IMPACT OF DISTURBANCE ON POPULATION AND GENETIC STRUCTURE OF **TROPICAL FOREST TREES**¹

R. Wickneswari¹, W.S. Ho¹, K.S. Lee¹ & C.T. Lee²

¹ School of Environmental and Natural Resource Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia

² Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia

ABSTRACT

Effects of selective logging on the population and genetic structure of Shorea curtisii, Dryobalanops aromatica and Scaphium macropodum were examined via two approaches: (1) to investigate the immediate effects by studying a same population before and after logging and, (2) to determine the long term effects by comparing regenerated stands with an adjacent unlogged stand, assuming that they were genetically identical before logging.

Reduction in basal area of trees from different size classes due to a single logging event ranged from -100 - 100% in S. curtisii, D. aromatica and S. macropodum with large trees >45 cm dbh generally being absent. Recruitment of seedlings and presence of saplings was generally high for the non-dipterocarp species, S. macropodum (100% increase) but low for the dipterocarp species, D. aromatica (45% decrease) and S. curtisii (53% decrease) in immediately logged-over forests. Damage to poles was high in S. curtisii (92% and 88% for basal area and tree density respectively), D. aromatica (33% and 57%) and S. macropodum (73% and 73%). These changes in population structure of some tree species can persist in regenerated forests even after 50 years of logging.

No significant change in genetic diversity was observed for adults of S. macropodum and saplings of D. aromatica and S. curtisii immediately after logging. However, genetic diversity of seedlings and adults of S. curtisii was reduced by 34% and 85% respectively for hypothetical gametic diversity, V_{gam} and 30% and 85% respectively for latent genetic potential, LP immediately after logging. Substantial genetic erosion was also detected for adults of S. curtisii (71% reduction in Vgam and 63% reduction in LP) and S. macropodum (31.5% reduction in Shannon diversity, H) in regenerated stands which were logged 50 years ago. Implications of these changes in population and genetic structure due to logging on sustainable management of genetic resources of tropical timber trees will be discussed in this paper.

INTRODUCTION

Tropical forests are found in more than 80 countries and account for about one third of the world's forest cover. Commercial harvesting of timber through logging is a major form of disturbance in many areas, but the variety of products harvested from tropical forests is immense: wood, fruit and other foods, medicinal plants, construction materials, and many more. Annually more than 4.0 million hectares of tropical rainforests are logged for timber (JONSSON & LINDGREN 1990). The volume of timber extracted varies from region to region according to the stocking of commercially valuable stems. The damage to the stand is generally related to the number of stems harvested per hectare and the nature of the logging operations.

Sustainable management of natural forests depends on their ability to regenerate after logging. Regeneration determines the genetic diversity in the future forests and their capacity for sustainable production (KOSKI & STAHL 2000). Hence, assessment of regeneration capacity and genetic diversity would be useful in developing sustainable forest management guidelines and effective conservation strategies. According to APPANAH and MOHD. RASOL ABD. MANAF (1990), dipterocarp forests managed under the Selective Management System (SMS) of harvesting practice in Malaysia have the capacity to regenerate after logging. They also reported that the smaller dipterocarp residuals (> 25 cm dbh) fruiting in recently logged forests.

Maintenance of genetic diversity in forest tree populations that are undergoing population changes, whether natural or human-induced, is seen to be the key to adaptability and continued evolution (MÜLLER-STARCK 1985; LEDIG 1988; NAMKOONG 1991; MÜLLER-STARCK et al. 1992). There is mounting evidence that tree populations that sustained genetic losses are susceptible to productivity decline and loss of environ-

¹ This paper has been presented at the IUFRO Symposium on Population and Evolutionary Genetics of Forest Trees held in Stará Lesná, Slovakia, on August 25-29, 2002.

mental fitness in the event of major environmental changes (MÜLLER-STARCK 1985; BERGMANN *et al.* 1990; RADDI *et al.* 1994). The population reduction can result in changes to local gene pools through various genetic mechanisms, including non-random selection, reduction in genetic richness of residual breeding populations, inbreeding, and genetic drift (BARNES 1989; LEDIG 1992; BUCHERT *et al.* 1997).

Loss of genetic diversity immediately after harvesting has been reported in Pinus strobus (BUCHERT et al. 1997) and a few tropical rainforest species (CHANGTRA-GOON 1997; HO et al. 1999; WICKNESWARI et al. 2000; HO et al. 2000; LEE et al. 2002). Inbreeding as a result of logging has been detected in Shorea megistophylla (MURAWSKI et al. 1994), D. aromatica (LEE 2000) and Pterocarpus macrocarpus (LIENGSIRI et al. 1998) indicating the reduction of mature individuals in the population and limited gene flow. Reduced crosspollination rates were observed in Shorea siamensis and also reduced pollination success of Dipterocarpus obtusifolius was detected after logging (GHAZOUL et al. 1998). However, outcrossing rates of some D. aromatica populations (KITAMURA et al. 1994) and Dipterocarpus obtusifolius (CHAISURISRI et al. 1997) were not affected by logging possibly because of high densities of flowering trees in those forests.

This study summarises: (1) the immediate effects of selective logging on population structure of *S. curtisii*, *D. aromatica* and *S. macropodum* and (2) the immediate and long term effects of selective logging on genetic structure of *Shorea curtisii*, *D. aromatica* and *S. macropodum* using different molecular markers.

Effects of Selective Logging on Population Structure

Immediate effects of selective logging under the Selective Management System or SMS (THANG 1988) on population structure of *S. curtisii*, *D. aromatica* and *S. scaphium* were investigated in Compartment 48, Serting Tambahan Forest Reserve (F. R.), Negeri Sembilan and Compartment 118, Ulu Sedili F. R., Johor in Peninsular Malaysia. Inventories of all trees more than 1 cm dbh were carried before felling and within 2½ years after felling. Details of the study sites and demographic survey are given in LEE *et al.* (2002) and Ho (2002).

Reduction in basal area of trees from different size classes due to a single logging event ranged from -100 – 100 % in *S. curtisii* (Table 1), *D. aromatica* (Table 3) and *S. macropodum* (Table 5). Generally, large trees >45 cm dbh of all the above three species were absent immediately after logging. NICHOLSON (1958) and WYATT-SMITH and FOENANDER (1962) observed lower (28–45 %) damages to small and mature trees in

Table 1. Mean basal area per hectare (m²ha⁻¹) by dbh in before logging (BF-C48) and logged stand (LS-C48) for *Shorea curtisii* in Compartment 48, Serting Tambahan Forest Reserve.

dbh	BFC48	LS-C48	Diff.	%
< 5	0.02	0.01	0.01	52.58
5 – 15	0.25	0.02	0.23	91.86
15 – 30	0.10	0.00	0.10	100.00
30 - 45	1.33	0.68	0.65	48.78
45 - 60	0.00	0.00	0.00	0.00
60 – 75	0.00	0.00	0.00	0.00
75 – 90	0.00	0.00	0.00	0.00
90 - 105	0.00	0.00	0.00	0.00
105 - 120	0.00	0.00	0.00	0.00
> 120	7.72	0.00	7.72	100.00
Total	9.41	0.71	8.7	92.45

Table 2. Mean tree density (no. of trees per hectare) by dbh in before logging (BF-C48) and logged stand (LS-C48) for *Shorea curtisii* in Compartment 48, Serting Tambahan Forest Reserve.

dbh	BF-C48	LS-C48	Diff.	%
< 5	95.00	45.00	50.00	52.63
5 – 15	40.00	5.00	35.00	87.50
15 – 30	5.00	0.00	5.00	100.00
30 - 45	10.00	5.00	5.00	50.00
45 - 60	0.00	0.00	0.00	0.00
60 – 75	0.00	0.00	0.00	0.00
75 – 90	0.00	0.00	0.00	0.00
90 - 105	0.00	0.00	0.00	0.00
105 - 120	0.00	0.00	0.00	0.00
> 120	5.00	0.00	5.00	100.00
Total	155	55	100	64.52

lowland forest after 2 years of logging under the Malayan Uniform System (MUS). However, their assessments did not include the trees being extracted for timber. They proposed that these changes in basal area after logging can lead to creation of space for seedlings to regenerate. This was only evident for the non-dipterocarp, S. macropodum where a 100 % increase in seedlings and saplings was observed (Table 6). The two dipterocarp species; S. curtisii and D. aromatica investigated showed a substantial decrease (53 and 45% respectively) in tree density for the seedling and sapling age cohorts (Table 2 and Table 4). Similarly, BORHAN et al. (1987) observed 38-57 % mortality of seedlings when the forest was logged by both tractor and heavy machine. GUARIGUATA (1998) monitored vegetative and demographic responses to

Table 3. Basal area (m²·ha⁻¹) by diameter classes for *Dryobalanops aromatica* - before logging (BL) & after logging (AL) in Compartment 118, Ulu Sedili F. R.

Diameter classes	BF	AL	Diff.	%
< 5	0.03	0.02	0.01	33.33
5 – 15	0.03	0.02	0.01	33.33
15 - 30	0.40	0.23	0.17	42.50
30 – 45	1.29	0.95	0.34	26.36
> 45	0.00	0.00	0.00	0.00
Total	1.75	1.22	0.53	30.29

Table 4. Tree density (no. of trees per hectare) by diameter classes *Dryobalanops aromatica* — before logging (BL) & after logging (AL) in Compartment 118, Ulu Sedili F. R.

Diameter classes	BL	AL	Diff.	%
< 5	73.00	40.00	33.00	45.21
5 – 15	7.00	3.00	4.00	57.14
15 - 30	7.00	3.00	4.00	57.14
30 – 45	10.00	7.00	3.00	30.00
> 45	0.00	0.00	0.00	0.00
Total	97	53	44	45.36

Table 5. Mean basal area per hectare $(m^2 \cdot ha^{-1})$ by dbh in before logging (BF-C48) and logged stand (LS-C48) for *Scaphium macropodum* in Compartment 48, Serting Tambahan Forest Reserve.

dbh	BF-C48	LS-C48	Diff.	%
< 5	0.01	0.02	-0.01	-100.00
5 – 15	0.30	0.08	0.22	73.33
15 – 30	0.19	0.35	-0.16	-84.21
30 – 45	0.50	0.53	-0.03	-6.00
> 45	0.00	0.00	0.00	0.00
Total	1	0.98	0.02	2

mechanical damages caused by logging on seedlings of *Alseis blackiana* (Rubiaceae), *Protium panamense*, *P. tenuifolium* and *Tetragastris panamensis* (Burseraceae) in lowland forest in central Panama. In these species, percentage mortality after 4 years of logging was significant; bent (21 %), snapped (13 %) and undamaged controls (6 %).

In this study, damage to poles was high in *S. curtisii* (92 % and 88 % for basal area and tree density respec tively), *D. aromatica* (33 % and 57 %) and *S.*

Table 6. Mean tree density (no. of trees per hectare) by dbh in before logging (BF-C48) and logged stand (LS-C48) for *Scaphium macropodum* in Compartment 48, Serting Tambahan Forest Reserve.

dbh	BF-C48	LS-C48	Diff.	%
< 5	60.00	37.00	23.00	38.33
5 – 15	37.00	10.00	27.00	72.97
15 – 30	3.00	10.00	-7.00	-233.33
30 - 45	3.00	3.00	0.00	0.00
> 45	0.00	0.00	0.00	0.00
Total	103	60	43	41.75

macropodum (73 % and 73 %). These changes in population structure of some tree species can persist in regenerated forests even after 50 years of logging (Ho 2002). BERTAULT & SIST (1997) reported that logging affected 40 % trees > 10 cm dbh, whilst WAN RAZALI (1989) and BERTAULT *et al.* (1993) suggested that mortality rate would remain high for years before returning to 1-2 % similar to that in primary forest. Generally, there is a tendency for non-dipterocarp species which are light demanding to dominate loggedover forests if disturbance is high.

Effects of Selective Logging on Genetic Structure

Direct immediate effects of selective logging under the SMS on genetic structure of *S. curtisii*, *D. aromatica* and *S. scaphium* from different age cohorts were investigated in the same study sites as for the population structure. Indirect long term effects of selective logging under the Malayan Uniform System or MUS (WYATT-SMITH 1963) on genetic structure of the above three species were investigated in compartments logged 50 years ago in Pasoh F. R., Negeri Sembilan and, Ulu Sedili F.R. and Panti F.R., Johor in Peninsular Malaysia. Details of the study sites, sampling procedures and genetic diversity assessments are given in LEE *et al.* (2002), Ho (2002) and LEE (2002).

Immediate and long term effects of logging on S. curtisii

Immediate and long term effects of logging on genetic diversity parameters estimated using 6 microsatellite loci for *S. curtisii* in Serting Tambahan F.R. and Ulu Sedili F.R. (immediate effects) and Panti F.R. (long term effect) are summarised in Tables 7 and 8. Details of the microsatellite analysis are given in HO (2002).

Generally, logging caused major changes in most of the Gregorius genetic multiplicity measures and diversity measures (Ho 2002). Large differences in observed

Stand	Age cohorts	Ν	Α	H_{e}	V	V_{gam}	LP
BF-C118	Seedling	0.0	19.2	2.9	6.0	34.3	30.2
vs	Sapling	2.5	-10.8	0.6	-0.4	37.3	-72.2
AF-C118	Adult	83.3	50.0	5.4	26.3	84.8	85.1

Table 7. Percentage reduction in genetic diversity parameters determined using six SSR loci for *Shorea curtisii* immediately after logging under the Selective Management System.

N = number of individuals per locus, A = mean number of alleles per locus, $H_e =$ mean expected heterozygosity per locus (Nei, 1978), V = genic diversity, $V_{gam} =$ hypothetical gametic diversity, LP = latent genetic potential. Negative values indicate increase. BF-C118: before felling of Compartment 118, Ulu Sedili F. R., AF-C118: after felling of Compartment 118, Ulu Sedili F. R.

Table 8. Percentage reduction in genetic diversity parameters determined using six SSR loci for *Shorea curtisii* 50 years after logging under the Malayan Uniform System.

Stand	Age cohorts	Ν	A	H _e	V	V_{gam}	LP
BF-C118	Seedling	18.0	14.9	0.6	0.9	-15.2	34.8
vs	Sapling	30.0	8.1	0.0	1.1	45.3	-14.8
RS-C69	Adult	76.7	37.5	2.0	16.5	71.3	63.4

N = number of individuals per locus, A = mean number of alleles per locus, $H_e =$ mean expected heterozygosity per locus (Nei, 1978), V = genic diversity, $V_{gam} =$ hypothetical gametic diversity, LP = latent genetic potential. Negative values indicate increase. BF-C118: before felling of Compartment 118, Ulu Sedili F. R., RS-C69: regenerated stand of Compartment 69, Panti F. R. regenerated stand of Compartment 69, Panti F. R.

and expected G_M were detected for seedlings and adults in Compartment 118, Ulu Sedili F.R. (Table 7). Ho (2002) also reported that the differences were mainly due to the losses of rare alleles in both classes (63.2 % and 100 % in seedlings and adults, respectively). Similarly, BUCHERT *et al.* (1997) in their study on *P.strobus* (Eastern White Pine) reported that 80 % of the rare alleles (p < 0.01) were lost and allelic richness reduced by 25 % after 75 % of the trees were harvested.

The reduction in genic diversity, V for seedlings and adult trees was 6.0 % and 26.3 %, respectively, meanwhile the genetic diversity for saplings was unchanged after a single selective logging event. In general, V like heterozygosity, H_e was not greatly influenced by allelic losses (BUCHERT *et al.* 1997; HO *et al.* 1999, 2000). Hypothetical multilocus gametic diversity, V_{gam} (which is a measure of producing genetically diverse gametes when mature) was reduced by about 35 % in seedlings and saplings after logging.

Hypothetical multilocus gametic diversity and latent genetic adaptive potential, LP of the adult trees decreased to about 85 %, suggesting that the ability of this gene pool to adapt to changing environmental conditions may have been compromised. Buchert *et al.* (1997) reported a similar phenomenon for *P. strobus* (Eastern White Pine) where harvesting reduced the *LP* of the residual gene pools to about one-half of that initially present in the pre-harvest gene pools. Reduction in the levels of G_M , V_{gam} and LP also suggests a possible reduction in long-term evolutionary potential in adult trees after logging. This was evident in Compartment 69 logged 50 years ago where V_{gam} and LP remain reduced (71% and 63% respectively) in adult trees (Table 8).

In contrast, LP increased in the saplings by about 72 % immediately after logging and about 15 %, 50 years after logging. This suggests that saplings have the capability to colonise or adapt to environmental changes in the long-term. BERGMANN et al. (1990) reported low levels of LP being correlated with forest decline in northern and central populations of European silver fir (Abies alba Mill.), whereas high levels appear to be correlated with healthy southern European populations. Under an adapative gene action hypothesis by BUCHERT et al. (1997), the low and rare frequency allozyme alleles in a population represent much of the genetic potential required for population adaptation to longterm environmental changes because alleles of higher frequencies have probably been selected for current or recent past environments.

The genetic diversity changes of *S. curtisii* due to selective logging imply that gene pools of naturally regenerated progeny stands may be quite different from the original parental stands, as reported by BUCHERT *et al.* (1997) and WICKNESWARI *et al.* (1997a). As these genetic diversity changes are very gradual, its conse-

quences may only be observable in the third or fourth rotation coupes of the forest management unit. Therefore, regeneration and genetic assessment of regenerants of *S. curtisii* from different age cohorts need to be further monitored for productivity and sustainability of the species.

Immediate and long term effects of logging on D. aromatica

Table 9 summarizes the genetic diversity measures assessed using four universal primers for seedlings and saplings of *D. aromatica* in Compartment 118 (immediate effect) and Compartment 69 (long term effect). Details of the universal primer analysis are given in Lee (2002).

LEE (2002) detected an increase (56 %) in number of alleles in seedlings but, a decrease (45 %) in saplings of *D. aromatica* in Compartment 118 immediately after logging. Shannon diversity (*H*) for seedlings increased by 14 %, from 0.228 before logging to 0.259 after logging (detected by M13 universal primer). Similarly, UP-PCR primers showed increment in *H* for seedlings. Though there was loss of alleles for saplings, an increase in *H* of 14 % and 5% respectively was observed using M13 universal primer and UP-PCR primers.

Generally, allelic richness in saplings (65–68 % reduction) was lower than that in seedlings (-33–20 % reduction) of *D. aromatica* in Compartment 69 which was logged 50 years ago (LEE 2002). Slightly higher *H* for seedlings (25 %) and saplings (21 %), was detected by M13 universal primer in Compartment 69. These results corresponded to UP-PCR primers. The UP-PCR primers detected 3% higher in *H* for seedlings. In contrast, *H* for saplings was lower by 12 % (Table 9).

Generally, genetic diversity of D. aromatica seedlings and saplings were not affected by logging both in the short or long term. LIM et al. (2002) demonstrated high heterozygosity ($H_{r} = 0.700$) and number of alleles ($A_a = 5.43$) for D. aromatica. The high abundance of D. aromatica in central Johor (WYATT-SMITH 1963) and pollination by bees may have contributed to its high outcrossing rate. KITAMURA et al. (1994) observed outcrossing rate of D. aromatica in primary and secondary forests ranging from 79-86 %. Furthermore, LEE et al. (2001) reported high outcrossing rate in primary forest ($t_m = 0.92$), followed by logged forest $(t_m = 0.77)$, artificial forest $(t_m = 0.66)$ and plantation forest ($t_m = 0.55$) for D. aromatica. KONUMA et al. (1999) noted that outcrossing rate might not be influenced by tree density if the species has a long-distance pollinator such as Apis or Trigona..

Immediate and long term effects of logging on S. *macropodum*

Immediate and long term effects of logging on genetic diversity measures of *S. macropodum* are summarised in Table 10 and 11 respectively. Immediate effect of logging was investigated in Serting Tambahan F.R. whilst long term effect was studied in Pasuh F.R. T-tests did not reveal any significant difference between the before and after logging gene pools of *S. macropod-um* adult, pole, sapling and seedling age cohorts in Serting Tambahan F.R. Mean H_e based on isozyme data for Serting Tambahan F.R. after logging was slightly lower than before logging (6.0 %) for the adults. Similarly, mean Shannon's diversity index, *H* for Serting Tambahan F.R. after logging was slightly lower (9 %). However, slight increments in the effective number of alleles, A_e (2.3 %) and H_e (7.1 %) based on

		No. of	No. of samples analysed			No. of p	No. of polymorphic loci (P)			Shannon diversity index (H)		
Age Primer	C 118			No. of fragments	C 118	8		C 118				
cohort		Before logging	After logging	RS-C69 scored	0	Before logging	After logging	RS-C69	Before logging	After logging	RS-C 69	
Seedling	M13 UP–P CR	1820	3029	4543	3429	15(44) 47(54)	25(74) 59(68)	20(59) 37(43)	0.228 0.218	0.259 0.270	0.284 0.224	
Sapling	M13 UP–P CR	2728	1211	2019	2925	19(66) 62(82	10(35) 28(37)	7(24) 18(24)	0.229 0.243	0.260 0.256	0.276 0.215	

Table 9. Mean percentage of polymorphic loci (P) and Shannon diversity index (H) per primer for seedlings and saplings of *Dryobalanops aromatica* in Compartment 118 and Compartment 69, Ulu Sedili F. R.

Number in parentheses refer to percentage of polymorphic loci.

© ARBORA PUBLISHERS

Sampling time	Molecular marker	Age cohort+	Р	Α	A _e	Н	Н	F _{is}
Before logging	Isozyme	adults (33)	100	3.3	1.71	0.415		0.132
	RAPD	Adults (33)	70.2	1.7	1.33	0.198	1.075	_
After logging	Isozyme	Adults (22)	100	3.0	1.64	0.390		- 0.036
		Poles (15)	100	2.5	1.5	0.318	-	0.382
		Saplings (31)	75	3.0	1.5	0.337	_	0.076
		Seedlings (33)	100	3.0	1.7	0.396	-	0.235
	RAPD	Adults (22)	68.1	1.7	1.36	0.212	0.978	_

Table 10. Estimates of genetic diversity measures for Scaphium macropodum in Serting Tambahan F. R.

P – percentage of polymorphic loci; A – mean number of alleles per locus; A_e – effective number of alleles per locus; H_e – Nei's (1973) gene diversity; H – mean Shannon's diversity index per primer; F_{is} – Fixation index. + Figures in brackets indicate sample size.

Table 11. Estimates of genetic diversity measures for Scaphium macropodum in Pasoh F. R.

Compartment	Molecular marker+	Р	A	A _e	H _e	Н	$oldsymbol{F}_{is}$
US	Isozyme (30) RAPD (30)	10079	3.5 1.8	1.6 1.4	0.381 0.225	_ 1.457	-0.037 -0.041
RS1	Isozyme (11) RAPD (11)	10055	3.0 1.5*	2.2 1.3*	0.541 0.163*	0.998*	0.155 0.073
RS2	Isozyme (18) RAPD (18)	7569.8	3.0 1.7*	2.0 1.4	0.498 0.218	- 1.400	0.175 0.143

P – percentage of polymorphic loci; A – mean number of alleles per locus; A_e – effective number of alleles per locus; H_e – Nei's (1973) gene diversity; H – mean Shannon's diversity index per primer; F_{is} – fixation index. + figures in brackets indicate sample size. * indicates significant difference at p<0.05.

RAPD data were observed after logging, probably due to random retention of more heterogeneous adult individuals.

RAPD analysis revealed a significant reduction ($p \le 0.05$) for all genetic diversity parameters surveyed for Regenerated Stand 1 (RS1) in Pasoh F.R. Percentage of polymorphic loci decreased by 31.0 %, while A_e dropped by 7.8 %. H_e was also reduced by 27.6 %. Meanwhile, no significant change in genetic diversity was detected for Regenerated Stand 2 (RS2) except in A, with 5.3 % reduction. There was a significant decrease (p < 0.05) in H of S. macropodum in RS1 (0.998) from Pasoh F.R. compared to Unlogged Stand (US, 1.457), which was equivalent to 31.5 % reduction. In contrast, RS2 showed a minor reduction of only 3.9 %. On the contrary, isozyme analysis revealed an increase in A_e and H_e for both RS1 and RS2 compared to US.

The reduction in basal area (trees > 5cm dbh) of compartment 48 from Serting Tambahan F.R. after

logging was about 57.5 % (LEE *et al.* 2002). However, logging did not cause adverse changes in genetic diversity of *S. macropodum*. This may probably be attributed to its high abundance in the forest management unit (FMU). *Scaphium macropodum* is one of the most abundant species in Serting Tambahan F.R., with the estimated adult tree (\geq 20 cm dbh) density of 10 trees ha⁻¹. Post-harvest inventory revealed that it was reduced to 8 trees ha⁻¹ after logging, still considerably high. This result concurs with the study using isozyme markers (WICKNESWARI *et al.* 1997a). WICKNESWARI *et al.* (1997a) also demonstrated a higher loss of genetic diversity (23.4 % reduction in H_e and 25.0 % in *A*) in *Shorea leprosula*, an important timber species, which was in contrast, of low abundance in the FMU.

Compared to compartment 48 of Serting Tambahan F.R., the mature tree density of *S. macropodum* in US of Pasoh F.R. was only about 2 trees ha^{-1} . As the three sub-populations of *S. macropodum* in Pasoh F.R. were

from a continuous population, it is assumed that they were genetically identical before logging. Hence, the significant reductions ($p \le 0.05$) observed across all the genetic diversity parameters for the RS1 (logged in 1951) indicate a substantial genetic diversity loss due to logging. In fact, the mean genetic distance among the three sub-populations of S. macropodum in Pasoh F.R. was the highest (0.062) among six species investigated by WICKNESWARI et al. (2000) indicating most probably change in allelic frequencies of sub-populations due to logging. On the contrary, S. macropodum from the RS2 which was relatively more disturbed in term of mean basal area reduction, suffered no genetic erosion. The result however, corroborates with the sample sizes of the respective stands. RS1 had the least number of samples available. This suggests that the genetic erosion may have been due to severe population decline after selective logging, resulting in increased genetic drift and reduced outcrossing rates.

Scaphium macropodum has unisexual flowers i.e., male and female flowers on separate inflorescences on the same tree (ASHTON 1988). KOCHUMMEN (1973) reported bees, flies, beetles and butterflies as its pollinators. Isozymes analysis of progeny arrays of three mature *S. macropodum* trees from Serting Tambahan F.R. revealed a substantially high mean t_m value, *i.e.*, 0.92 (unpublished data). Owing to the presumably smaller number of individuals left in RS1 after logging, selfing might have been enhanced and caused a further loss of genetic diversity in that FMU.

CONCLUSIONS

Figures 1 and 2 show the generalized changes in basal area and tree density of *S. curtisii*, *D. aromatica* and *S. macropodum* by age cohorts immediately after a single logging event. Most large trees >45 cm dbh were harvested and damage to poles was high compared to seedlings and small/large trees. Canopy opening encouraged regeneration of trees \leq 5 cm dbh especially the non-dipterocarps Some trees \leq 5 cm dbh suffered damage caused mainly by tree felling and road construction. Trees in the 30–45 cm dbh class were in adequate numbers after logging. However, APPANAH and WEINLAND (1990) reported many trees that are only partially affected during logging may appear well initially, but could die several years later.

The reductions of genetic diversity measures are in the following sequence: saplings < seedlings < adults. Generally, logging caused loss in genetic diversity and long-term evolutionary potential of adult trees in the logged stands. However, these immediate losses in genetic diversity which can persist in the long term may

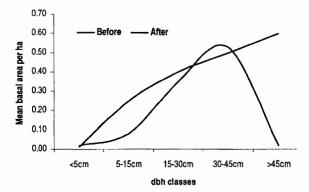


Figure 1. Immediate effect of logging on basal area of tropical tree species from different diameter classes (or age cohorts).

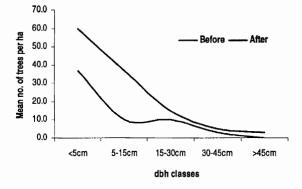


Figure 2. Immediate effect of logging on tree density of tropical tree species from different diameter classes (or age cohorts).

be compensated for by an existing good seed or seedling bank in the forest management unit or by migration from nearby undisturbed forest areas. It is thus, crucial to allocate adequate buffer zones whilst at the same time leaving behind sufficient undamaged good quality adolescent or bigger trees to ensure good regeneration in the residual stands.

Assessment of genetic erosion should be carried out using more than one molecular marker analysis if one of them shows no significant difference. Results of these studies show that species' vulnerability to the threat of genetic erosion posed by selective logging is highly correlated with its abundance in a particular forest management unit (FMU). Timber species of high abundance and high heterogeneity in a FMU are likely to have higher capacity to buffer genetic erosion compared to those of low occurrence. Tree density of species can be a useful indicator in reflecting the risk of genetic erosion rather than the overall disturbance level based on reduction in basal area of all trees.

More studies involving different species in different forest types are essential to gain better understanding of the effect of a single selective logging event on the genetic resources of tropical forest. If significant genetic erosion is detected, remedial actions such as enrichment planting of affected species could be carried out to mitigate the negative impacts to avoid risk of irreversible genetic erosion.

ACKNOWLEDGEMENTS

This work was supported by the Malaysian Government (IRPA Grant 01-02-02-0022), the Center for International Forestry Research (CIFOR) and the International Plant Genetic Resources Institute (IPGRI) in collaboration with the Forest Research Institute Malaysia (FRIM) and Universiti Kebangsaan Malaysia.

REFERENCES

- APPANAH, S. & MOHD. RASOL ABD. MANAF. 1990: Smaller trees can fruit in logged dipterocarp forests. J. Trop. For. Sci. 3(1): 80 – 87.
- APPANAH, S. & WEINLAND, G. 1990: Will management systems for hill dipterocarp forests, stand up? J. Trop. For. Sci. 3(2): 140–158.
- ASHTON, P.S. 1988: Manual of the non-dipterocarp trees of Sarawak. Vol. II. Dewan Bahasa dan Pustaka, Kuala Lumpur.
- BARNES, B.V. 1989: Old-growth forests of the northern lake states: a landscape ecosystem perspective. *Nature Areas* J. 9: 45–57.
- BERGMANN, F., GREGORIUS, H.R. & LARSEN, J.B. 1990: Levels of genetic variation in European silver fir (*Abies alba*) – Are they related to the species' decline? *Genetica* 82: 1–10.
- BERTAULT, J-G., DUPUY, B., MAÎTRE, H-F. 1993: Silvicultural research of sustainable management of rainforest. Proceedings of the Tropical Silviculture Workshop, IUFRO Centennial Conference, Berlin, 1–3 September 1992. Pp. 1–14.
- BERTAULT, J-G., SIST, P. 1997: An experimental comparison of different harvesting intensities with reduced-impact and conventional logging in East Kalimantan, Indonesia. *For. Ecol. Manage.* 94:209–218.
- BORHAN, M., JOHARI, B., QUAH, E.S. 1987: Studies on logging damage due to different methods and intensities of harvesting in a hill dipterocarp forest of Peninsular Malaysia. *Malay. Forest.* **50** (1–2):135–147.
- BUCHERT, G. P., RAJORA, O. P., HOOD, J. V., DANCIK, B. P. 1997: Effects of harvesting on genetic diversity in oldgrowth eastern white pine in Ontario, Canada. *Conserv. Biol.* 11: 747–758.
- CHAISURISRI, K., WUNGPLONG, P., LIEWLAKSANEEYANAWIN, C., BOYLE, T.J.B. 1997: Impacts of disturbance on genetic diversity of some forest species in Thailand. Paper presented at Wrap-up Workshop of the CIFOR-IPGRI Impact of Disturbance Project, Bangalore, India, 18–22 August 1997.

- CHANGTRAGOON, S. 1997: Impact of disturbance on genetic diversity of Cycas siamensis in Thailand. Paper presented at Wrap-up Workshop of the CIFOR-IPGRI Impact of Disturbance Project, Bangalore, India, 18–22 August 1997.
- GHAZOUL, J., LISTON, K.A. & BOYLE, T.J.B. 1998: Disturbance induced density dependent seed set in *Shorea* siamensis (Dipterocarpaceae), a tropical forest tree. *J. Ecol.* **86**: 462–473.
- GUARIGUATA, M.R. 1998: Response of forest tree saplings to experimental mechanical damage in lowland Panama. *For. Ecol. Manage.* **102**, 103–111.
- HO, W.S., WICKNESWARI, R. & MAHANI.M.C. 1999: Effects of selective logging on demographic genetic structure of *Shorea curtisii* Dyer ex King. Poster paper presented at the *Symposium Biology In The Next Millennium: Challenges In Biology Education and Research*, 1–3 December 1999, Malaysia.
- HO, W.S., WICKNESWARI, R. & MAHANI.M.C. 2000: Changes in population structure and genetic diversity of Shorea curtisii Dyer ex King due to selective logging. Proceedings of the XXI IUFRO World congress 2000: Forests and society – The role of research. Kuala Lumpur, Malaysia. Pp. 52.
- Ho, W.S. 2002: Effects of selective logging on forest structure and genetic diversity of *Shorea curtisii* Dyer ex King (Dipterocarpaceae). Ph.D. Thesis. Universiti Kebangsaan Malaysia, Malaysia.
- JONSSON, T. & LINDGREN, P. 1990: Logging Technology for Tropical Forests – for or against? The Forest Operations Institute 'Skogsarbeten', Sweden. 128 p.
- KITAMURA, K., MOHAMAD YUSOF, A.R., OCHIAI O. & YOSHIMARU, H. 1994: Estimation of outcrossing rate on Dryobalanops aromatica Gaertn. F. in primary and secondary forests in Brunei, Borneo, Southeast Asia. Plant Spec. Biol. 9: 37–41.
- KOCHUMMEN, K. M. 1973: Sterculiaceae (from the genus *Sterculia*). *Tree Flora of Malaya* **2**: 353–372.
- KOSKI, V. & STAHL, P. 2000: Impacts of silviculture and forest management on genetic diversity of trees. Proceedings of the XXI IUFRO World congress 2000: Forests and society – The role of research. Kuala Lumpur, Malaysia. pp110–119.
- LEDIG, F.T. 1988: The conservation of diversity in forest trees. *Bioscience* 38: 471–479.
- LEDIG, F.T. 1992: Human impacts on genetic diversity in forest trees. *Oikos* 63: 87–108.
- LEE, C.T., WICKNESWARI, R., MAHANI, M.C. & ZAKRI, A.H., 2002: Effect of selective logging on the genetic diversity of Scaphium macropodum. Biol. Conserv. 104: 107–118.
- LEE, K.S. 2002: Effects of logging on genetic diversity of *Dryobalanops aromatica* and *Koompassia malaccensis* (in Malay). M.Sc. Thesis. Universiti Kebangsaan Malaysia, Malaysia.
- LEE, S.L. 2000: Mating system parameters of *Dryobalanops* aromatica Gaertn. F. (Dipterocarpaceae) in three different forest types and a seed orchard. *Heredity* 85: 318 -345.
- LIENGSIRI, C., BOYLE, T.J.B. & YEH, F.C. 1998: Mating system *in Pterocarpus macrocarpus* Kurz in Thailand. *J. Hered.* **89**:216–221.

- LIM, L.S., WICKNESWARI, R., LEE, S.L. & LATIFF, A. 2002: Genetic variation of *Dryobalanops aromatica* Gaertn. F. (Dipterocarpaceae) in Peninsular Malaysia using microsatellite DNA markers. *For. Genet.* 9(2): 127–138.
- KONUMA, A., TSUMURA, Y., LEE, C.T., LEE, S.L. &OKUDA, T. 1999: Estimation of gene flow in the tropical-rainforest tree *Neobalanocarpus heimii* (Dipterocarpaceae), inferred from paternity analysis. *Mol. Ecol.* 9: 1843–1852.
- MÜLLER-STARCK, G. 1985: Genetic differences between "tolerant" and "sensitive" beeches (*Fagus sylvatica* L.) in an environmentally stressed adult forest stand. *Silvae Genet.* 34: 241–247.
- MÜLLER-STARCK, G., BARADAT, P. & BERGMANN, F. 1992: Genetic variation within European tree species. *New Forests* 6: 23–47.
- MURAWSKI, D. A., GUNATILLEKE, I.A.U.N. & BAWA, K. S. 1994: The effects of selective logging on inbreeding in *Shorea megistophylla* (Dipterocarpacea) from Sri Lanka. *Conserv. Biol.* 8: 997–1002.
- NAMKOONG, G. 1991. Biodiversity issues in genetics, forestry and ethics. *For. Chron.* **68**: 438–443.
- NICHOLSON, D.I. 1958. A analysis of logging damage in tropical rainforest, North Borneo. *Malay. Forest.* **21**(4): 235–245.
- RADDI, S.F., STEFANINI, M., CAMUSSI, A. & GIANNINI, R. 1994: Forest decline index and genetic variability in *Picea abies* (L.) Karst. *For. Genet.* 1: 33–40.
- THANG, H.C. 1988. Selective management system: Concept and practice (Peninsular Malaysia). Forest Department

Headquaters, Kuala Lumpur.

- WAN RAZALI, W. 1989: Summary of growth and yield studies in tropical mixed forests. Proj. Pap. UNDP/RAS/86/049, Forest Research Institute, Malaysia, Kepong, FRIM Rep. No. 49, pp. 17–83.
- WYATT-SMITH, J. 1963: Manual of Malayan Silviculture for Inland Forests. *Malay. For. Rec.* No. **23**(1).
- WYATT-SMITH, J. & FOENANDER, E.C. 1962: Damage to the regeneration as the result of logging. *Malay. Forest.* **25**(1): 40–44.
- WICKNESWARI, R., LEE, C. T., NORWATI, M. & BOYLE, T.J.B. 1997a: Immediate effects of logging on the genetic diversity of five tropical rainforest species in a ridge orest in Peninsular Malaysia. Paper presented at Wrap-up Workshop of the CIFOR-IPGRI Impact of Disturbance Project, Bangalore, India, 18–22 August 1997.
- WICKNESWARI, R., LEE, C.T., NORWATI, M. & BOYLE, T.J.B. 1997b: Effects of logging on the genetic diversity of six tropical rainforest species in a regenerated mixed dipterocarp lowland forest in Peninsular Malaysia. Paper presented at Wrap-up Workshop of the CIFOR-IPGRI Impact of Disturbance Project, Bangalore, India, 18–22 August 1997.
- WICKNESWARI, R., LEE, C.T., NORWATI, M. & BOYLE, T.J.B. 2000: Impact of logging on genetic diversity in humid tropical forests. *In*: Mátyás (ed.), Forest Genetics and Sustainability, Vol. 63, 171–181.