The Republic of the Union of Myanmar
Ministry of Environmental Conservation and Forestry
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Genetic Variation of Teak (*Tectona grandis* Linn. f.*)* in Myanmar revealed by Amplified Fragment Length Polymorphisms (AFLPs)

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မြန်မာနိုင်ငံရှိ ကျွန်းသစ်တောများ၏ မျိုးရိုးဗီဇစုံလင်ကွဲပြားမှုကို AFLPs မျိုးရိုးဗီဇ အမှတ်အသားများ အသုံးပြုလေ့လာခြင်း

ဒေါက်တာရာဇာမင်း
လက်ထောက်ကထိက
သစ်တောတက္ကသိုလ်

မြန်မာနိုင်ငံရှိ ကျွန်းသစ်တောများ၏ မျိုးရိုးဗီဇစုံလင်ကွဲပြားမှုကို **Amplified Fragment Length Polymorphisms (AFLPs)** မော်လီကျူလာမာကာဖြင့်လေ့လာခြင်းဖြစ်ပါသည်။ မြန်မာပြည် မြောက်ပိုင်းနှင့်တောင်ပိုင်း (၄)နေရာတွင် နီးကပ်စွာတည်ရှိသော ရွေးချယ်ခုတ်လှဲထားသည့် (ဦးရေစု) ကျွန်းတောနှင့် ရွေးချယ်ခုတ်လှဲခြင်းမပြုရသေးသည့်(ဦးရေစု) ကျွန်းတောများမှ စာရင်းကောက်ယူခြင်း ဖြစ်ပါသည်။ ဦးရေစုတောတစ်တောတွင် ကျွန်းပင်ကြီး (၅၀)ပင်နှင့် မျိုးဆက်ပင်ငယ်(၅၀)များမှ သစ်ရွက်နမူနာများကို စုဆောင်းကောက်ယူပါသည်။

လေ့လာတွေ့ရှိချက်များမှာ ကျွန်းသစ်တောများ၏ မျိုးရိုးဗီဇစုံလင်မှုမှာ မြင့်မားလျက်ရှိခြင်းနှင့် ရွေးချယ်ခုတ်လှဲခြင်းသည် ကျွန်းသစ်တောများ၏ မျိုးရိုးဗီဇအပေါ် သက်ရောက်မှုမရှိခြင်းတို့ ဖြစ်ပါသည်။ ထို့ပြင် မြောက်ပိုင်းရှိ ကျွန်းသစ်တောများသည် တောင်ပိုင်းရှိ ကျွန်းသစ်တောများထက် မျိုးရိုးဗီဇစုံလင်မှုပမာဏမှာ မြင့်မားလျက်ရှိခြင်းနှင့် ရွေးချယ်ခုတ်လှဲခြင်း မပြုရသေးသည့် တောများတွင် အပင်ကြီးများ၏ မျိုးရိုးဗီဇစုံလင်မှုမှာ မျိုးဆက်ပင်ငယ်တို့ထက် မြင့်မားရှိခြင်းတို့ဖြစ်ပါသည်။

ဦးရေစုတောများအကြား မျိုးရိုးဗီဇကွဲပြားမှုအခြေအနေတွင် တောင်ပိုင်းရှိ ကျွန်းသစ်တောများနှင့် မြောက်ပိုင်းရှိ ကျွန်းသစ်တောများမှာ သီးခြားအုပ်စုများအဖြစ် ကွဲပြားခြားနားလျက် ရှိသည်ကို တွေ့ရပါသည်။ ထို့ပြင် မျိုးရိုးဗီဇ အကွာအဝေးနှင့် ပထဝီမြေပြင်အကွာအဝေးများမှာ သိသာသော ဆက်နွယ်ချက်များရှိခြင်းနှင့် ကျွန်းသစ်တောဦးရေစု အားလုံးကြားတွင်လည်း သိသာသော မျိုးရိုးဗီဇ ကွဲပြားချက်ရှိခြင်းတို့ဖြစ်ပါသည်။ သို့ဖြစ်၍ အကွာအဝေးတခုစီတိုင်းတွင် ပေါက်ရောက်နေသည့် ကျွန်းသစ်တောများကို မျိုးရိုးဗီဇကာကွယ် ထိန်းသိမ်းခြင်းတွင် ထည့်သွင်းရန်နှင့် အထူးသဖြင့် တောင်ပိုင်းနှင့် မြောက်ပိုင်းဒေသကြီး နှစ်ခုကို ကျွန်းသစ်မျိုးရိုးဗီဇ ကာကွယ်ထိန်းသိမ်းရေး နယ်မြေကြီး နှစ်ခုအဖြစ်သတ်မှတ်၍ ဆောင်ရွက်သင့်ကြောင်း အကြံပြုပါသည်။

ယခုတင်ပြသည့် စာတမ်းမှာ လက်တွေ့ကွင်းဆင်းသုတေသနကို အခြေခံထားခြင်းမျိုးမဟုတ်ပဲ သစ်တောဓြေများနှင့် သစ်တောစိုက်ခင်းများ စီမံအုပ်ချုပ်ခြင်း၊ ဒေသခံများနှင့် ပုဂ္ဂလိက ကုမ္ပဏီများ၏ ပဋိပက္ခများ၊ ဒေသခံများနှင့် ပုဂ္ဂလိက ကုမ္ပဏီများအကြား မတူကွဲပြား သည့် အစုအဖွဲ့များ ဖွဲ့စည်း၍ အဆိုပါပဋိပက္ခများကို ကျော်လွှားရန် အဖြေရှာသည့် နည်းလမ်းများ စသည်တို့ ပါရှိသည့် အကိုးအကားများနှင့် စာအုပ်စာတမ်းများကို လေ့လာ၍ သုတေသန ပြုထားခြင်းဖြစ်ပါသည်။ ယခု သုတေသနသည် ပြည်သူကို အခြေခံသည့် သစ်တောစီမံအုပ်ချုပ်မှု အစီအစဉ်များ၏ အရဲကိုးစွန့်စားရမှုများအား ထာဝစဉ်တည်တံ့စေသော ဖွံ့ဖြိုးမှုကို ဦးတည်သည့် မှန်ကန်စွာဖြေရှင်းနိုင်မည့် အခွင့်အလမ်းကောင်းများအဖြစ် ပြောင်းလဲနိုင်မည့် နည်းလမ်းကို မီးမောင်းထိုးပြသနိုင်ရန် မျှော်မှန်းပါသည်။ ယခုသုတေသနကို နိုင်ငံ၊ ပုဂ္ဂလိကနှင့် ဒေသခံပြည်သူတို့ စုပေါင်းဆောင်ရွက်ခြင်းဖြင့် သဘာဝပတ်ဝန်းကျင် အတွက် သင့်လျော်ခြင်း၊ လူမှုရေးအရအကျိုးများခြင်း၊ စီးပွါးရေးအရ အလားအလာကောင်းခြင်း တို့နှင့်ပြည့်စုံပြီး မြန်မာနိုင်ငံ၏ လက်ရှိဖြစ်ပေါ်ပြောင်းလဲမှု များနှင့် သဟဇာတဖြစ်မည့် ပုံစံတစ်ခုကို တည်ဆောက်တင်ပြခြင်းဖြင့် နိဂုံးချုပ်ထားပါသည်။

Genetic Variation of Teak (*Tectona grandis* Linn. f.) in Myanmar revealed by Amplified Fragment Length Polymorphisms (AFLPs)

Yazar Minn

Abstract

Genetic variation of teak (*Tectona grandis* Linn. f.) was characterized using 71 Amplified Fragment Length Polymorphisms (AFLPs). Fifty adult trees and 50 seedlings from young regeneration were sampled in selectively logged and unlogged populations in four regions, each in the Northern and Southern parts of Myanmar. In general, genetic diversity within teak populations was relatively high. We failed to detect the impact of logging on genetic variation of teak. Genetic diversity was significantly higher in Northern than in Southern populations of Myanmar. Furthermore, genetic diversity of adult trees was significantly higher than in the teak regeneration in unlogged populations. Cluster analysis revealed two major clusters: one with northern populations and another one with southern populations of Myanmar. A Mantel test showed significant positive correlations between genetic and geographical distances among populations. The F_{ST} values were significantly different among all teak populations and higher between than within the regions in Myanmar. We suggest inclusion of many different populations for

conservation and more importantly, designation of two major conservation regions for Northern and Southern Myanmar.

Key words: AFLPs, conservation, genetic diversity, genetic differentiation, natural regeneration, selective logging, teak

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Genetic Variation of Teak (*Tectona grandis* Linn. f.*)* in Myanmar revealed by Amplified Fragment Length Polymorphisms (AFLPs)

1. Introduction

Teak (*Tectona grandis* Linn. f.) is a diploid species (2n=36) (Gill *et al.*, 1983). It belongs to the family Verbenaceae (also placed in the family Lamiaceae (Anon., 2012; Cantino, 1992)). Teak naturally occurs in the South and South East Asian countries, within the range of latitudes between 9°-25°30′ N and longitudes between 73°-104° 30′ E (Gyi and Tint, 1998; Kaosa-ard, 1986). Mostly, teak occurs in the central and western parts of India, in the most parts of Myanmar, in the northern parts of Thailand and some western parts of Laos (Troup, 1921; Kaosa-ard, 1986; Gyi and Tint, 1998). According to Gyi and Tint (1998), the total area of natural teak forests in those countries was about 27.9 million ha: 8.9 million ha in India, 16,000 ha in Laos, 16.5 million ha in Myanmar and 2.5 million ha in Thailand. However, high deforestation rates across the region lead to the actual occurrence of natural teak forests mostly in some parts of India and Myanmar nowadays (Gyi and Tint, 1998).

The patterns of genetic variation of forest trees are being assessed using different genetic markers. Genetic variation of teak has been characterized using isozyme markers (Kjaer *et al.*, 1996), Random Amplified Polymorphic DNA (RAPD) (Nicodemus *et al.*, 2003; Parthiban *et al.*, 2003), Amplified Fragment Length Polymorphisms (AFLPs) (Minn, 2007; Shrestha et al., 2005)) and nuclear Simple Sequence Repeats (SSRs) (Fofana *et al.*, 2009). In Myanmar, genetic variation of teak from three populations in Bago Yoma and one population in the fringe of the central dry zone has been successfully assessed using AFLPs (Minn, 2007). Due to limited number of samples and populations, Minn (2007) suggested further studies with populations from different geographical regions to provide more comprehensive information for sustainable utilization and conservation of teak resources.

Selective logging is one of the major tools in the management of teak forest in Myanmar. It is frequently referred as dysgenic selection due to selection against desirable phenotypic trees. Moreover, it is also argued for reduction in genetic diversity of the forest tree species. For example, logging significantly reduces genetic diversity of *Pinus strobus* (Buchert *et al.*, 1997). and *Araucaria angustifolia* (Medri *et al.*, 2003). However, no impact of logging has been reported for some tree species. For example, selective logging does not significantly affect genetic structure of *Scaphium macropodum* (Lee *et al.*, 2002). The impact of selective logging on genetic variation of teak in Myanmar is not known yet.

Not only genetic variation of adult trees but also genetic variation of regeneration are equally important because regeneration plays an important role for shaping the genetic structures of future forests and sustainable productivity (Koski and Stahl, 2000). Moreover, different tree species and their temporal stages reveal different intensity of changes on the level of genetic diversity after logging activities (Wickneswari *et al.*, 2004). Currently, genetic structures of teak regeneration in unlogged and selectively-logged forests are unknown.

The present study thus deals with the application of AFLPs to assess the patterns of genetic variation of teak forests, to examine the impacts of selective logging on genetic variation of teak and to assess genetic structures of adults and regeneration of teak forests in Myanmar.

2. Materials and Methods

2.1. Study areas

Sampling was conducted in four population pairs in the northern region of Myanmar and another four population pairs in the southern region of Myanmar between October 2009 and January 2010 (Fig. 1 and Table 1).

A population pair consisted of unlogged and selectively-logged teak stands. Those two populations were situated adjacent to each other in the area. A population was selected as an unlogged population if there was no recent logging but target diameter trees were highly abundant. In most cases, information for previous logging in the unlogged populations was not available. Nonetheless, most unlogged populations were designated by the Forest Department for subsequent logging in a few years. In the same region, another adjacent natural population was selected as a selectively-logged population where there had been recent teak logging operations in the stand. Generally, target diameter teak trees were scarce in these selectively-logged stands.

2.2. Plant materials

Leave samples were collected for the analyses. The sampled leaves were immediately stored in silica gel to prevent fungal contamination. Silica gel was periodically checked and replaced to keep material dry.

To minimize the risk of sampling related trees, minimum distance between consecutive sampled adult trees was approximately 100 m. Leaf samples were collected from teak regeneration which were the nearest to sampled adult teak trees.

Samples were collected from 50 adults and 50 seedlings from natural regeneration in each population. The total numbers of leaf samples collected from Myanmar were 1600. However, due to unambiguous amplification of some samples, the number of sample size used for the analyses was 1494.

2.3. DNA isolation

Genomic DNA was isolated from dried leaves by using the protocol of Qiagen DNA isolation Plant Mini Kit (Qiagen, Hilden, Germany). DNA was stored at – 20°C.

2.4. Genotyping of AFLPs

AFLP analysis was performed according to the protocol of Vos et al. (1995) with slight modifications. Two restriction enzymes *Eco*RI and *Mse*I were used to digest total genomic DNA. The *Eco*RI and *Mse*I adaptors were ligated to the ends of the restriction fragment. The restriction-ligation reaction was performed overnight at room temperature to generate DNA templates for PCR amplification consisting of two successive steps. The pre-selective amplification was carried out by using the primer combination of E01/M03, each consisting of one selective nucleotide A and G, respectively. The selective amplification was conducted by the primer combination of E41/M74 having the three selective nucleotides AGG and GGT, respectively. E41 was labelled with 6-FAM at its 5′-end in order to analyze fragment sizes on a capillary sequencer (ABI 3100 Genetic Analyzer). Both PCRs were carried out in a Peltier Thermal Cycler (PTC-0200 version 4.0, MJ Research). Amplified fragments were resolved on an ABI 3100 Genetic Analyzer with an internal size standard (GS 500 ROX fluorescent dye) from Applied Biosystems.

The size of AFLP fragments were identified by Gene Scan ver. 3.7 and were scored by Genotyper version 3.7 computer programs (Applied Biosytems). The fragments were manually scored and controlled from 50 bp to 500 bp. A reproducibility test was carried out with 8 samples from three different independent runs. Seventy-one reproducible and reliable fragments were observed and chosen for the data analyses.

2.5. Data analyses

The percentage of polymorphic loci (*PPL*) and Nei's (1978) gene diversity (H_j) estimated with AFLP-SURV ver. 1.0 (Vekemans, 2002) considering only loci with frequencies of band presence below $1 - (3/N)$, where N is the total sample size (Lynch and Milligan, 1994). Allelic frequencies were computed using a Bayesian approach with non-uniform prior distribution of allele frequencies (Zhivotovsky, 1999) with slight deviation from Hardy-Weinberg equilibrium using an inbreeding value $f = 0.037$ (mean value computed by SSRs, in prep).

The analyses of variance (ANOVA) were applied to analyze variance components to detect significant differences between estimates of genetic diversity (Sokal and Rohlf, 1994). Significant values were estimated for differences between adults and regeneration, the logging types and the two regions based on the estimators of *PPL* and H_j using MICROSOFT EXCEL 2007.

Pairwise F_{ST} and significant values were estimated based on 1000 permutations using ARLEQUIN ver. 3.5.1.2 (Excoffier and Lischer, 2010).

The cluster analysis was performed based on the UPGMA method (Sneath and Sokal, 1973) derived from Nei's genetic distances (1978). One thousand bootstrapped replicated matrices of pairwise Nei's genetic distances were calculated using AFLP-SURV ver. 1.0 (Vekemans, 2002) and the results were used as inputs for computing UPGMA

dendrogram using NEIGHBOUR (UPGMA algorithm) and CONSENSE (expanded majority rule approach) of the package PHYLIP ver. 3.69 (Felsenstein, 1989). The dendrogram was visualized by TREEVIEW ver. 1.6.6 (Page, 1996). Principle Coordinate Analysis (PCA) was generated by Nei's (1978) genetic distances among populations using GENALEX ver. 6.4 (Peakall and Smouse, 2006).

Mantel test (Mantel, 1967) was used to estimate correlation between genetic (F_{ST}/(1-F_{ST})) and natural logarithm of geographic distances between sampled populations using GENALEX ver. 6.4 (Peakall and Smouse, 2006). Slaktin's (1995) pairwise genetic differentiation (F_{ST} /(1- F_{ST})) was calculated using ARLEQUIN ver. 3.5.1.2 (Excoffier and Lischer, 2010).

Genetic diversity at each level (i.e., adult, regeneration, each management type and each region) and two or more hierarchical levels (i.e., between adults and regeneration , between unlogged and selectively-logged populations, between regions) was partitioned by ARLEQUIN ver. 3.5.1.2 (Excoffier and Lischer, 2010) after estimating Analyses of Molecular Variances (AMOVA) based on pairwise differences between molecular phenotypes using the estimators of Weir and Cockerham (1984). The p -values were estimated for both markers after 1000 random permutations.

3. Results

3.1. Genetic diversity within populations

Genetic diversity varied among populations (Table 2). Similarly, genetic diversity of *T. grandis* also varied among adult and regeneration populations (Table 2). Genetic diversity of adult teak was higher than that of regeneration in population pairs in Aunglan, Mabein and Pyinmana and only in unlogged populations in Bamauk, Indaw, and Pinlebu. However, genetic diversity of adults was lower than that of regeneration in Tharawaddy and in selectively-logged populations in Indaw and Letpadan.

ANOVA tests revealed that the estimates of genetic diversity of *T. grandis* for overall adults and regeneration were not significantly different (Table 3). However, in the unlogged *T. grandis* populations, genetic diversity (H_j) for adults was significantly higher than for regeneration ($p < 0.5$) while the other estimate (*PPL*%) was not significantly different. Conversely, the genetic diversity of regeneration is slightly higher in selectively-logged than in unlogged *T. grandis* populations though the estimates were not significant.

All estimates of genetic diversity of *T. grandis* for the selectively-logged and unlogged populations were not significantly different ($p > 0.05$; Table 3). Meanwhile, genetic diversity of the northern populations was significantly higher than that of the southern populations (Table 3). Genetic diversity of adult trees was significantly higher in the northern populations.

3.2. Pairwise genetic differentiation

There was significant genetic differentiation between almost all population pairs except MUA and MSA populations as indicated by pairwise F_{ST}s (data not shown). The highest pairwise differentiation was detected between populations of the two regions (F_{ST} =

0.288, PLUR and TSA). Genetic differentiation (pairwise F_{ST}) among adult populations and among regeneration populations was significant except one adult population pair (MU vs. MS) (Table 4). The highest genetic differentiations were observed between the northern and southern populations (F_{ST} = 0.277 for adults (PLS vs. TS); F_{ST} = 0.207 for regeneration (PLU vs. AS); Table 4). Meanwhile, the lowest genetic differentiations were observed within the regions (F_{ST} = 0.004 for adults (MU vs. MS); F_{ST} = 0.014 for regeneration (PLU vs. PLS); Table 4).

3.3. Cluster analysis

UPGMA dendrogram revealed two major clusters: one for the northern populations and another one for the southern populations (Fig. 2). Within each cluster, adult populations were mostly clustered together with adjacent adult populations while regeneration populations were also clustered together with adjacent regeneration populations.

3.4. Principle Coordinate Analysis (PCA)

The two axes explained 64.08 % of the overall genetic variability (Fig.3). The first axis (40.81%) separated two groups: the northern populations and the southern populations. The second axis (23.27%) illustrated that the northern *T. grandis* populations were genetically more differentiated than the southern populations.

3.5. Mantel tests

Mantel tests revealed significant and positive correlations between geographic and genetic distances among *T. grandis* populations for adults (R = 0.638, $p < 0.01$; Fig. 4) and regeneration (R = 0.772, $p < 0.01$). Simiarly, significant and positive correlations were detected for adults and regeration in populations within the southern regions (R = 0.637, $p < 0.01$ for regeneration; R = 0.501, $p < 0.05$ for adults) and within northern region (R = 0.577, $p < 0.05$ for adults, R = 0.369, $p < 0.05$ for regeneration).

3.6. Analyses of Molecular Variance (AMOVA)

Genetic variation mostly resided within populations (87 %; Table 5). The genetic variation among all populations in Myanmar was highly significant (Φ_{ST} = 0.123, $p < 0.001$; Table 5). More than 80% of genetic variation was observed within populations for each sample stage and management types while genetic differentiation among populations was also significant (data not shown). Noticeably, the genetic differentiation among adult *T. grandis* in selectively-logged populations (Φ_{ST} = 0.163) was considerably higher than in unlogged populations (Φ_{ST} = 0.112).

Genetic variation partitioned between unlogged and selectively-logged *T. grandis* populations was not significantly different (-0.72%, Φ_{CT} = -0.007, $p > 0.05$; Table 5). Meanwhile, genetic differentiation between adults and regeneration were low but significant (1.5 %, Φ_{CT} = 0.015, $p < 0.05$; Table 5). The genetic differentiation of *T. grandis* between the two regions was highly significant ($p < 0.001$; Table 5).

4. Discussion

4.1. Genetic diversity within populations

Tropical trees are generally found to be high level of genetic diversity within populations (Hamrick *et al.*, 1992). Species with broad ranges and larger population size has higher level of genetic diversity than species with limited ranges and small populations (White et al., 2007). Similarly, we observed a relatively high level of genetic diversity of teak which still has broad ranges and large population size in Myanmar (Table 2). However, the current estimates of AFLPs are lower than the previous investigation of four adult *T. grandis* populations in Myanmar investigated with 69 AFLP loci from the same primer combination (n = 85, H_j = 0.315, PPL = 94.23) (Minn, 2007). The difference in the estimates of genetic diversity could be largely due to the different selected loci, different number of samples, sample stages and populations. Our observations are comparable to other tropical tree species investigated by AFLP markers and our estimates are quite similar to *Diperocarpus cf. condorensis* (H_j = 0.215, *PPL* = 71.20) (Luu, 2005) but lower than in *Tectona hamiltoniana* (H_j = 0.305, *PPL* = 90.23) (Minn, 2007) and higher than estimates of *Shorea leprosula* (H_j = 0.161, *PPL* = 53.23) and *Shorea parvifolia* (H_j = 0.138, *PPL*= 51.79) (Cao *et al.*, 2006) and nine Dipterocarps (H_j = 0.100 to H_E = 0.165) (Cao *et al.*, 2009).

4.2. Genetic structure of adult trees and teak regeneration

Genetic diversity of tropical and subtropical forest trees is not greatly different among different temporal stages (Hall *et al.*, 1994; Spain and Lowe, 2011). We also observed similar genetic diversity (H_j *and PPL*) for overall adults and regeneration (Table 3). Nonetheless, the genetic diversity (H_j) of adults was significantly higher than that of regeneration in the unlogged stands (Table 3). AMOVA correspondingly showed that there was significant genetic differentiation between adults and regeneration at AFLPs (1.5 %, p <0.05; Table 5). Such difference between adults and regeneration was due to the small effects of many different AFLP loci (data not shown) and some of them might be under selection.

Significant positive F_{ST}s between parental trees (adults) and young cohorts (regeneration) would be expected if many genes come from differentiated populations and young cohorts showing reduction in genetic diversity relative to parental population (Spain and Lowe, 2011). We also observed significant genetic differentiation (pairwise F_{ST}s) between adults and regeneration in each stand (data not shown). UPGMA further supports different genetic structures between two sample stages in the same stand. This genetic similarity of the same sample stages could be explained by natural selection in young regeneration stages. Thus, most of the representing genotypes of regeneration which has been selectively favored at young stages are not likely to reach adult stages due to natural selection.

Additionally, life history and ecological characteristics of tree species can also collectively define their genetic structure (Yeh, 2000). Generally, teak regeneration is abundant in logged stands since teak needs full light for its survival and growth. The genetic structure of (offspring) regeneration and (parental) adults will differ if the number of offsprings are small (White *et al.*, 2007). Thus, restricted abundance of regeneration

under light-restricted unlogged stands might also influence genetic diversity of teak regeneration.

As a rule, genetic diversity for the adults and regeneration in the same stand are expected to be similar. However, the unintentional change of genetic structure of natural regeneration can not be ruled out, even though the transmission of genes from the parent generation to the progenies implies a limited potential for drastic changes in their genetic structures (Finkeldey and Ziehe, 2004).

4.3. The impacts of selective logging on genetic variation of *T. grandis*

We detected no impact of selective logging on genetic diversity of *T. grandis.* This could be largely due to the existence of a high level of genetic diversity of *T. grandis* which has sufficient capacity to resist and recover from the human-induced genetic effects (Reusch *et al.*, 2005). Thus, the selection felling applied in these investigated stands is still considered to be a good management practice. However, logging may induce increasing genetic differentiation among populations and decreasing genetic variation within populations (Hartl and Clark, 2007; Slatkin, 1995; Young et al., 1996). Similar trends were observed in this study though the estimates were not significant.

Selective logging is mainly based on selective removal of large diameter trees. Diameter of the trees is quantitative trait which is influenced by many adaptive gene loci. In this study, we used anonymous AFLP markers which may not be relevant to judge the intensity of impacts on the diameter of *T. grandis* trees. Thus, the current finding, no impact of logging on the genetic variation of teak, is just preliminary only and simultaneously, the study strongly recommends further investigating the impact of selective logging on genetic structure of *T. grandis* forests using adaptive genetic markers.

4.4. Genetic variation and structure of *T. grandis* among populations and regions

Genetic diversity was significantly higher in the northern *T. grandis* populations, and this significant estimate was mostly attributed by adult *T. grandis* populations (Table 3). Different historical evolutionary factors like genetic drift and gene flow could be responsible for different level of genetic diversity in two regions.

Genetic variation mainly resided within populations of *T. grandis* (> 80 %), which agrees the observation because woody species with large geographic ranges and outcrossing breeding maintains more genetic diversity within species and populations but less variation among populations (Hamrick *et al.*, 1992). The result is comparable to the genetic variation within populations of *T. grandis* originating from India, Indonesia and Thailand (Changtragoon and Szmidt, 2000; Shrestha *et al.*, 2005), (Nicodemus *et al.*, 2003). It is also comparable to the study conducted by Minn (2007). The current study showed significant genetic differentiation among populations. This result is comparable to the majority of the tropical tree species (Ekue *et al.*, 2011; Minn, 2007)

Positive and significant correlations between geographic and genetic distances among populations indicate an existence of isolation by distance (IBD). This phenomenon can be characterized by increasing genetic divergence and decreasing gene flow within increasing geographical distances (Crispo and Hendry, 2005).

All the results support strong genetic differentiation between two regions. This significantly higher level of genetic differentiation could be attributed to differential selection due to different environmental conditions and reduction of population size (genetic drift) in either populations from one region and no migration between populations of the two regions and elevated rate of mutation in populations in the two regions (White *et al.*, 2007). Generally, in populations in equilibrium between drift and migration, genetic differentiation among populations is expected to increase with the geographic distance (Slatkin, 1994). All the findings indicate limited gene flow or migration between populations in the northern and southern regions, thus leading to a strong genetic differentiation. This could also be explained that the existence of the geographic barrier like the large dry area without natural *T. grandis* forests lying between the two regions might have prevented effective gene flow and migration between the regions.

Low levels of F_{ST} values within each northern and southern region indicate higher gene exchanges within the regions than between the regions. There are significant correlations between gene flow and mode of reproduction, resulting higher levels of gene flow for outcrossing or mixed mating species than for selfing species (Morjan and Rieseberg, 2004). This is mainly true for the populations within the regions in this study.

5. Implications for conservation and sustainable utilization

Teak in Myanmar still has a high level of genetic diversity. Therefore, *in situ* and *ex situ* conservation should be effectively implemented to maintain these genetic resources. Moreover, the northern and southern regions should be regarded as two different conservation regions due to strong genetic differentiation between them. Many spatially-isolated populations should also be included in the conservation programs as there is the presence of IBD and significant genetic differentiation among teak populations.

Furthermore, provenances for transfer of seeds or seedlings should be delineated based on the significant genetic differentiation among populations. Thus, seeds or reproductive materials should be collected from many different populations for gene bank storage, provenance trials and other ex-situ plantations.

Genetic structure of teak populations was unaffected by logging in this study. In other word, the selective logging applied in all investigated stands is still not dysgenic selection practice for teak forests. Nonetheless, care should be taken as excessive and intensive logging may lead to genetic erosion.

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8. Tables

Table 1 Populations, regions, logging types, sample types, geographic information and logged years of the sampled populations of *T. grandis*.

No.	Populations	Region	UL/SL	Adults Abbr.	Regen. Abbr.	Latitude	Longitude	Altitude (m)	Year (Logged)
1	Aunglan	S	UL	AUA	AUR	N19°21'10.5"	E95°48'06.8"	448	NA
2	Aunglan	S	SL	ASA	ASR	N19°19'10.7"	E95°47'38.2"	355	2005
3	Letpadan	S	UL	LUA	LUR	N18°04'42.0"	E96°06'55.9"	219	N/A
4	Letpadan	S	SL	LSA	LSR	N18°05'33.6"	E96°06'53.3"	253	2008
5	Tharawaddy	S	UL	TUA	TUR	N17°53'55.0"	E96°00'57.6"	177	N/A
6	Tharawaddy	S	SL	TSA	TSR	N17°54'23.9"	E96°01'03.5"	167	2007
7	Pyinmana	S	UL	PMUA	PMUR	N19°32'23.7"	E96°29'08.9"	794	N/A
8	Pyinmana	S	SL	PMSA	PMSR	N19°31'49.5"	E96°29'03.2"	512	2005
9	Bamauk	N	UL	BUA	BUR	N24°13'41.0"	E95°55'44.8"	203	N/A
10	Bamauk	N	SL	BSA	BSR	N24°22'51.2"	E95°55'10.0"	132	2008
11	Indaw	N	UL	IUA	IUR	N24°05'35.3"	E96°10'36.4"	281	N/A
12	Indaw	N	SL	ISA	ISR	N24°07'26.1"	E96°10'03.0"	196	2007
13	Pinlebu	N	UL	PLUA	PLUR	N23°49'54.7"	E95°22'51.7"	249	N/A
14	Pinlebu	N	SL	PLSA	PLSR	N23°49'57.6"	E95°34'21.7"	566	2007
15	Mabein	N	UL	MUA	MUR	N23°52'41.3"	E96°43'51.9"	102	N/A
16	Mabein	N	SL	MSA	MSR	N23°55'42.6"	E96°38'58.1"	171	2007

S Southern Myanmar, *N* Northern Myanmar, *UL* unlogged population, *SL* selectively-logged population, *Regen.* regeneration, *Abbr.* abbreviations, *N/A* data not available.

Table 2 Genetic diversity within populations of *T. grandis* at AFLPs.

Area	Populations	*n*	*PPL*	H_j
Aunglan	ASA	48	70.4	0.207
	ASR	49	69.0	0.198
	AUA	45	69.0	0.212
	AUR	46	73.2	0.194
Bamauk	BSA	48	73.2	0.201
	BSR	47	76.1	0.209
	BUA	38	84.5	0.257
	BUR	49	74.6	0.210
Indaw	ISA	35	83.1	0.243
	ISR	45	94.4	0.268
	IUA	43	83.1	0.245
	IUR	45	71.8	0.179
Letpadan	LSA	49	52.1	0.185
	LSR	48	52.1	0.198
	LUA	47	62.0	0.197
	LUR	47	49.3	0.191
Mabein	MSA	34	78.9	0.253
	MSR	45	67.6	0.200
	MUA	43	84.5	0.256
	MUR	49	74.6	0.204
Pinlebu	PLSA	43	60.6	0.182
	PLSR	48	70.4	0.199
	PLUA	45	74.6	0.222
	PLUR	48	39.4	0.165
Pyinmana	PMSA	49	69.0	0.219
	PMSR	47	36.6	0.151
	PMUA	47	67.6	0.199
	PMUR	48	63.4	0.171
Tharawaddy	TSA	47	42.3	0.155
	TSR	49	70.4	0.202
	TUA	46	36.6	0.158
	TUR	48	53.5	0.194
Myanmar		45	72.2	0.215

n number of samples, *PPL* percent of polymorphic loci, H_j gene diversity (Nei, 1978)

Table 3 Differences in genetic diversity within *T. grandis* at AFLPs.

	N	*PPL*	H_j
Sample types (adults vs. regeneration)			
Adults	16	68.2	0.212
Regeneration	16	64.8	0.196
Management types (UL vs. SL)			
UL	16	66.4	0.203
SL	16	66.6	0.204
Regions (northern vs. southern)			
Northern	16	74.5 [a]**	0.218 [a]**
Southern	16	58.5 [b]**	0.189 [b]**
SL (adults vs. regeneration)			
Adult	8	66.2	0.206
Regen.	8	67.1	0.203
UL (adults vs. regeneration)			
Adults	8	70.2	0.218 [a*]
Regen.	8	62.5	0.188 [b*]
Adults (SL vs. UL)			
UL	8	70.2	0.218
SL	8	66.2	0.206
Regeneration (SL vs. UL)			
UL	8	62.5	0.188
SL	8	67.1	0.203
Adults (northern vs. southern)			
Northern	8	77.8 [a**]	0.232 [a**]
Southern	8	58.6 [b**]	0.191 [b**]
Regeneration (northern vs. southern)			
Northern	8	71.1	0.204
Southern	8	58.4	0.187

SL selectively logged populations, *UL* unlogged populations, *N* number of populations, H_j gene diversity (Nei, 1978), *PPL %* percent of polymorphic loci.Values followed by different letters with (*) (**) and (***) are significant at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. All other values are not significant.

Table 4 Pairwise F_{ST} for adults (below diagonal) and regeneration (above diagonal) in *T. grandis* populations at AFLPs.

	AS	AU	BS	BU	IS	IU	LS	LU	MS	MU	PLS	PLU	PMS	PMU	TS	TU
AS		0.023	0.151	0.161	0.117	0.109	0.080	0.056	0.141	0.141	0.169	0.207	0.068	0.099	0.045	0.064
AU	0.021		0.134	0.140	0.086	0.093	0.095	0.069	0.139	0.138	0.152	0.200	0.090	0.106	0.068	0.094
BS	0.211	0.176		0.018	0.063	0.046	0.163	0.145	0.032	0.034	0.038	0.051	0.157	0.114	0.143	0.147
BU	0.097	0.094	0.082		0.059	0.046	0.169	0.161	0.037	0.039	0.036	0.068	0.161	0.121	0.165	0.163
IS	0.148	0.115	0.071	0.029		0.058	0.157	0.147	0.068	0.081	0.101	0.143	0.126	0.096	0.139	0.145
IU	0.111	0.079	0.090	0.029	0.018		0.129	0.116	0.048	0.056	0.052	0.089	0.121	0.108	0.100	0.138
LS	0.112	0.080	0.234	0.131	0.179	0.116		0.017	0.159	0.143	0.159	0.199	0.110	0.139	0.057	0.062
LU	0.116	0.063	0.203	0.115	0.119	0.082	0.079		0.143	0.127	0.151	0.183	0.096	0.127	0.042	0.041
MS	0.123	0.106	0.117	0.055	0.081	0.075	0.130	0.135		0.037	0.057	0.091	0.139	0.098	0.141	0.141
MU	0.119	0.111	0.130	0.059	0.074	0.069	0.130	0.131	0.004^{ns}		0.069	0.101	0.159	0.116	0.132	0.130
PLS	0.244	0.202	0.143	0.109	0.064	0.061	0.245	0.176	0.181	0.170		0.014	0.190	0.145	0.147	0.157
PLU	0.159	0.124	0.040	0.041	0.024	0.037	0.171	0.141	0.094	0.092	0.059		0.237	0.188	0.178	0.191
PMS	0.034	0.036	0.232	0.099	0.148	0.100	0.088	0.093	0.134	0.126	0.236	0.158		0.035	0.075	0.058
PMU	0.029	0.028	0.183	0.084	0.135	0.078	0.102	0.102	0.116	0.116	0.207	0.127	0.020		0.094	0.073
TS	0.127	0.108	0.266	0.169	0.191	0.139	0.104	0.102	0.185	0.174	0.277	0.199	0.108	0.116		0.045
TU	0.100	0.092	0.255	0.144	0.175	0.123	0.109	0.106	0.181	0.176	0.256	0.182	0.080	0.089	0.031	

Populations: the last letter; *S* selectively-logged *T. grandis* population and *U* unlogged *T. grandis* population; the first letters; *A* Aunglan, *B* Bamauk, *I* Indaw, *L* Letpadan, *M* Mabein, *PL* Pinlebu, *PM* Pyinmana and *T* Tharawaddy, *ns* not significant and all others are significant at $p < 0.05$.

Table 5 Analyses of Molecular Variance (AMOVA) for different groups of *T. grandis* at AFLPs.

Source of variation	d.f.	S.S.	V.C.	% V	Φ statistics	*p* value
All Myanmar populations						
Among populations	31	1541.54	0.93	12.3	$\Phi_{ST} = 0.123$	< 0.001
Within populations	1462	9603.81	6.57	87.7		
Adults and regeneration						
Among groups	1	130.88	0.112	1.5	$\Phi_{CT} = 0.015$	< 0.05
Among populations within groups	30	1410.67	0.867	11.5	$\Phi_{SC} = 0.117$	< 0.001
Within populations	1462	9603.81	6.569	87.0	$\Phi_{ST} = 0.130$	< 0.001
Unlogged and selectively-logged populations						
Among groups	1	11.05	-0.054	-0.72	$\Phi_{CT} = -0.007$	> 0.5
Among populations within groups	30	1530.49	0.952	12.8	$\Phi_{SC} = 0.127$	< 0.001
Within populations	1462	9603.81	6.569	88.0	$\Phi_{ST} = 0.120$	< 0.001
Northern and southern regions						
Among groups	1	497.15	0.620	8.0	$\Phi_{CT} = 0.080$	< 0.001
Among populations within groups	30	1044.39	0.605	7.8	$\Phi_{SC} = 0.084$	< 0.001
Within populations	1462	9603.81	6.569	84.3	$\Phi_{ST} = 0.157$	< 0.001

d.f. degree of freedom, *S.S.* sum of square, *V.C.* variance components, *% V* percentage of variation. *p* -values were obtained after 1000 permutations.

9. Figures

Fig. 1 Map showing locations of sampled *T. grandis* populations in Myanmar

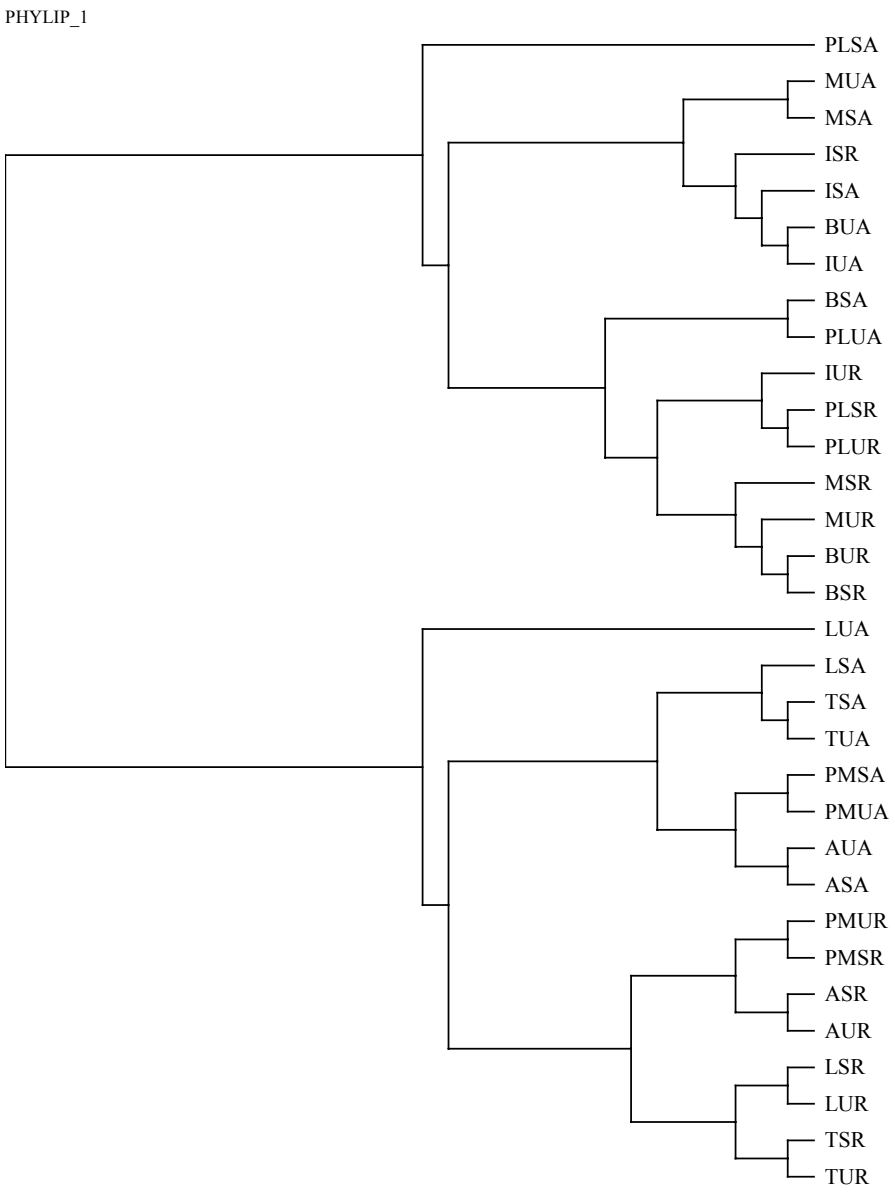
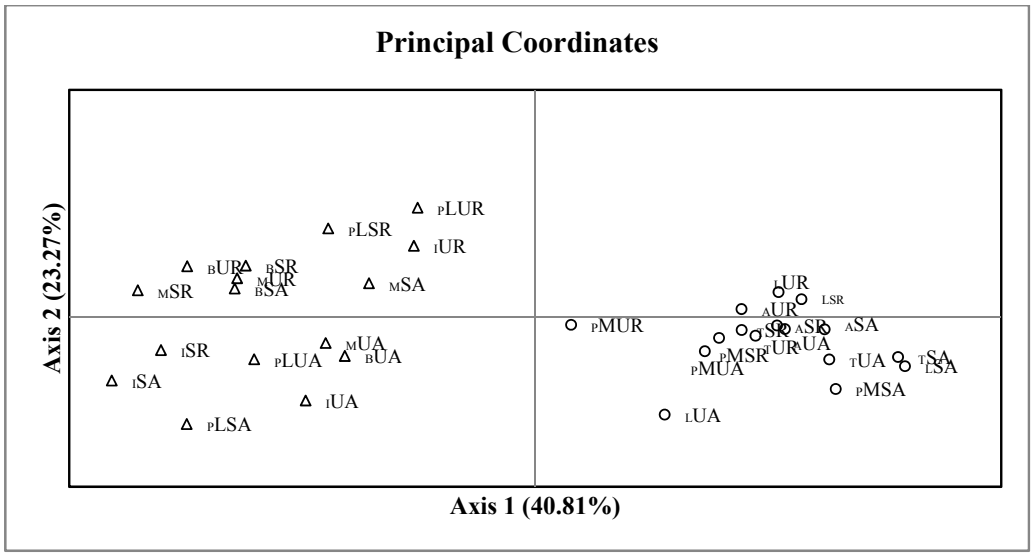


Fig. 2 UPGMA dendrogram based on Nei's genetic distances (1978) at AFLPs. The robustness of the tree was supported by bootstrapping values based on 1000 replications.



northern populations, southern populations

Fig. 3 Principal Coordinate Analysis (PCA) of *T. grandis* populations at AFLPs.

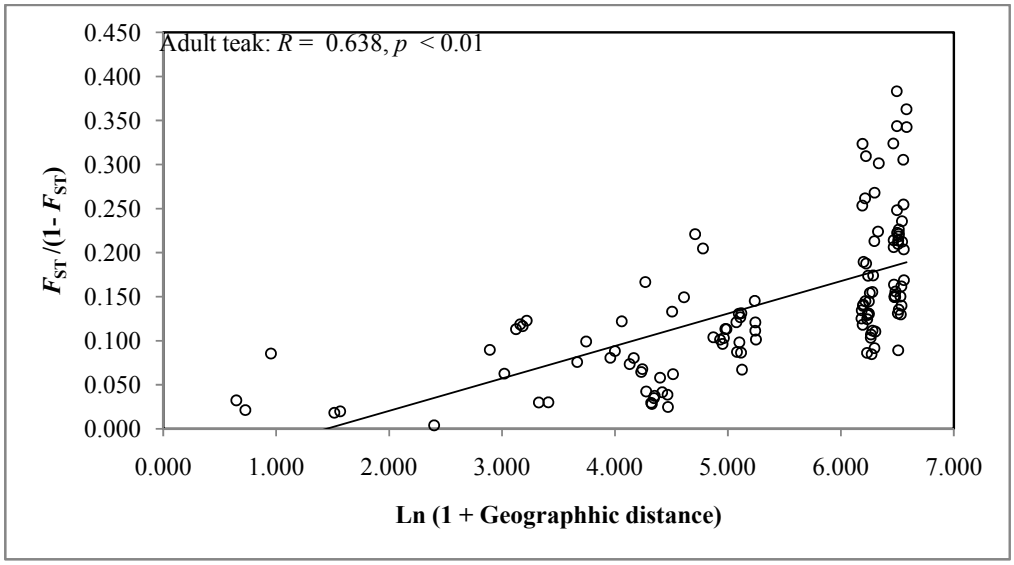


Fig.4 Relationship between geographic and genetic distances among adult *T. grandis* populations.

Curriculum Vitae

1. Title of Paper: : Genetic Variation of Teak (*Tectona grandis* Linn. f.) in Myanmar revealed by Amplified Fragment Length Polymorphisms (AFLPs)

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6. Publications

Thein, H.M., Kanzaka, M., Fukushima, M., Minn, Y., 2007. Structure and composition of a teak-bearing forest under Myanmar Selection System: Impacts of logging and bamboo flowering; *South East Asian Studies* 45: 303-316.

Fukushima, M., Kanzaki, M., Thein, H. M., Minn, Y., 2007. Recovery Process of Fallow Vegetation in the traditional Karen Swidden Cultivation System in the Bago Mountain Range, Myanmar. South East Asian Studies 45: 317-333.

Minn, Y., Prinz, K., Finkeldey, R., 2013 (submitted) Genetic variation of teak (*Tectona grandis* Linn. f.) in Myanmar revealed by microsatellites

Master thesis

Minn, Y., 2007. Genetic diversity within and among populations of teak (*Tectona grandis* Linn f.) and dahat (*Tectona hamiltoniana* Wall.) in Myanmar detected by AFLPs and cpSSRs. Master Thesis, Forest Genetics and Forest Tree Breeding, Goettingen University, Germany.

Ph.D. thesis

Minn, Y., 2012. Investigation of genetic variation of teak (*Tectona grandis* Linn. f.) in Myanmar for conservation and sustainable utilization of genetic resources. Ph.D. thesis. Forest Genetics and Forest Tree Breeding, Goettingen University, Germany.