera (*Shorea*, *Hopea*, *Anisoptera*, and *Vatica*), consisting of six (ASHTON, 1982) to seven species (NEWMAN, *et al.*, 1998c).
- Maluku, with a total of four genera (*Shorea*, *Hopea*, *Anisoptera*, and *Vatica*), consisting of six (ASHTON, 1982) to seven species (NEWMAN, *et al.*, 1998c).
- Irian (including Papua New Guinea), with a total of three genera (*Hopea*, *Anisoptera*, and *Vatica*), consisting of 15 species (ASHTON, 1982; NEWMAN, *et al.*, 1998c).

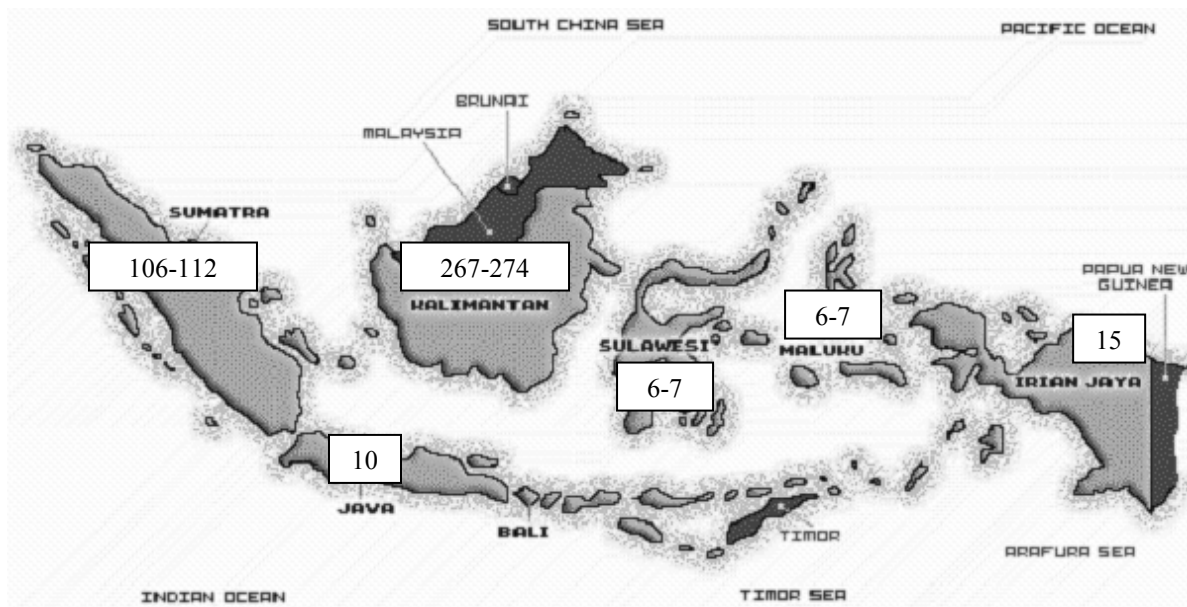


Figure 1. The distribution of Dipterocarpaceae in Indonesia. The total number of species in each island / isles after ASHTON (1982) and NEWMAN *et al.*, (1996a, 1996b, 1998a, 1998b, 1998c) is shown.

1.1.2. Reproductive biology

Dipterocarpaceae have bisexual flowers which are pollinated by a variety of insects as vectors (APPANAH, 1981; APPANAH and CHAN, 1981; CORLETT, 2004; MOMOSE *et al.*, 1998; SAKAI *et al.*, 1999a). Pollen flow of dipterocarps can reach more than 500 m in *Neobalanocarpus heimii* (KONUMA *et al.*, 2000) and approximately 200 m in *Dipterocarpus tempehes* (KENTA *et al.*, 2004). On the basis of controlled pollination, three kinds of breeding systems of dipterocarps are recognized: obligatory outbreeding species in most dipterocarps (BAWA, 1998, CHAN, 1981; SAKAI *et al.*, 1999b); inbreeding species, for example, *Dipterocarpus oblongifolius* (CHAN, 1981); and apomictic species, such as in *Shorea ovalis* ssp. *sericea* and *Shorea agamii* (KAUR *et al.*, 1978). Genetic variation was found in seedlings from a

polyembryonic seed of *Hopea odorata* (WICKNESWARI *et al.*, 1995), which indicated that multiple seedlings may not necessarily involve apomixis (BAWA, 1998).

Outcrossing rates (t_m) of dipterocarps have been estimated using isoenzyme and microsatellite markers in different forest types and species, such as *Dryobalanops aromatica* ($t_m= 0.77$ in logged forest and $t_m= 0.92$ in primary forest; LEE, 2000a), *Shorea megistophylla* ($t_m= 0.71$ in logged forest and $t_m= 0.87$ in primary forest; MURAWSKI *et al.*, 1994b), *Shorea curtisii* ($t_m= 0.52$ in logged forest and $t_m= 0.96$ in primary forest; OBAYASHI *et al.*, 2002), *Shorea congestiflora* ($t_m= 0.87$ in logged forest; MURAWSKI *et al.*, 1994a), *Shorea trapezifolia* ($t_m= 0.54-0.62$ in logged forest; MURAWSKI *et al.*, 1994a), *Shorea leprosula* ($t_m= 0.84$ in primary forest; LEE *et al.*, 2000c) and *Stemonoporus oblongifolius* ($t_m= 0.84$ in primary forest; MURAWSKI and BAWA, 1994). Several factors may influence the outcrossing rate, such as flowering tree density (MURAWSKI and HAMRICK, 1992), density of pollinators (LEE, 2000a), and the types and behavior of pollinators governing the pollen movement (GHAZOUL *et al.*, 1998). In summary, most dipterocarps are predominantly outcrossing, but selfing occurs in many species.

An important character of the family in the non-seasonal region is its flowering behaviour. Flowering time does not occur annually, but at irregular intervals with a mass production in a short (2 – 3.5 weeks) flowering period (ASHTON *et al.*, 1988; CHAN and APPANAH, 1980). They do not flower simultaneously with the different dipterocarp species (LAFRANKIE and CHAN, 1991) or in different elevations (SASAKI *et al.*, 1979). Observations in Kalimantan and Peninsular Malaysia revealed that most dipterocarps flower in March-April and the fruits of most species matured and fell in September-October (CHAN and APPANAH, 1980; WOOD, 1956).

General flowering of Dipterocarpaceae in an aseasonal climate is a supra annual cycle of plant reproduction that takes place at irregular intervals of two to ten years (APPANAH, 1985, 1993; COCKBURN, 1975; NG, 1977; WOOD, 1956, YASUDA *et al.*, 1999). Several environmental factors have been suggested as the floral triggers for general flowering in Dipterocarpaceae, including prolonged drought (APPANAH, 1985; MEDWAY, 1972), increase of photoperiod (NG, 1977; VAN SCHAİK, 1986; WYCHERLEY, 1973), and drop of minimum air temperature at night associated with cloudless weather (ASHTON *et al.*, 1988). Satiation of generalist seed predators has been considered a primary force for general flowering (JANZEN, 1975; SAKAI, 2002).

Seed dispersal of dipterocarps can be divided as follows (ASHTON, 1982; MURAWSKI and BAWA, 1994; SUZUKI and ASHTON, 1996): by wind in most species which have wing-like structure (aliform) sepals, by water in many species which have short sepals and grow in swamps or river banks, and simply by falling on the ground in species without wing-like sepals. Seeds disseminated by water can potentially disperse over longer distances than by wind.

Natural hybridization in dipterocarps has been frequently reported. *Shorea* species flower at the same time and are pollinated by the same insect groups (APPANAH and CHAN, 1981); therefore, the occurrence of interspecific gene exchange is possible. The successful fruit formation resulting from a cross between *Shorea splendida* and *Shorea stenoptera* shows the potential of natural hybridization of closely related species (CHAN, 1981). Putative hybrids between *Shorea acuminata* and *Shorea leprosula* were marked with nucleotide sequences in the *GapC* region (ISHIYAMA *et al.*, 2003). The polyploid condition indicates the possibility of hybridization which might have arisen in several species, such as triploidy in *Hopea beccariana*, *Hopea latifolia*, *Hopea subalata*, *Hopea odorata* and *Shorea resinosa*, and tetraploidy in *Hopea nutans*, *Shorea ovalis* ssp. *sericea* (ASHTON, 1982; JONG and KAUR, 1979; KAUR *et al.*, 1978; SOMEGO, 1978).

1.1.3. Ecology, silviculture and economic importance

Dipterocarpaceae is the most important forest tree family in natural and close-to-nature forests in Southeast Asia. The many different species of dipterocarps have widely varying site requirements, as illustrated by the fact that they can be found on entirely different site types and in nearly all of the different forest types of Southeast Asia (LAMPRECHT, 1989). Dipterocarps usually grow in mixed tropical rain forests, where they often constitute the dominant floristic element (WEIDELT, 1996). The highest species diversity is observed in evergreen rainforests in Peninsular Malaysia, Sumatra and Kalimantan (ASHTON, 1982; SYMINGTON, 1943; WHITTEN *et al.*, 1987). The latter island is the main centre of dipterocarps with the highest number of endemic species (155 species). Approximately one quarter of all trees in most lowland forests of Kalimantan are dipterocarps (ASHTON, 1982; SIST, 1996; SLIK *et al.*, 2003). The greatest richness in terms of abundance of species is attained in the emergent stratum in Sarawak and Brunei, Northwest Kalimantan (WHITMORE, 1975).

The symbiosis with ectomycorrhiza improves the physiological adaptability and is important for the growth of dipterocarps, especially in nutrient poor conditions (SMITS, 1994). Thus, the inoculation of ectomycorrhiza is crucial for the establishment of dipterocarp plantations. Silvicultural treatment, such as liberation thinning, also increases the periodic annual diameter increment (PAI) in larger trees (diameter at breast height / DBH>20 cm) of the Red Meranti group and smaller trees (DBH=10-20 cm) of other *Shorea* spp. and some *Hopea* spp. (KAMMESHEIDT *et al.*, 2003).

The polycyclic silvicultural system has been applied for dipterocarp forest management in Indonesia, namely *Tebang Pilih Indonesia - TPI* (the Indonesian selective cutting system) in 1972, followed by *Tebang Pilih Tanam Indonesia - TPTI* (the Indonesian selective cutting and planting system) since 1989 (DJPH, 1993). Several essentials in the latter system are: stand inventory of all growth stages, limitation of 50 cm minimum of DBH, and maintaining the residual stand with a minimum of 25 nucleus trees per hectare.

Dipterocarpaceae is the pre-eminent timber family in Indonesia, since more than 70% of the world's demand for plywood made from hardwoods has been supplied by Indonesia, principally from dipterocarp species (CHOONG and ACHMADI, 1996). The various wood varieties of dipterocarps are used for veneers and for outdoor and indoor construction (LAMPRECHT, 1989). Additionally, resin is also obtained from various species. Several dipterocarps species, mainly of the genus *Shorea*, produce a nut with an edible fat, identical to that of cocoa, and an excellent substitute for cocoa butter in the manufacture of chocolate and cosmetics (SEIBERT, 1996). The harvesting operation in Indonesia and other countries has a decisive impact on the amount and quality of the residual forest stand. Many of the dipterocarp forest in Southeast Asia have been badly damaged by logging and relogging in the same areas. Several species have been threatened, even coming to the brink of extinction (KORSGAARD, 1985).

Most of dipterocarp species in Indonesia are presently commercial. The vernacular name is usually applied for the timber trading purposes. As a genus consisted of the greatest number of species member, *Shorea* is the most popular timber of Dipterocarpaceae in Indonesia with vernacular name Meranti. Even SYMINGTON (1943) used vernacular name to divide *Shorea* into four groups, namely Balau (Selangan Batu), White Meranti (Meranti Pa'ang), Yellow Meranti (Meranti Damar Hitam) and Red Meranti. NEWMAN *et al.* (1996a, 1996b, 1998a, 1998b, 1998c) described the other common timber names of Indonesian dipterocarps related

to the genus, namely Giam / Merawan (*Hopea*), Keruing (*Dipterocarpus*), Kapur (*Dryobalanops*), Mersawa (*Anisoptera*), White Seraya (*Parashorea*), and Resak (*Vatica*, *Cotylelobium*, and *Upuna*).

1.1.4. Phylogenetics

The taxonomy of Dipterocarpaceae has been studied quite intensively due to their great value in the timber market (ASHTON, 1982), but the phylogenetic relationships among the taxa of Dipterocarpaceae have not been closely studied. Recently, phylogenetic research using molecular markers has been developed because of the simplicity of obtaining large amounts of data and the higher reliability as compared to morphological data for constructing phylogenetic trees (CHASE *et al.*, 1993).

Phylogenetic studies on Dipterocarpaceae have been conducted at various taxonomic levels. A study using nucleotide sequence data of angiosperm taxa showed that Dipterocarpaceae grouped with order Malvales (CHASE *et al.*, 1993; HILU, *et al.*, 2003) and in one clade together with Sarcolaenaceae (ALVERSON *et al.*, 1998; MORTON *et al.*, 1999) supported with a high bootstrap value (80 and 100%). The close relationships of Dipterocarpaceae and Sarcolaenaceae were also supported by DAYANDANAN *et al.* (1999) based on *rbcL* gene sequences. The systematic positions of subfamily Monotoideae and of monotypic *Pakaraimaea dipterocarpea* have been problematic. They were considered to have closer relationships to Tiliaceae (KOSTERMANS, 1978, 1985) or Dipterocarpaceae (ASHTON, 1982). KOSTERMANS (1989) declared Monotaceae to be a new family consisting of three genera, i.e. *Monotes*, *Marquesia* and *Pakaraimaea*. However, molecular data supported the monotypic subfamily Pakaraimoideae (represented by *Pakaraimaea dipterocarpea*) to cluster together with subfamilies Monotoideae and Dipterocarpoideae as a monophyletic clade of Dipterocarpaceae (DAYANANDAN *et al.*, 1999; MORTON *et al.*, 1999).

There are several phylogenetic studies of Asiatic dipterocarps (subfamily Dipterocarpoideae) using various outgroups belonging to subfamily Dipterocarpoideae (KAMIYA *et al.*, 1998; TSUMURA *et al.*, 1996), Monotoideae (GAMAGE *et al.*, 2003), family Bixaceae and Rhopalocarpaceae (DAYANANDAN *et al.*, 1999) and Tiliaceae (KAJITA *et al.*, 1998; LI *et al.*, 2004). Various marker types observing chloroplast DNA variation were investigated, such as PCR-RFLP (TSUMURA *et al.*, 1996), nucleotide sequences of *matK*, *trnL* intron, the *trnL-trnF* intergeneric spacer region (GAMAGE, 2003; KAJITA *et al.*, 1998; KAMIYA *et al.*, 1998; LI,