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Original article

Dynamics of Species Composition over 16 years in Long-term Dynamic Plots of Sakaerat Deciduous Dipterocarp Forest, Northeastern Thailand

Pongsak Sahunalu

Independent Researcher, Kasetsart University, Chatuchak, Bangkok, 10900, Thailand
E-mail: fforpss@ku.ac.th

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ABSTRACT

The species composition (DBH ≥ 4.5 cm) of a deciduous dipterocarp forest in Sakaerat, northeastern Thailand, was studied over a 16-year period. Changes occurred contemporaneously by the addition of new tree species and the loss of some initial tree species in the plots that were 1 ha in size in each of four stands, as a result of tree mortality and recruitment. In stands 1 to 4, the permanent loss of initial tree species was 5, 3, 1 and 1 species, respectively, while new tree species with individual trees having a DBH reaching 4.5 cm were 10, 20, 27 and 6 species, respectively. The gains and losses in tree species affected the importance value index (IVI) of each tree species in the stand, with some tree species experiencing an increase and some a decrease in their IVI values. The initial dominant tree species demonstrated their declining IVI differently in each stand. Stand 1 demonstrated its association type change clearly, while the other three stands maintained the initial association types throughout the study period. The most notable change was the shift of the IVI of most legume tree species from a lower rank in the stands to a higher rank. The final results of the 16-year investigation demonstrated that 19, 17, 16 and 23 tree species increased their IVI value and 19, 16, 16 and 14 tree species decreased their IVI value in stands 1 to 4, respectively. Each stand of the deciduous dipterocarp forest community in Sakaerat exhibited a dynamic equilibrium in gaining and losing IVI differently, with those having a prominent gain being mostly legume tree species in the four stands, together with some relatively fast growing tree species newly recruited into the stands to compensate for declining IVI values of some initially leading tree species.

Keywords: deciduous dipterocarp forest, dynamic equilibrium, species composition change, Sakaerat

INTRODUCTION

Forest community dynamics involve spatial and temporal changes in the community structure, mortality, recruitment and growth of the living and newly recruited tree species over time. There are continuous gains and losses in the tree species population that result in maintenance of the structure and function, as well as the species composition and species diversity in those communities.

Thailand has recently become aware of the loss of natural forest resources through various destructive and deteriorating processes.

The conservation of the remaining patchy forest communities has been given an urgent and high priority, especially to preserve most of the relatively good and representative stands of each forest community type, at least for the purpose of *in-situ* plant conservation and to provide the functional services that the dry deciduous forest (DDF) type can contribute to ecology. Most of the protected areas are classified as National Parks, Wildlife Sanctuaries, Biosphere Reserves and other national forest reserves, which are considered to be the most effective way of *in-situ* conservation of plant genetic resources in their original or native distributing sites. In addition, *ex-situ* conservation practices are attempted to introduce native tree species to ameliorate or restore degraded forest or fragmented forest tracts. Knowledge of species composition changes through time under natural conditions in any protected forest type is therefore very necessary for future planning of intensive forest management to achieve sustainable conservation of the forests, maintain the habitats of various kinds of wildlife and protect the land from severe environmental hazards. Emphasis is given to the deciduous dipterocarp forest community (DDF), particularly as it occurs in the Sakaerat Biosphere Reserves (SDDF) in northeast Thailand as one of the representatives of tropical dry forest community types that has been neglected and has lacked long-term study in this region and in this country as a whole.

It has been demonstrated that during the period of 16 years of the investigation and monitoring of the deciduous dipterocarp forest in the Reserves, the community has apparently changed in terms of its dominant tree species as a result of tree mortality and recruitment, showing an imbalance between the two mechanisms (Sahunalu, 2009b). The whole SDDF community has gained a considerable number of trees while maintaining a relatively stable tree size distribution (Sahunalu, 2009a) which has been evidenced by its gain in total community basal area (Sahunalu, 2010). It is also apparent that numerous tree species have been recruited into the stands that are different from the initial dominant tree species, with the new species tending to become the dominant species over the period of 16 years. As the dynamics of the stands have occurred over such a relatively long-term period, it is, therefore, interesting to investigate to what extent the SDDF community has undergone its change in species composition and what tree species have become the most successful in occupying the habitat.

This paper reports the results of a study over 16 years on the species composition changes in the long-term and into the large scale permanent forest dynamics monitored using SDDF plots under natural conditions with minimum anthropogenic disturbances, as well as no apparent and severe or episodic catastrophic disturbance over a relatively long period. The knowledge gained from this study will improve understanding of the ecology and dynamics of one type of dry tropical forest, particularly the DDF and provide a guideline for formulating further the forest management and conservation strategies and manipulation planning for this precious forest community type.

MATERIALS AND METHODS

Recorded data used for this study were based on species composition together with tree DBH in the four stands dominated by different major tree species from the repeated censuses at approximately 1-year intervals over 16 years from 1984 to 2000. Tree species performance in each stand was analyzed by evaluating tree IVI similar to the procedures reported in Sahunalu (2009a). The balance between IVI gains and losses of 10 selected prominent tree species was also investigated in the four stands to elucidate the dynamic equilibrium of each species in the four representative stands.

RESULTS AND DISCUSSION

Species Composition Changes

Monitoring the four stands for 16 years in SDDF, involved evaluating the IVI of each tree species, including lianas and some unidentified perennial plants (all DBH ≥ 4.5 cm). The net changes are shown in Tables 1 to 4.

Table 1 IVI (%) of trees (DBH ≥ 4.5 cm) in stand 1 in 2000 and their net changes in IVI during 1984-2000. * indicates newly appearing species after 1984; D indicates species that have disappeared from the stand.

species	IVI	Net change in IVI[1]
Albizia odoratissima (L.f.) Benth.	6.793	5.826
Antiaris toxicaria Lesch.	0.457	-0.510
Antidesma ghaesembilla Gaerth.	0.463	-0.034
Antidesma laurifolium Airy Shaw	0.425	-0.517
Aporosa villosa (Wall. ex Lindl.)Baill.	3.145	-1.559
Bauhinia sp.	1.338	0.642
Bombax insigne Wall.	0.585	-0.427
Buchanania lanzan Spreng.	1.223	*
Canarium subulatum Guillaumin	0.420	*
Careya sphaerica Roxb.	2.151	-0.540
Cratoxylum formosum (Jack) Dyer	2.245	1.792
Dalbergia cultrata Graham ex Benth.	7.082	-0.272
Dalbergia nigrescens Kurz	1.861	*
Dalbergia oliveri Gamble	2.215	0.957
Dillenia obovata (Blume) Hoogland	7.313	-6.346
Diospyros ehretioides Wall. ex G.Don	2.833	-1.586
Diospyros mollis Griff.	D	D
Dipterocarpus intricatus Dyer	39.046	-0.924
Flacourtia sp.	0.411	*
Gardenia sootepensis Hutch.	0.428	-0.033
Grewia sp.	2.094	*
Irvingia malayana Oliv. ex A.W. Benn.	4.405	2.414
Ixora ebarbata Craib	D	D
Kydia calycina Roxb.	0.691	0.011
Lannea coromandelica (Houtt.) Merr.	8.173	5.239
Mangifera caloneura Kurz	4.161	-1.544
Mitragyna rotundifolia (Roxb.) Kuntze	13.555	-1.336
Morinda coreia Ham.	6.008	1.917
Morinda elliptica Ridl.	0.826	*
Nauclea officinalis (Pierre ex Pit.) Merr. & Chun	0.413	*
Phyllanthus emblica L.	D	D
Pterocarpus macrocarpus Kurz	41.553	8.055
Quercus kerrii Craib	17.074	-25.662
Rothmannia wittii (Craib) Bremek.	0.603	*
Shorea obtusa Wall.ex Blume	22.615	-1.071
Shorea roxburghii G.Don	42.437	-3.572
Shorea siamensis Miq.	8.952	2.586
Sindora siamensis Teijsm. & Miq.	7.666	-0.498
Syzygium cumini (L.) Skeels	0.612	0.007
Terminalia chebula Retz. var. *chebula*	D	D
Unidentified	0.481	-0.576
Unidentified (Liana)	D	D
Vitex peduncularis Wall.ex Schauer	6.944	-1.478
Xylia xylocarpa var. *kerrii* (Craib & Hutch) I.C. Nielsen	30.302	14.563
Total species		44
Total new species		8
Total disappeared species		5
Total IVI gained species		12
Total IVI lost species		19

Note: [1] Figures with negative sign (-) in the last column indicate that the IVI decreased.

Table 2 IVI (%) of trees (DBH ≥ 4.5 cm) in stand 2 in 2000 and their net changes in IVI during 1984-2000. * indicates newly appearing species after 1984; D indicates species that have disappeared from the stand.

Species	IVI	Net change in IVI (%)[1]
Albizia odoratissima (L. f.) Benth.	8.180	3.048
Aporosa villosa (Wall. ex Lindl.) Baill.	0.280	-0.165
Bauhinia saccocalyx Pierre	3.470	-0.396
Bauhinia sp.	2.093	*
Bombax insigne Wall.	0.590	*
Buchanania lanzan Spreng.	0.395	-0.051
Canarium subulatum Guillaumin	8.283	7.717
Canthium parvifolium Roxb.	0.567	*
Carallia brachiata (Lour.) Merr.	0.395	*
Careya sphaerica Roxb.	0.578	0.107
Cratoxylum formosum (Jack) Dyer	5.492	*
Croton roxburghii N.P. Balakr.	0.876	*
Dalbergia cochinchinensis Pierre	0.276	*
Dalbergia cultrata Graham ex Benth.	2.754	0.774
Dalbergia nigrescens Kurz	0.558	*
Dalbergia oliveri Gamble	1.952	*
Dillenia obovata (Blume) Hoogland	0.664	-0.338
Diospyros castanea Fletcher	0.280	*
Diospyros ehretioides Wall. ex G.Don	0.948	-0.071
Dipterocarpus intricatus Dyer	5.155	-1.202
Erythrophleum succirubrum Gagnep.	0.283	-0.756
Gardenia sootepensis Hutch.	6.659	2.161
Grewia sp.	0.303	*
Irvingia malayana Oliv. ex A.W. Benn.	3.173	0.641
Kydia calycina Roxb.	0.590	0.133
Lannea coromandelica (Houtt.) Merr.	2.452	1.346
Lithocarpus polystachyus (Wall. ex A.DC.) Rehder	4.970	4.033
Mallotus philippensis Mull.Arg.	0.284	*
Mangifera caloneura Kurz	12.823	-1.776
Mitragyna rotundifolia (Roxb.) Kuntze	4.377	-0.439
Morinda coreia Ham.	4.744	-2.077
Morinda elliptica Ridl.	0.554	*
Nauclea officinalis (Pierre ex Pit.) Merr. & Chun	0.278	*
Parinari anamense Hance	0.541	-0.105
Pavetta tomentosa Roxb. ex Sm. var.*canescens* Craib	0.555	*
Pterocarpus macrocarpus Kurz	23.537	-4.984
Quercus kerrii Craib	8.251	0.310
Rothmannia wittii (Craib) Bremek.	5.459	4.082
Shorea obtusa Wall. ex Blume	85.464	-38.191
Shorea roxburghii G. Don	2.631	-1.433
Shorea siamensis Miq.	54.212	3.916
Sindora siamensis Teijsm. & Miq.	2.354	-2.379
Siphonodon celastrineus Griff.	0.559	*
Syzygium cumini (L.) Skeels	0.712	0.215
Terminalia chebula Retz. var. *chebula*	0.291	-0.173
Terminalia triptera Stapf	0.281	*
Unidentified	4.257	1.220
Vaccinium sprengelii (G.Don) Sleumer	D	D
Vitex canescens Kurz	0.875	0.418
Vitex peduncularis Wall. ex Schauer	2.377	1.017
Vitex pinnata L.	0.282	*
Wendlandia tinctoria (Roxb.) DC.	3.594	*
Xantolis cambodiana (Pierre ex Dubarb) P. Royen	0.659	*
Xylia xylocarpa var. *kerrii* (Craib & Hutch) I.C. Nielsen	17.832	3.652
Total species		54
Total new species		20
Total disappeared species		1
Total IVI gained species		17
Total IVI lost species		16

Note: [1] Figures with minus (-) in the last column indicate that the IVI decreased.

Table 3 IVI (%) of tree species (DBH ≥ 4.5 cm) in stand 3 in 2000 and their net changes in IVI during 1984-2000. * indicates newly appearing species after 1984; D indicates species that have disappeared from the stand.

Species	IVI	Net change in IVI (%)[1]
Afzelia xylocarpa (Kurz) Craib	0.245	*
Albizia odoratissima (L.f.) Benth.	6.775	1.899
Antidesma laurifolium Airy Shaw	0.794	0.344
Aporosa villosa (Wall. ex Lindl.) Baill.	4.019	3.557
Artocarpus lacucha Roxb.	0.772	0.327
Bauhinia sp.	5.238	2.275
Bombax anceps Pierre var. *anceps*	0.661	*
Buchanania lanzan Spreng.	0.491	*
Canarium subulatum Guillaumin	2.853	2.394
Careya sphaerica Roxb.	2.609	-1.360
Catunaregam tomentosa (Blume ex DC.) Tirveng.	0.248	*
Cratoxylum cochinchinense (Lour.) Blume	0.249	*
Cratoxylum formosum (Jack) Dyer	16.132	*
Croton roxburghii N.P. Balakr.	0.763	*
Dalbergia cultrata Graham ex Benth.	0.242	*
Dalbergia nigrescens Kurz	3.669	0.720
Dalbergia oliveri Gamble	1.919	-0.364
Dillenia obovata (Blume) Hoogland	0.571	-0.386
Diospyros ehretioides Wall. ex G. Don	2.626	-0.082
Diospyros oblonga Wall. ex G. Don	1.713	-0.263
Dipterocarpus intricatus Dyer	14.658	-4.646
Erythrophleum succirubrum Gagnep.	3.050	1.591
Flacourtia sp.	1.023	*
Gardenia sootepensis Hutch.	11.096	8.747
Gomphia serrata (Gaertn.) Kanis	0.488	*
Grewia eriocarpa Juss.	0.253	*
Grewia sp.	0.492	*
Haldina cordifolia (Roxb.) Ridsdale	0.246	*
Hibiscus macrophyllus Roxb. ex Hornem.	0.248	*
Hymenodictyon orixense (Roxb.) Mabb.	0.244	*
Irvingia malayana Oliv. ex A.W. Benn.	1.378	0.329
Ixora ebarbata Craib	0.493	*
Lannea coromandelica (Houtt.) Merr.	15.237	*
Mangifera caloneura Kurz	0.851	-0.076
Memecylon scutellatum Naudin	0.242	*
Mitragyna rotundifolia (Roxb.) Kunze	5.698	-2.362
Morinda coreia Ham.	7.967	-0.411
Parinari anamense Hance	1.842	-0.189
Pavetta tomentosa Roxb. ex Sm. var. *canescens* Craib	2.388	*
Phyllanthus emblica L.	3.116	2.585
Pterocarpus macrocapus Kurz	34.424	-3.465
Quercus kerrii Craib	1.672	-0.468
Semecarpus reticulate Lecomte	1.176	-0.341
Shorea obtusa Wall. ex Blume	92.909	-64.121
Shorea roxburghii G.Don	11.163	3.354
Shorea siamensis Miq.	0.253	*
Sindora siamensis Teijsm. & Miq.	10.428	-0.918
Siphonodon celastrineus Griff.	2.749	1.836
Syzygium cumini (L.) Skeels	2.106	-1.462
Terminalia chebula Retz. var. *chebula*	0.748	*
Ternstroemia gymnanthera (Wight & Arn.) Bedd.	0.268	*
Unidentified	1.766	1.307
Unidentified (liana)	0.242	*
Vitex pinnata L.	0.521	*
Xantolis cambodiana (Pierre ex Dubarb) P. Royen	0.517	*
Xylia xylocarpa var. *kerrii* (Craib & Hutch) I.C. Nielsen	13.865	6.064
Total species		57
Total new species		25
Total disappeared species		-
Total IVI gained species		16
Total IVI lost species		16

Note: [1]Figures with minus (-) in the last column indicate that the IVI decreased.

Table 4 IVI (%) of tree species (DBH ≥ 4.5 cm) in stand 4 in 2000 and their net changes in IVI during 1984-2000. * indicates newly appearing species after 1984; D indicates species that have disappeared from the stand.

Species	IVI	Net change in IVI (%)[1]
Albizia odoratissima (L.f.) Benth.	5.950	1.495
Antiaris toxicaria Lesch.	0.392	-0.007
Antidesma laurifolium Airy Shaw	1.231	0.003
Aporosa villosa (Wall. ex Lindl.)Baill.	1.911	-1.398
Bauhinia saccocalyx Pierre	1.496	0.072
Bauhinia sp.	0.913	*
Berrya cordifolia (Willd.) Burret	0.382	*
Bombax insigne Wall.	0.778	*
Canarium subulatum Guillaumin	2.318	1.405
Careya sphaerica Roxb.	1.548	-0.055
Cratoxylum formosum (Jack) Dyer	2.888	0.543
Dalbergia assamica Benth.	D	D
Dalbergia cultrata Graham ex Benth.	5.409	-2.106
Dalbergia oliveri Gamble	5.003	1.981
Dillenia obovata (Blume) Hoogland	0.416	0.017
Diospyros ehretioides Wall. ex G.Don	0.783	-0.019
Diospyros mollis Griff.	0.472	0.007
Dipterocarpus intricatus Dyer	9.320	-0.066
Gardenia sootepensis Hutch.	7.880	1.779
Irvingia malayana Oliv. ex A.W. Benn.	2.029	0.442
Lannea coromandelica (Houtt.) Merr.	0.769	*
Lithocarpus polystachyus (Wall. ex A.DC.) Rehder	4.462	0.669
Mitragyna rotundifolia (Roxb.) Kunze	11.683	3.306
Morinda coreia Ham.	11.541	1.763
Nauclea officinalis (Pierre ex Pit.) Merr. & Chun	0.783	-0.803
Nauclea orientalis (L.) L.	0.418	0.001
Parinari anamense Hance	1.813	0.098
Phyllanthus emblica L.	0.380	-0.813
Premna pyramidata Wall. ex Schauer	0.462	0.009
Pterocarpus macrocarpus Kurz	23.862	2.740
Quercus kerrii Craib	20.911	-3.498
Shorea obtusa Wall. ex Blume	0.598	-0.388
Shorea roxburghii G.Don	51.597	-22.138
Shorea siamensis Miq.	90.174	9.430
Sindora siamensis Teijsm. & Miq.	11.321	0.476
Spondias pinnata (L.f.) Kurz	0.390	*
Stereospermum neuranthum Kurz	0.711	0.114
Syzygium cumini (L.) Skeels	0.864	-0.375
Terminalia chebula Retz. var. *chebula*	0.421	0.018
Unidentified	0.763	-0.581
Vitex peduncularis Wall. ex Schauer	3.137	-0.426
Vitex pinnata L.	0.391	*
Xylia xylocarpa var. kerrii (Craib & Hutch) I.C. Nielsen	11.412	3.235
Total species		43
Total new species		6
Total disappeared species		1
Total IVI gained species		22
Total IVI lost species		14

Note: [1]Figures with minus (-) in the last column indicate that the IVI decreased.

Due to annual tree species mortality and recruitment, there appears to have been five tree species lost from stand 1. These tree species are *Diospyros mollis, Ixora ebarbata, Phyllanthus emblica, Terminalia chebula* and a species of unidentified liana. Stand 2 lost one tree species, namely *Vaccinium sprengelii*, while stand 4 also lost only one species, namely *Dalbergia assamica*. Stand 3 had no species loss. On the contrary, there were numerous new tree species. This occurred in stand 1, where eight new tree species were recorded as their diameters increased by recruitment above the threshold DBH of 4.5 cm and over. Stand 2 had 20 new additional tree species, whilst stand 3 had 25 new tree species by recruitment. Stand 4 had only six new tree species. It was apparent that numerous new species were added to the four stands, creating a sizable change in species composition, which is discussed below.

Evaluation of the IVI of each species after the 16-year period showed that all species in the four stands had changed their IVI values from their original values at the onset of the investigation in 1984 (Tables 1 to 4), with some increases and decreases in IVI due to tree recruitment and mortality. Some tree species were entirely new to the stands having been below the threshold DBH of 4.5 cm during the previous census periods and they just appeared and were included in the stands during the intermediate and final tree census periods.

Investigation of the same tree species in the four stands during the 16-year period revealed that tree species initially growing in the four stands had changed their IVI value to different degrees, indicating their variable performance in successfully occupying the same habitat in the same forest community (Tables 1 to 4). Within the total of 44 tree species found in stand 1, 12 tree species gained in IVI value and 19 tree species reduced their IVI value, providing a relatively imbalance between the two attributes. The most prominent tree species that increased their IVI remarkably in stand 1 were: *Albizia odoratissima, Lannea coromandelica, Pterocarpus macrocarpus, Shorea siamensis* and *Xylia xylocarpa* var. *kerrii*. (Table 1). The most notable tree species that increased their IVI in stand 2 were: *A. odoratissima, Canarium subulatum, Lithocarpus polystachyus, Rothmannia wittii, S. siamensis* and *X. xylocrpa* var. *kerrii* (Table 2). Meanwhile, stand 3 had several tree species that increased their IVI, such as *A. odoratissima, Aporosa villosa, Bauhinia* sp., *C. subulatum, Gardenia sootepensis, P. emblica, Shorea roxburghii* and *X. xylocarpa* var. *kerrii* (Table 3). Notable tree species that increased their IVI in stand 4 were: *A. odoratissima, Mitragyna rotundifolia, P. macrocarpus,* and *X. xylocarpa* var. *kerrii* (Table 4).

The most notable tree species in stand 1 that had a decline in their IVI were: *A. villosa, Dillenia obovata, Diospyros ehretioides, Quercus kerrii, S. roxburghii* and some other minor species. In stand 2, many species reduced their IVI, such as *Dipterocarpus intricatus, Mangifera caloneura, P. macrocarpus, Shorea obtusa, S. siamensis* and other minor species. Stand 3 showed that various dominant species had a reduction in their IVI, namely: *D. intricatus, M. rotundifolia, P. macrocarpus, S. obtusa,* and some of their minor associated species. Notable tree species that had a reduced IVI in stand 4 included *A. villosa, Dalbergia cultrata, Q. kerrii, S. roxburghii* and some other minorspecies. It is apparent that in stand 1 where *S. roxburghii* and *Q. kerrii* were the two dominant species in the initial period, there was some change in the major association species, with *S. roxburghii* and *P. macrocarpus* being the two leading tree species having the highest IVI values. Stand 2 was dominated initially by *S. obtusa* and *S. siamensis* and this did not change, though their IVI values changed from their initial values. Stand 3 was dominated initially by *S. obtusa* and *P. macrocarpus* and these two species ratined their dominance, although their IVI values declined considerably. Stand 4 was initially dominated by *S. siamensis* and *S. roxburghii* and again they retained their dominance, although the former species had a substantial reduction in its IVI, while the latter one substantially increased its IVI.

After the 16-year study period, the

number of tree species that increased their IVI value was 12, 17, 16 and 22 in stands 1, 2, 3 and 4, respectively, whilst the number that decreased their IVI value was 19, 16, 16 and 14 species in the four stands, respectively. The net increase in the number of species was 8, 20, 25 and 6, respectively, in stands 1, 2, 3 and 4. The number of newly recruited tree species that contributed to the increase in species composition was 8, 20, 25 and 6, respectively, in stands 1, 2, 3 and 4. Net losses of tree species were 5, 1 and 1 tree species, respectively in stands 1, 2 and 4. Stand 3 had no species loss (Tables 1 to 4). As IVI is an index derived from the summation of the percentages of relative density, frequency and dominance of each tree species (Curtis and McIntosh, 1951), it is usually interpreted as an indicator of successful performance of those tree species in a given habitat. Change in IVI is, therefore, referred to as the overall capability of each tree species to grow in each stand. SDDF has been managed to maintain a minimum anthropogenic disturbance and the whole DDF community has been well controlled by keeping forest ground fires to a minimum over a long period by the Biosphere Reserves strategies. Therefore, it is considered that changes in the IVI of each tree species are the result of their responses to the natural conditions over time or have resulted from temporal change that might progressively or retrogressively alter the species composition in each stand. Tree species that had permanently disappeared from the four stands were: *D. mollis, P. emblica, I. ebarbata, T. chebula, V. sprengelii, D. assamica* and a species of unidentified liana. All the tree species that disappeared had relatively low IVI values initially. Some tree species appear to have been new entries recruited into the stands and have exhibited their success in occupying the habitat in different ways in each stand, suggesting that there have been spatial variations in such tree replacement events. Long-term monitoring of various forest community types by several investigators also recorded the change in the initial tree species to new ones. A dendrochronological study by tree ring analysis of an old-growth white oak forest on the Atlantic side, northern Virginia, USA, by Abrams and Copenheaver (1999) discussed the history of the decline of white oak (*Quercus alba*), a former dominant tree species on the site that was replaced by a *Fagus, Liriodendron* and *Acer rubrum* forest community. Schnitzler and Closset (2003) found a birch (*Betula pedula*) community changed to beech (*Fagus sylvatica*) as the new dominant tree species in Vosges, France after 50 years of forest dynamic monitoring. Dynamics study over 5 years of an old-growth forest dominated by *Chamaecyparis obtusa* in the Asakawa Forest Reserve, Kiso district, central Japan also found a tendency to change to a dominant tree species of Tsujopsis dolabrata, with the latter tree species being an understorey tree initially (Yamamoto, 1993). A result of a 36-year investigation in old-growth *Pseudotsuga-Tsuga* forest in the Cascade Range of southern Washington, USA, by Franklin and DeBell (1988) concluded that stand dominance shifted slowly from *Pseudotsuga menziesii* to *Tsuga heterophylla*, although both species had similar mortality rates as there was no recruitment of shade-tolerant former tree species. Adjacent stands of seasonal dry evergreen forest or seasonal evergreen rain forest (SERF) in Sakaerat, northeastern Thailand dominated by *Hopea ferrea* (Bunyavejchewin, 1999) also showed a tendency for stand degeneration after observation for 10 years, but there were many possibilities that the stand might be dominated by other tree species rather than maintaining the same initial dominant tree species, as the recruitment rate of this dominant tree species was found to be lower than the mortality rate, except for a stand dominated by Shorea henryana that seemed to maintain the same dominant tree species. Over a 16-year observation period in sub-boreal conifer-hardwood mixed forest, northern Japan, Takahashi *et al*. (2003) noted the tendency of *Quercus crispula*, a dominant canopy tree, to produce its own saplings only rarely to recruit successfully underneath the same mother tree, although its mortality was quite low. The stand was still changing and had not stabilized in terms of both species composition and tree size structure. A study on dynamics over 30 years of an old-growth mixed mesophytic forest in Dysart Woods, northern Ohio, USA found that beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) were predicted to be important while the dominance of white oak (*Quercus alba*) would decrease, due to the high mortality in large size classes of this tree species and decreasing density due to regeneration failure (McCarthy *et al*., 2001). The deciduous dipterocarp forest community in Sakaerat (SDDF) was also no exception, as very few saplings of the overstorey and dominant conspecific tree species were observed underneath or in the vicinity of mother trees or elsewhere inside the stands. It has always been thought that most tree species in dry forests can regenerate well by sprouting under favorable conditions. However, without disturbance induction, sprouting of those tree species might not occur easily, particularly in this forest community type. An observation in a scrub forest type originally recognized as deteriorated DDF in Ratchaburi, western Thailand (personal observation) suggested that remnant tree species readily grew relatively fast by sprouting after all trees in the stand were clear cut at the base of the stem and under strict forest fire control conditions for a brief period. Gap-phase regeneration or regeneration by seeds may play an insignificant role in inducing natural regeneration of this dry forest type. This observation is supported by a result of a study on coppicing regrowth in a disturbed tropical dry forest in Jamaica (McLaren and McDonald, 2003), where coppice regrowth after cutting was observed to be vigorous among and within the species cut in this forest type and 81% of the 51 tree species were reported to have recovered by using strong coppicing. Coppicing has been known for a long time as the stand regeneration mechanism in most dry forest sites where the stem and root remain in place (Ewel, 1977; Murphy and Lugo, 1986; Murphy *et al*., 1983, 1995).

Dynamic equilibrium in species composition

Investigations on the species dynamic equilibrium in the four stands was carried out by selecting 10 high IVI ranking tree species initially recorded in each stand; their gains and losses in IVI during the 16-year period are shown in Figure 1.

It is clear that in stand 1, *P. macrocarpus* and *X. xylocarpa* var. *kerrii*, which are legume tree species, showed a prominent increase in their IVI values, while *Q. kerrii* reduced its IVI greatly, without any sign of an increase, as was observed similarly for *D. obovata*. Equilibrium in maintaining species IVI in this stand is, therefore, attributable to the greatest mortality occurring in *Q. kerrii*, but *P. macrocarpus* and *X. xylocarpa* var. *kerrii* had greater recruitment, together with new entry tree species, such as *L. coromandelica* and *S. siamensis* that shifted their IVI ranking higher to replace *D. obovata* and *Vitex peduncularis* (Figure 1).

In stand 2, S. obtusa was the most dominant tree species and tended to have the greatest reduction in IVI without any species having significant gains, though other tree species, such as *P. macrocarpus, M. rotundifolia, Morinda coreia, M. caloneura and D. intricatus,* all increased their IVI values slightly. Tree species that appeared to have notable increases in their IVI values to compensate for the IVI loss by *S. obtusa* were: *S. siamensis, X. xylocarpa* var. *kerii*, A. *odoratissima* and three new entry additional species, namely *C. subulatum, Cratoxylum formosum* and *Gardenia sootepensis* (Figure1).

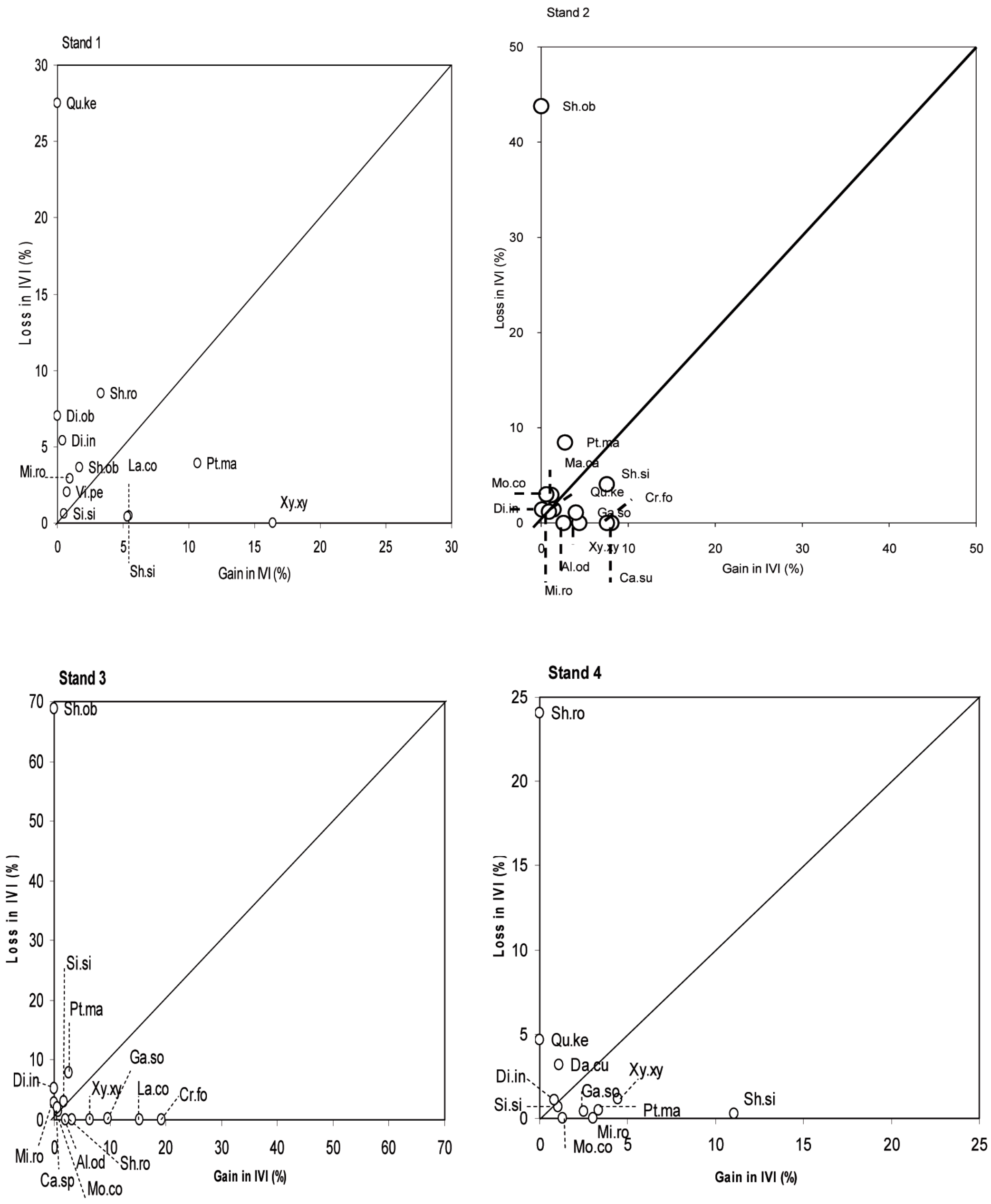

Figure 1 Relationships between gains and losses in IVI of 10 selected dominant tree species in the four stands. Tree names are abbreviated from the first two genera and species names of these tree species as they appear in Tables 1 to 4.

Stand 3 was dominated by *S. obtusa* and *P. macrocarpus* and these two species tended to maintain their dominance, despite a noticeable reduction in their IVI values, in a similar manner to *Sindora siamensis*, *M. coreia*, *D. intricatus* and *M. rotundifolia*. However, the notable three newly recruited trees species of *C. formosum*, *L. coromandelica* and *G. sootepensis* were able to compensate for the IVI reductions of the other tree species in stand 3.

Stand 4 was dominated by *S. siamensis* and *S. roxburghii*, which had the top two IVI rankings initially, maintained their ranking order differently, with the former having a large increase in its IVI, while the latter consequently reduced its IVI greatly (Figure 1). Due to the relatively open stand condition, mainly composed of large sized trees, such as *Q. kerrii* and *D. intricatus*, these species saw reductions in their IVI values, with numerous small-sized trees recruited, together with increases in the IVI of the initial trees, resulting in numerous tree species showing gains in their IVI values in stand 4. Considerable gains in IVI were noted for *X. xylocarpa* var. *kerrii*, *P. macrocarpus* and *M. rotundifolia*. The new entry tree species that emerged with a high IVI was *G. sootepensis*, that resulted in this stand being composed of several trees with IVI values that had gained more than those species that had a reduction in their IVI values, which is considered to be a phenomenon of population flux that is important for maintaining stand dynamic equilibrium conditions.

The most remarkable feature of the SDDF community was the species composition dynamics as shown by the reduction in IVI values of most of the initial dominant tree species, such as *S. obtusa*, *S. siamensis*, *S. roxburghii* and *D. intricatus* and the IVI values increasing in most legume tree species, such as *P. macrocarpus*, *X. xylocarpa*, *Sindora siamensis* and *A. odoratissima* to compensate for the reductions in IVI by the former species. Thus, it may be hypothesized tentatively that while those initial dominant tree species had losses in IVI, the potential of the habitat condition might be more or less reduced. For instance the soil nutrient availability could be declining and there could be a reduction in tree competition as the availability of more open ground space would provide favorable habitat conditions for those tree species that had some special requirements, such as light demanding and being pioneer species were capable of occupying the open habitat and building up soil nutrients to compensate for the declining soil nutrient. The latter species are usually trees which are capable of natural nitrogen fixation, such as most legumes, that can replace the former losses in dominant trees and restore the deteriorated habitat. Further study on the roles of legume tree in this forest type is therefore essential and deserves encouragement. Sahunalu (1994; 1997a, b; 1999) initiated ecological studies on legume tree species in DDF that have been progressed somewhat, but more aspects remain for future intensive study in this essential tree group.

CONCLUSION AND RECOMMENDATION

The species composition (DBH ≥ 4.5 cm) of SDDF over the period of 16 years changed through the addition of new entry tree species and the loss of some initial tree species in the four stands, as a result of tree mortality and recruitment contemporaneously. The number of permanent losses of initial tree species was 5, 1 and 1 in stands 1, 2 and 4, with no loss in number for stand 3. The number of new tree species having a DBH of 4.5 cm and over that were added to the stands was 8, 20, 25 and 6 species, respectively, in stands 1 to 4. These additions and reductions in tree species caused changes in the IVI value of each tree species in the stand, with some values increasing and some decreasing. The notable number of tree species showing an increase in IVI value was 12, 17, 16 and 23 tree species in stands 1 to 4, respectively, while 19, 16, 16 and 14 tree species exhibited declines in IVI in the four stands, respectively. The initial dominant tree species in each stand demonstrated declines in IVI differently. Stand 1 dominated by *S. roxburghii* and *Q. kerrii* altered its association type to *S. roxburghii-P. macrocarpus*, as *Q. kerrii* had a large decline in its IVI value, so that it was lower than the IVI for *P. macrocarpus*. The other three stands maintained the same association types throughout the study period, even though their dominant tree species showed a range of positive and negative changes in their IVI values.

The most notable change in IVI was the increase in IVI for almost all legume tree species during the period. Changes in the dominance of tree species in long-term dynamics is believed to be a common phenomenon, as it has been found in several forest communities in many regions.

Each stand of SDDF exhibited a continuity of population flux by demonstrating a dynamic equilibrium of different IVI gains and losses, with the most prominent gains by most legume tree species in the four stands, together with some relatively fast-growing tree species newly recruited into the stands to compensate for the IVI declining in some of the initial leading tree species.

The long-term dynamics of species composition, particularly in DDF, which is a dry forest type among many forest community types distributed in Thailand and commonly found retained as patches in several pieces of protected areas, have been little studied and it is not clear to what extent each tree species component is maintained under natural conditions, if the stand is kept undisturbed for a long period. The present study revealed that in the long-term, at least during a 16-year period, each tree species responded to a phenomenon of tree population flux depending on its capability to sustain self-maintenance processes and resistance and tolerance to external disturbances. SDDF is considered to have had minimum anthropogenic disturbance, as it is controlled under the Biosphere Reserves scheme. The capability of each tree species population to maintain its abundance, perform successfully and maintain vigorous growth was clearly demonstrated, exhibiting as changes in IVI, which is the combination of distributional density, frequency of occurrence and dominance in covering a given habitat. Few major tree species in SDDF had a good balance between gains and losses in their IVI, except for most of the legume tree group co-occurring with the major tree species of the Dipterocarpaceae that were quite successful at self-maintenance. *Q. kerrii*, which is a component species belonging to the Fagaceae, one of the largest families and a widely distributed tree group next to the Dipterocarpaceae, showed a very weak capability to maintain its population dominance in the long-term, especially in SDDF and it is considered that this species will be lost permanently. In the future it is considered that SDDF will be dominated by most of the legume tree group: *P. macrocarpus, Sindora siamensis, X. xylocarpa*. This may be quite desirable and offers many clues to assist with future stand management operations. Further studies should clarify demographic, regeneration and phonological aspects of each leading tree species in this dry forest type, in order to gain further knowledge that will be useful for future stand management under the protected area scheme and in operations to restore disturbed areas.

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