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Community-level Physiological Profiling in Monitoring Rehabilitative Effects of *Acacia auriculiformis* Plantation on Degraded Land in Sakaerat, Thailand

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This study was conducted to investigate the rehabilitative effects of planting *Acacia auriculiformis* trees on degraded land by observing variations in soil bacterial community profiles provided by community-level physiological profiling. Soil bacterial and physicochemical comparisons between an original evergreen forest and the *Acacia* plantation plot, established on an area severely degraded as a result of deforestation, showed that most soil characteristics were rehabilitated 18 to 19 years after the plantation of *Acacia* according to single variables, Shannon and Simpson diversity indices based on the community-level physiological profiles, principal component analysis and redundancy analysis. However, a more strict statistical comparison, discriminant analysis, completely discriminated between the *Acacia* plantation and the evergreen forest soils when the community-level physiological profiles were compared. Thus, the *Acacia* plantation soil was shown to still be in the process to full recovery. Here, we discuss the relevance of planting *A. auriculiformis* in land rehabilitation schemes in savanna regions.

Keywords *Acacia auriculiformis*, community-level physiological profile, land degradation and rehabilitation, multivariate analysis, soil bacterial community
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1 Introduction

Deforestation has emerged as a challenge to socio-economic development in Thailand (The tenth national… 2006) as in many other countries. In the past four decades, forest areas in Thailand as a whole are estimated to have declined by 50% or more (Fisher and Hirsch 2008). In the tropics, deforestation often leads to land degradation and results in degraded soils under tropical climatic conditions (Eden and Parry 1996). Deforestation is seen as a major cause of increasingly severe problems of drought and flood (Krairapanond and Atkinson 1998). Since the late 1980s, the Thai government has been taking measures to rehabilitate the degraded lands. Reforestation is one of the rehabilitation measures, and trees have been planted on the degraded lands under a subsidy scheme of the government (Sharp and Nakagoshi 2006). Because the native tree species are prone to fail to survive due to the degraded soil conditions, in the reforestation strategy, exotic plant species are often introduced to rehabilitate the degraded lands with harsh soil conditions (Ashton et al. 2001). However, the strategy is often criticized because the introduced exotic species may result in biological deserts (Wuethrich 2007). Another critical opinion is that the exotic tree species may escape to adjacent areas, threatening native species (Hartley 2002). When considering these constraints, we question whether introducing an exotic tree species is truly rehabilitative.

There has been some evidence of the rehabilitative effects of reforestation. The aboveground diversity of plant species draws attention relatively well. Surveys of the distribution of plant species following reforestation have been used to demonstrate the success or failure of the reforestation in terms of recovery of the original ecosystems (Kamo et al. 2002). In addition to the aboveground plant community structure, soil quality has also been used as an indicator of rehabilitative effects of reforestation (Young 1997). On the other hand, soil biotic changes are not well documented in investigations of the rehabilitative effects of reforestation, while the changes have been reported as responses to land degradation caused by deforestation. When soil microbes function well, the soil may support trees and other plants in the ecosystem (Beare et al. 1995). Soil bacteria, as a part of the soil microbial community, contribute to plant growth by mineral solubilization (Derylo and Skorupska 1992), nitrogen fixation (Albrecht et al. 1981) and production of plant growth hormones (Nieto and Frankenberg 1989). Therefore, an indicator of rehabilitation is the recovery of soil microbes and their functions, though they have seldom been monitored in investigations of the rehabilitative effects of reforestation.

Rehabilitative effects of reforestation are shown by comparing soils of the rehabilitated area with reforestation and the adjacent degraded land without reforestation. To compare the soils, we have used community-level physiological profiling of soil bacterial community as a method for multivariate profiling of the soils (Garland and Mills 1991). This method reveals the functional potential of the soil bacterial community through observation of the utilization pattern of different carbon sources. In this study, we profiled soils over a land degradation-rehabilitation gradient in Sakaerat, Thailand (Doi and Ranamukhaarachchi 2007). The original vegetation type of Sakaerat is dry evergreen forest. But human activities, mainly slash-and-burn cultivation, have deforested some parts of Sakaerat. Some areas were cultivated and abandoned after intensive exploitation of the soil resources, causing the ground to become bare. In some spaces, the bare ground was rehabilitated by planting *Acacia auriculiformis* trees (Sakai et al. 2009). Bare ground was the most degraded vegetation type, and the rehabilitated *Acacia* plantation plots and the dry evergreen forest represented a land degradation-rehabilitation gradient. The main objective of this study was to investigate the rehabilitative effects of the *Acacia* plantation by profiling the gradient in a wet-to-dry seasonal change.

2 Materials and Methods

2.1 Site Description

This study was conducted in Sakaerat Environmental Research Station, Thailand. The details were described elsewhere (Doi and Ranamukhaarachchi 2007, Doi and Sakurai 2004). The annual precipitation is 1260 mm and the average

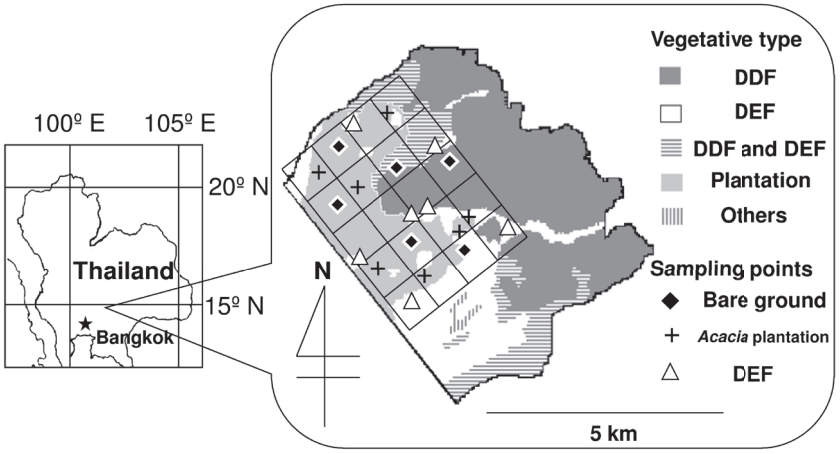

Fig. 1. The vegetation types of the Sakaerat Environmental Research Station and the sampling points. DDF and DEF indicate dry deciduous forest and dry evergreen forest, respectively.

temperature is 26 °C. The climate is classified as savanna (Köppen 1931). The soil is originally an Orthic Acrisol, according to the FAO/UNESCO scheme (FAO/UNESCO 1979).

We compared soils of dry evergreen forest (the original vegetation), *Acacia* plantation and bare ground (the most degraded vegetation). These vegetation types represent a land degradation-rehabilitation gradient. The vegetation types were randomly distributed. Thus, the vegetation mosaic was regarded as a completely randomized design (Fig. 1, Doi and Sakurai 2004). The numbers of replications were 7, 7 and 6 for dry evergreen forest, *Acacia* plantation and bare ground, respectively. All the sampling points were on slight slopes (less than 10°).

The dry evergreen forest is primarily dominated by *Hopea ferrea* and *Shorea* spp. that form the upper storey 20 to 40 m above ground. A typical dry evergreen forest contains more than 1000 trees (trunk diameter at breast height > 5 cm) ha^{-1}, the total basal area at 1.3 m height exceeds 30 m^2 ha^{-1} and the above ground biomass is over 200 tons ha^{-1} (Kanzaki et al. 1995).

The *Acacia auriculiformis* plantation plots are scattered in the area (Fig. 1). The *Acacia* plots were established in 1986 and 1987 in the parts that used to be subjected to slash-and-burn shifting cultivation (Kaeonium et al. 1976). In these spaces, the original vegetation had been removed and the biomass had been burned. The cleared land had been cultivated for a few years, and then abandoned when the soil quality deteriorated to the extent that could not support crop production. Some of the abandoned parts of Sakaerat had been converted to plantation plots of *Acacia mangium*, *Eucalyptus camaldulensis* and other tree species. *A. auriculiformis* was one of the introduced tree species.

The bare ground soil has been intensively deprived of nutrients and has lost conditions seen in forest soils. At these sampling points, recovery of vegetative cover did not occur since the harsh conditions for plants make the bare ground to remain so. Morphological features of bare ground can still be seen at some points in the site. For typical bare ground, the A horizon can not be recognized. The uppermost horizon is reddish brown (Doi and Ranamukhaarachchi 2007) rich in gravel, and has few roots and other plant organs/debris. The boundary between the uppermost horizon and the deeper horizon is not clear, while the horizon deeper than 50 cm is pale orange.

2.2 Soil Sampling and Physicochemical Profiling

Soils were sampled on Sep 25 and 26, Nov 25 and 26 and Dec 24 and 25, 2005 (Fig. 2). The

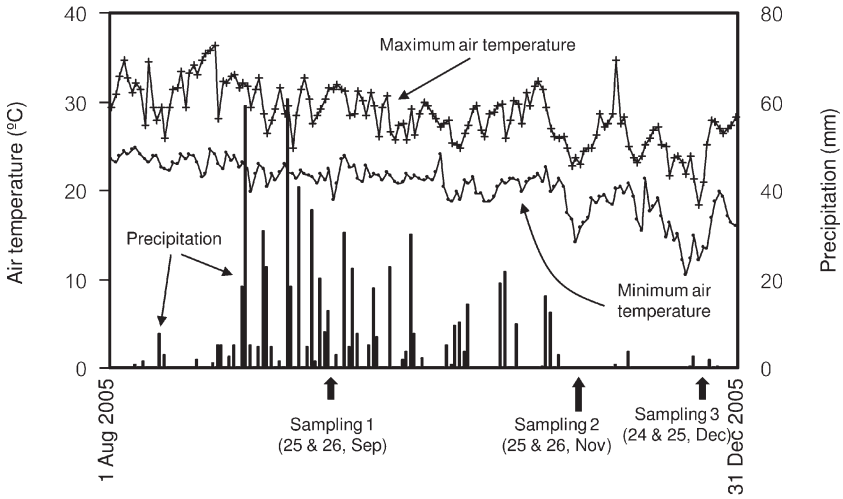

Fig. 2. Changes in temperature and precipitation during the research period.

sampling was done within 26 hours, in which the site had negligible precipitation (< 1 mm). At each sampling point, hundred-mL core samplers, 5 cm in diameter, were inserted from the surface to a depth of 5.1 cm. A circle, 10 m in diameter was established, and 8 soil cores were randomly taken within the circle. In addition, two other cores were randomly taken in the circle for soil moisture and bulk density measurements. The 8 soil cores were immediately placed into a single plastic bag, mixed and brought to the laboratory. For community-level physiological profiling, the moist soil was immediately passed through 2 mm sieve and was brought to the laboratory within 12 h. For soil physicochemical profiling, the soil samples were air-dried, passed through 2 mm sieve then analyzed. Physicochemical profiling of soils were performed as previously described (Doi and Ranamukhaarachchi 2007).

2.3 Community-level Physiological Profiling

The bacterial community in each composite sample was profiled with three Biolog EcoPlates as previously described (Doi 2005). Five grams of each soil sample were suspended in 45 mL of sterilized 0.85% (w/v) NaCl and reciprocally shaken at room temperature for 30 min at 120 rpm. The suspension was centrifuged at 1000 g for 5 min, decanted, and the pellet was re-suspended in 45 mL of the NaCl solution. Then, the centrifugation and suspending was repeated twice. The soil suspension was left still for a minute, and 10 mL of the uppermost section was diluted 40-fold with the NaCl solution. This suspension was used to inoculate Biolog EcoPlate at a rate of 0.1 mL/well. Oxidation of each carbon source was measured by quantifying purple color development as a result of the reduction of tetrazolium violet. The plates were incubated at 26°C in the dark and absorbance at 405 nm was read using a microplate reader (Perlong DNM-9602G, Nanjing, PR China) at 4 to 12 h intervals for 7 days. During the incubation, the plates were wrapped in a plastic film to avoid desiccation. Values for the above mentioned three pseudo-replicates were averaged, and used for the following statistical analyses.

2.4 Data Analyses

The following analyses were performed using the statistical software, SPSS 10.0.1 (SPSS Inc.). Repeated measures analysis of variance for each of the soil physicochemical characteristics was performed. As the post-hoc test, Dunnett T3 t-test

was performed to examine the significant differences between means.

Community-level physiological profiles of the soils were analyzed to construct data sets for using the information. The average well color development approach (AWCD, Garland and Mills 1991) was employed as the first choice. AWCD at a particular time was calculated using the following equation.

$$\text{Average well color development (AWCD)} = \Sigma(\text{ABS}i\text{t} - \text{ABSct})/31 \quad (1)$$

where ABS*i*t is the absorbance at 405 nm for the i-th carbon source at the time (t) and ABSct is the absorbance for the control well, including no carbon sources, at the time (t). In this study, values of AWCD for the bare ground soil samples at the convergence stage were obviously poor, then comparable to that for the forest soil samples at the exponential stage. This made it impossible to use profiles of the forest soils at their convergence stages because the color development for the bare ground soils did not reach to the color intensity that the forest soil samples manifested. Therefore, the kinetic approach proposed by Lindstrom et al. (1998) was applied. Values of AWCD in the color development were used to determine the asymptote (K) statistically. The value of parameter K was regarded as the asymptote that the value of AWCD finally reaches. The 0.5 K time point was regarded as the exponential stage (Lindstrom et al. 1998) and the 0.95 K time point as the convergence stage. This approach provided 0.5 K and 0.95 K data sets. In addition to these data sets, another data set, called area data set, was constructed (Hackett and Griffiths 1997). Then, a multivariate profile of the soil sample was obtained. A ratio-transformation was employed, i.e., each observation was divided by the sum of all the observations for the sample and used for statistical analyses.

To compare the data sets in discriminating among the soils, discriminant analysis was performed. The 31 values for each soil sample were used for discriminant analysis of the community-level physiological profiles. Raw soil physicochemical data were used for discriminant analysis of soil physicochemical profiles. The putting-independents-together method was chosen.

Principal component analysis was performed to extract principal components from the data set on physicochemical profiles or the community-level physiological profiles. Then, the principal component scores were used for describing the land degradation-rehabilitation gradient.

It had been demonstrated that the intensity of the land degradation in Sakaerat was solely described by the first principal component derived from the physicochemical data set (Doi and Sakurai 2004). Hence, multiple regression analysis was performed to obtain a regression model for describing the land degradation-rehabilitation gradient based on the data set on the community-level physiological profiles. Scores on the first principal component derived from the physicochemical data set were examined if the variation has significant linear relationships with scores on principal components extracted from the data set on the community-level physiological profiles. The multiple regression analyses involved only the significant principal components having eigenvalues of 1 or greater (Kaiser 1960). The stepwise method at the default criteria ($p = 0.05$ for inclusion and 0.10 for removal) was chosen.

We calculated biodiversity indices based on the carbon source utilization pattern by the soil bacterial community (Staddon et al. 1997). Shannon diversity, Shannon evenness and Simpson indices were calculated. The Shannon diversity and evenness indices indicate diversity and evenness of distribution pattern of the community, while the Simpson index indicates dominance by a particular portion of the community (Staddon et al. 1997). Repeated measures analysis of variance was performed for analyzation, determination and comparison of sources of variations of the diversity indices. Dunnett T3 t-test was chosen as the post-hoc t-test.

CANOCO for Windows 4.02 and CanoDraw 3.10 (Microcomputer Power, NY) were used for redundancy analysis of the relationships among the soil physicochemical variables, the soil bacterial community profiles and the values of Shannon diversity index (ter Braak and Šmilauer 1998). The sampling dates were used as the co-variable to take the temporal changes into account.

3 Results

The climatic conditions are summarized in Fig. 2. The site had heavy precipitation in September and October, but received less water in November and December, resulting in a wet-to-dry transition.

Most soil physicochemical variables reflected the degradative/rehabilitative effects significantly (Table 1, $p<0.05$). The land degradation was explained by high values of bulk density and exchangeable acidity (Al, H), and the low values of moisture content, pH, organic matter content, basic cation contents (K, Ca, Mg), and available phosphorus. The values for the *Acacia* plantation soil were not significantly different from those for the evergreen forest soil, except for the bulk density value in September. The bare ground soil was shown to be significantly poorer than the other soils in some soil physicochemical variables. *Acacia* plantation soil showed rehabilitative effects of the plantation on the degraded soil. The effects of the wet-to-dry seasonal change were pronounced as changes in soil moisture content, bulk density, and pH.

Fig. 3 shows community-level physiological profiles of the soils. Some significant differences were found between the vegetation types. The bare ground soil was significantly different from the others, but there were fewer cases in which the means for the *Acacia* plantation and the evergreen forest were differentiated at a significance level of $p=0.05$. These results again indicate that the soil of the *Acacia* plantation plot was progressively recovering the original community-level physiological profile. To extend the use of the data, multivariate analyses were performed.

Table 2 indicates the results of principal component analysis. Regarding variation in scores on the first principal component extracted from the overall physicochemical data set, vegetation type was a significant source ($p=0.001$), but the sampling time ($p=0.908$) and the interaction ($p=0.798$) were not. Thus, the first principal component was confirmed to be a measure of the intensity of land degradation in Sakaerat (Doi and Sakurai 2004). The bacterial data sets provided larger numbers of significant principal components (eigenvalue > 1) than the physicochemical data set. For the overall data sets on the community-level physiological profiles, repeated measures analyses of variance were performed to determine the principal components explaining the seasonal change. When sampling time was examined as a source of the variation, the principal components having the smallest p values were the fifth (0.5 K), the eighth (0.95 K), and the third (Area). Thus, seasonality was found to be a minor source of the variation.

Fig. 4 summarizes the regression models that describe the land degradation-rehabilitation gradient. These models show that the first bacterial principal components had significant linear relationships with the land degradation-rehabilitation gradient. The soil sample groups of the evergreen forest and the *Acacia* plantation overlap while the bare ground samples are separated in the diagrams. It was indicated that the soil of the *Acacia* plantation plot was recovering the original physiological functions.

The discriminant analyses of the bacterial data sets properly classified all the soil sample groups in all three sampling times and resulted in no misclassification. On the other hand, discriminant analysis of the physicochemical data sets resulted in two cases of misclassification: an *Acacia* sample was misclassified as an evergreen forest sample in September and November, respectively. Hence, the bacterial data sets enabled discrimination among the soils at least as well as the physicochemical data set.

Analysis of the biodiversity indices revealed significant sources of the variation (Table 3). Sampling time and vegetation type were significant ($p<0.003$) for all the data sets and all the indices. No significant interactions between these sources of variation were recognized ($p>0.212$); consistent variation patterns among the sampling times or the vegetation types were seen. For example, the diversity indices tended to be greater in September and smaller in December. The bacterial community in the evergreen forest soil tended to have the highest functional diversity, and that in the bare ground soil had the poorest. In most comparisons, the diversity indices of the soil bacterial community of the evergreen forest were not significantly different from those of the *Acacia* plot. Therefore, it was again shown that the soil of the *Acacia* plot was increasing in similarity to that of the evergreen forest during the rehabilitation period. This was indicated by recovering values of average well color development as well.

Table 1. Soil physicochemical characteristics and results of repeated measures analysis of variance.

Physicochemical characteristics	Separation of means for the vegetation types at each sampling time									Significance of sources of variation (p value)		
	September			November			December					
	BG*	*Acacia*	DEF	BG	*Acacia*	DEF	BG	*Acacia*	DEF	Vegetation type (V)	Sampling time (S)	V × S
Moisture content (%)	11.9b†	24.1a	25.7a	4.45b	18.1a	21.7a	3.43b	8.67a	10.1a	0.000	0.000	0.000
Bulk density (kg L^{-1})	1.15ab	1.12a	1.00b	1.40a	1.16b	1.02b	1.43b	1.12ab	0.96a	0.000	0.008	0.011
pH	5.88a	6.30a	5.88a	5.52a	6.01a	5.83a	5.90a	6.30a	6.37a	0.129	0.028	0.619
Organic matter (%)	3.61b	6.33a	4.95a	3.73b	5.22ab	5.31a	3.13b	5.52ab	5.58a	0.004	0.780	0.269
Bray II P (mg kg^{-1} dry soil)	2.50a	4.16a	5.61a	2.71a	3.93a	4.68a	4.07a	5.05a	4.69a	0.008	0.167	0.224
Exch K (m eq kg^{-1} dry soil)	2.99a	4.73a	4.57a	2.97a	5.84a	4.19a	2.38b	4.50a	4.38a	0.009	0.728	0.890
Exch Ca (m eq kg^{-1} dry soil)	12.1b	31.6a	17.2ab	15.1a	35.6a	31.8a	15.8a	31.5a	31.7a	0.018	0.220	0.632
Exch Mg (m eq kg^{-1} dry soil)	19.7a	34.4a	29.6a	20.4a	32.2a	33.7a	20.1b	38.1ab	43.2a	0.020	0.206	0.578
Exch Na (m eq kg^{-1} dry soil)	0.29a	0.26a	0.19a	0.22a	0.33a	0.15a	0.21a	0.17a	0.12a	0.149	0.239	0.644
CEC** (m eq kg^{-1} dry soil)	42.3a	72.7a	55.9a	48.3a	77.8a	75.6a	48.3a	77.1a	80.8a	0.053	0.268	0.777
Exch Al (m eq kg^{-1} dry soil)	1.90a	0.40a	0.87a	2.38a	1.10a	1.68a	2.08a	1.05a	1.00a	0.074	0.204	0.947
Exch H (m eq kg^{-1} dry soil)	6.30a	1.39a	3.41a	7.33a	2.72a	4.08a	7.78a	1.83a	0.49a	0.151	0.744	0.857

* BG, *Acacia*, and DEF in the mean separation columns indicate bare ground, *Acacia* plantation and dry evergreen forest, respectively, for each month and each soil physicochemical characteristic.
** CEC, cation exchange capacity.
† The means indexed by the same letter do not differ significantly at p=0.05 according to the Dunnett T3 t-test.

Table 2. Structures of the data sets.

Sampling time	Data set	Statistic	Principal components							
			1	2	3	4	5	6	7	8
September	0.5 K	Eigenvalue	9.1*	6.5	3.7	2.8	2.3	1.6	1.2	0.8
		Variation explained (%)	29.3	20.9	12.0	9.0	7.5	5.1	3.9	2.6
	0.95 K	Eigenvalue	11.3	4.9	3.3	2.1	2.0	1.6	1.5	1.1
		Variation explained (%)	36.4	15.9	10.8	6.7	6.4	5.2	4.7	3.6
	Area	Eigenvalue	13.2	5.5	3.9	2.4	1.7	1.0	0.7	0.6
		Variation explained (%)	42.7	17.8	12.7	7.6	5.6	3.2	2.3	1.8
	Physicochemical	Eigenvalue	5.2	2.1	1.8	1.1	0.5	0.5	0.3	0.2
		Variation explained (%)	43.3	17.6	15.0	9.2	4.5	3.8	2.8	1.9
November	0.5 K	Eigenvalue	11.5	5.0	2.7	2.4	1.8	1.5	1.3	1.1
		Variation explained (%)	37.1	16.0	8.6	7.6	5.7	4.7	4.2	3.5
	0.95 K	Eigenvalue	13.1	4.1	2.7	2.3	1.7	1.5	1.3	1.0
		Variation explained (%)	42.4	13.3	8.8	7.4	5.5	5.0	4.3	3.2
	Area	Eigenvalue	14.4	3.9	2.3	2.1	2.0	1.4	1.1	0.8
		Variation explained (%)	46.4	12.6	7.3	6.9	6.4	4.6	3.4	2.7
	Physicochemical	Eigenvalue	5.8	2.2	1.9	0.9	0.5	0.3	0.2	0.1
		Variation explained (%)	48.3	18.3	15.9	7.6	3.8	2.6	1.7	0.9
December	0.5 K	Eigenvalue	12.1	5.3	3.3	2.1	1.5	1.2	1.1	0.9
		Variation explained (%)	39.0	17.0	10.5	6.7	4.9	3.8	3.5	2.8
	0.95 K	Eigenvalue	14.2	4.0	3.1	2.1	1.4	1.2	1.2	0.8
		Variation explained (%)	45.8	13.0	9.9	6.7	4.7	3.8	3.7	2.5
	Area	Eigenvalue	16.4	4.4	2.4	1.7	1.2	1.0	0.9	0.6
		Variation explained (%)	52.9	14.2	7.8	5.6	3.8	3.2	2.8	1.9
	Physicochemical	Eigenvalue	6.1	2.5	1.5	0.7	0.5	0.4	0.2	0.1
		Variation explained (%)	50.8	20.7	12.4	5.4	4.2	2.9	1.6	1.0
September, November, and December	0.5 K	Eigenvalue	7.0	6.1	3.1	1.9	1.6	1.3	1.1	1.0
		Variation explained (%)	22.6	19.5	9.9	6.1	5.2	4.3	3.6	3.4
	0.95 K	Eigenvalue	9.2	4.8	2.8	2.4	1.7	1.4	1.1	1.0
		Variation explained (%)	29.6	15.5	9.0	7.7	5.4	4.5	3.7	3.5
	Area	Eigenvalue	10.7	5.7	2.8	2.4	1.3	1.1	1.0	0.8
		Variation explained (%)	34.5	18.5	9.0	7.7	4.2	3.6	3.3	2.7
	Physicochemical	Eigenvalue	5.3	2.1	1.5	0.9	0.7	0.6	0.4	0.2
		Variation explained (%)	43.8	17.7	12.7	7.4	5.9	4.8	3.1	1.9

* The underlined figures indicate that the principal component is significant according to the Keiser's criterion (eigenvalue ≥ 1, Keiser 1960).

Fig. 3. Community-level physiological profiles of the soil bacterial communities of the bare ground (solid bar), the *Acacia* plantation (open bar), and the evergreen forest (gray bar) in each month and for each data set. The means indexed by different letters differ significantly at p = 0.05 according to the Dunnett T3 t-test. The means without indexing letters indicate no significant differences among the vegetation types. The error bar indicates the standard deviation. (n = 6, bare ground; n = 7, *Acacia* plantation and evergreen forest)

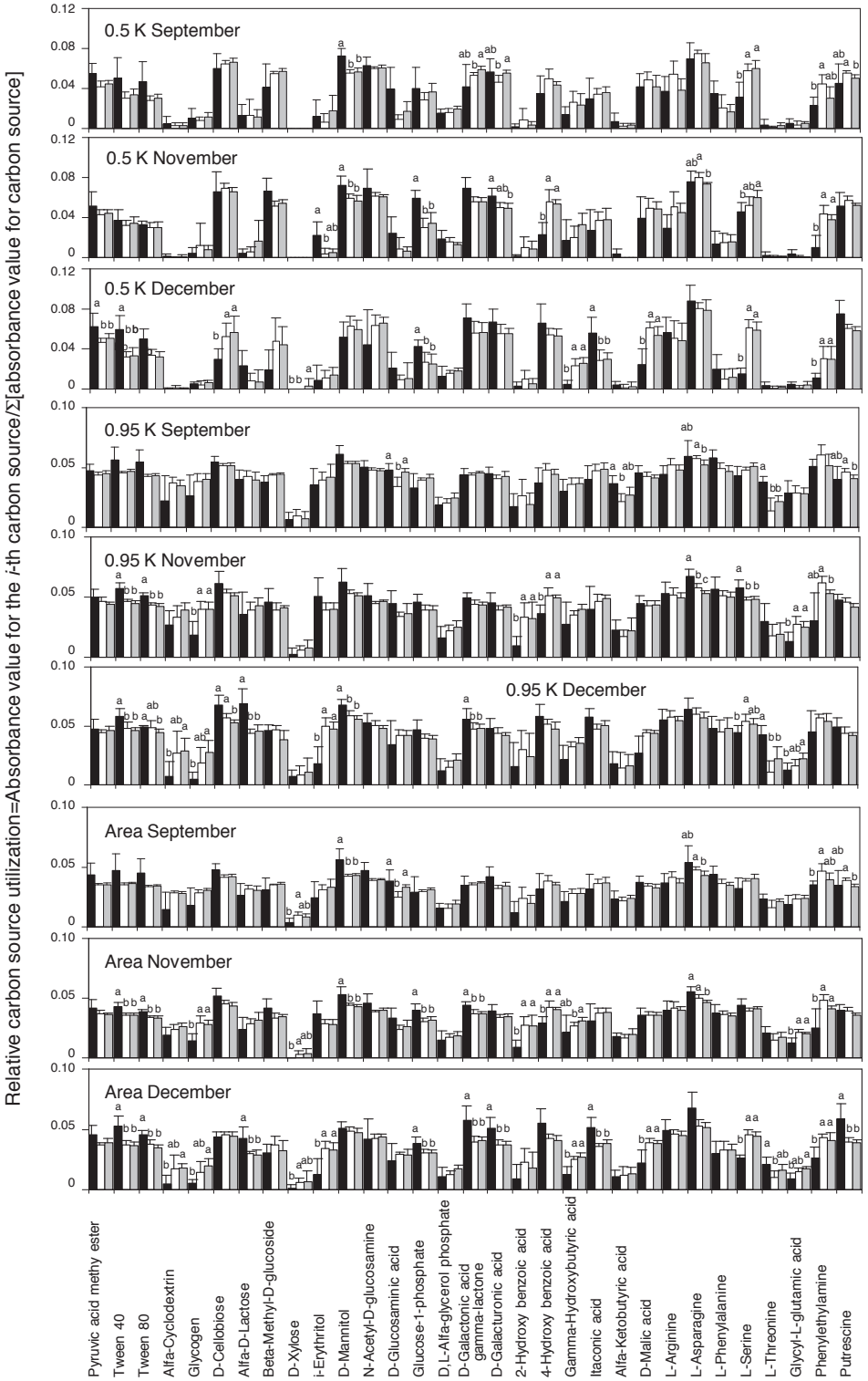
Relative carbon source utilization=Absorbance value for the i-th carbon source/Σ[absorbance value for carbon source]
0.5 K September
0.5 K November
0.5 K December
0.95 K September
0.95 K November
0.95 K December
Area September
Area November
Area December
Pyruvic acid methy ester
Tween 40
Tween 80
Alfa-Cyclodextrin
Glycogen
D-Cellobiose
Alfa-D-Lactose
Beta-Methyl-D-glucoside
D-Xylose
i-Erythritol
D-Mannitol
N-Acetyl-D-glucosamine
D-Glucosaminic acid
Glucose-1-phosphate
D,L-Alfa-glycerol phosphate
D-Galactonic acid gamma-lactone
D-Galacturonic acid
2-Hydroxy benzoic acid
4-Hydroxy benzoic acid
Gamma-Hydroxybutyric acid
Itaconic acid
Alfa-Ketobutyric acid
D-Malic acid
L-Arginine
L-Asparagine
L-Phenylalanine
L-Serine
L-Threonine
Glycyl-L-glutamic acid
Phenylethylamine
Putrescine

Table 3. Values of the biodiversity indices for the soil bacterial communities of the vegetation types and the descriptive statistics at each sampling time based on community-level physiological profiling.

Data set	Diversity index or descriptive statistic	September			November			December			Significance of land degradation/ rehabilitation (vegetation type, V) and sampling time (S) as sources of variation (p value)		
		Bare ground	*Acacia* plantation	Evergreen forest	Bare ground	*Acacia* plantation	Evergreen forest	Bare ground	*Acacia* plantation	Evergreen forest	V	S	V × S
0.5 K	Shannon	$3.084^{ab\ A}$*	$3.102^{b\ A}$	$3.145^{a\ A}$	$2.993^{a\ A}$	$3.042^{a\ B}$	$3.075^{a\ B}$	$2.984^{a\ A}$	$3.049^{a\ AB}$	$3.076^{a\ AB}$	0.002	0.001	0.926
	Shannon evenness	$0.898^{a\ A}$	$0.903^{a\ AB}$	$0.916^{a\ A}$	$0.872^{a\ A}$	$0.886^{a\ B}$	$0.896^{a\ B}$	$0.869^{a\ A}$	$0.888^{a\ A}$	$0.896^{a\ AB}$	0.001	0.000	0.289
	1/Simpson	$20.0^{a\ A}$	$20.7^{a\ A}$	$21.5^{a\ A}$	$18.3^{b\ A}$	$19.7^{b\ B}$	$20.4^{a\ B}$	$17.7^{a\ A}$	$19.4^{a\ AB}$	$19.9^{a\ AB}$	0.000	0.000	0.899
	Average well color development (AWCD)	$0.585^{b\ A}$	$0.724^{ab\ A}$	$0.766^{a\ A}$	$0.508^{b\ A}$	$0.656^{a\ A}$	$0.710^{a\ A}$	$0.521^{c\ A}$	$0.648^{b\ A}$	$0.744^{a\ A}$	0.000	0.029	0.918
	Number of carbon sources with AWCD>0	$28.2^{a\ A}$	$27.7^{a\ A}$	$29.1^{a\ A}$	$25.8^{a\ A}$	$25.6^{a\ A}$	$26.1^{a\ B}$	$28.5^{a\ A}$	$26.6^{b\ A}$	$28.0^{a\ A}$	0.043	0.000	0.667
0.95 K	Shannon	$3.340^{a\ A}$	$3.371^{a\ A}$	$3.381^{a\ A}$	$3.286^{b\ A}$	$3.369^{ab\ A}$	$3.380^{a\ A}$	$3.246^{a\ A}$	$3.322^{a\ A}$	$3.358^{a\ A}$	0.000	0.001	0.304
	Shannon evenness	$0.973^{a\ A}$	$0.982^{a\ A}$	$0.985^{a\ A}$	$0.957^{a\ A}$	$0.981^{a\ A}$	$0.984^{a\ A}$	$0.945^{a\ A}$	$0.967^{a\ A}$	$0.978^{a\ A}$	0.000	0.001	0.213
	1/Simpson	$27.8^{a\ A}$	$28.9^{a\ A}$	$29.4^{a\ A}$	$25.9^{b\ A}$	$28.8^{a\ A}$	$29.4^{a\ A}$	$24.7^{b\ A}$	$27.3^{ab\ A}$	$28.5^{a\ A}$	0.000	0.001	0.381
	Average well color development (AWCD)	$1.000^{b\ A}$	$1.247^{ab\ A}$	$1.334^{a\ A}$	$0.964^{b\ A}$	$1.247^{a\ A}$	$1.349^{a\ A}$	$0.989^{c\ A}$	$1.218^{b\ A}$	$1.413^{a\ A}$	0.000	0.889	0.863
	Number of carbon sources with AWCD>0	$30.7^{a\ A}$	$30.9^{a\ A}$	$30.7^{a\ A}$	$30.0^{a\ A}$	$30.9^{a\ A}$	$30.9^{a\ A}$	$30.5^{a\ A}$	$30.4^{a\ A}$	$30.9^{a\ A}$	0.076	0.596	0.206
Area	Shannon	$3.299^{a\ A}$	$3.386^{a\ A}$	$3.396^{a\ A}$	$3.295^{b\ A}$	$3.365^{a\ B}$	$3.378^{a\ B}$	$3.202^{b\ A}$	$3.329^{ab\ B}$	$3.348^{a\ B}$	0.000	0.000	0.439
	Shannon evenness	$0.968^{a\ A}$	$0.986^{a\ A}$	$0.989^{a\ A}$	$0.969^{a\ A}$	$0.981^{a\ B}$	$0.985^{a\ AB}$	$0.939^{b\ A}$	$0.971^{ab\ B}$	$0.977^{a\ B}$	0.000	0.000	0.327
	1/Simpson	$26.2^{a\ A}$	$29.4^{a\ A}$	$30.0^{a\ A}$	$26.0^{c\ A}$	$28.6^{b\ B}$	$29.2^{a\ B}$	$22.8^{b\ A}$	$27.2^{a\ B}$	$27.9^{a\ C}$	0.000	0.000	0.615
	Area (Absorbance × hour)	$3470^{b\ A}$	$5121^{ab\ A}$	$5464^{a\ A}$	$2915^{b\ A}$	$4021^{a\ B}$	$4292^{a\ B}$	$3161^{b\ A}$	$4779^{a\ A}$	$5150^{a\ A}$	0.000	0.000	0.159
	Number of carbon sources with>0 AWCD	$30.2^{a\ A}$	$31.0^{a\ A}$	$31.0^{a\ A}$	$30.0^{a\ A}$	$30.9^{a\ A}$	$30.9^{a\ A}$	$30.0^{a\ A}$	$30.9^{a\ A}$	$30.7^{a\ A}$	0.000	0.528	0.996

* For each month and each diversity index, the means indexed by the same small letter do not differ significantly among the vegetation types at p=0.05 according to the Dunnett T3 t-test. For each index and each vegetation type, the means indexed by the same capital letter do not differ significantly among the sampling times at p=0.05 according to the t-test.

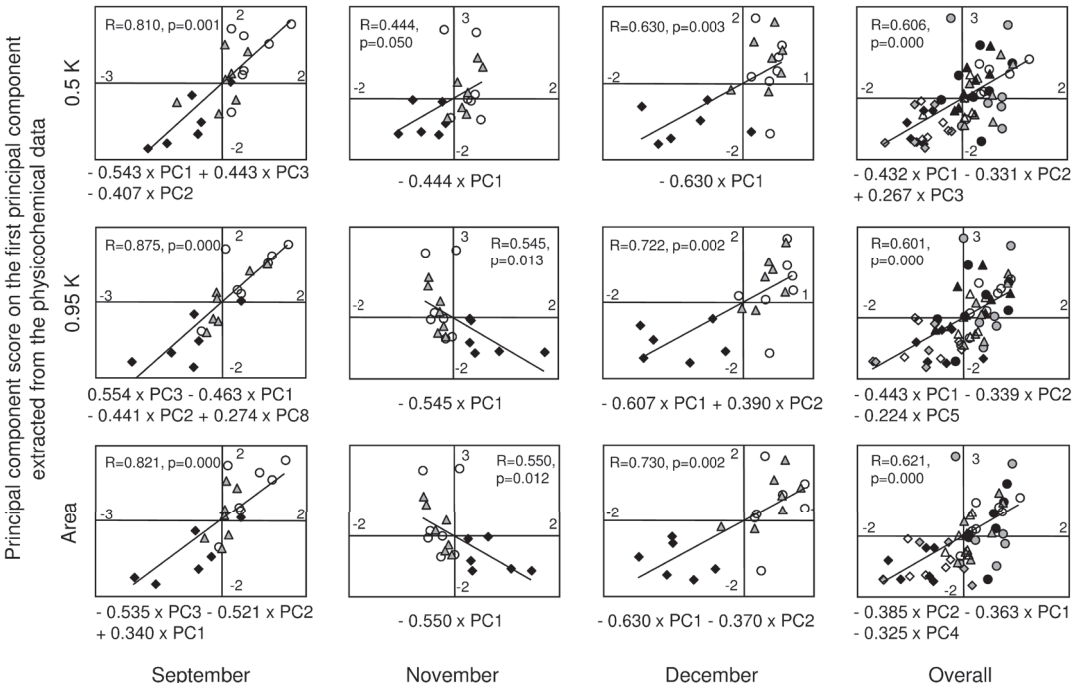

Fig. 4. Regression models describing the land degradation-rehabilitation gradient shown as the variations of score on the first principal components derived from the physicochemical data sets. For each month, the solid diamond, the open circle and the gray triangle indicate bare ground, *Acacia* plantation and evergreen forest, respectively. The formulae along the horizontal axes were provided by the multiple regression analysis. PC*i* indicates the score on the *i*-th principal component for the soil sample. The p value following the R value indicates the significance of the regression model. For the overall data sets, the diamond, the circle and the triangle indicate bare ground, *Acacia* plantation and evergreen forest, respectively. The solid, the gray and the open symbols indicate the soil samples taken in September, November and December, respectively.

By direct gradient analyses, the first and second axes were extracted to explore the relationships between the values of the Shannon diversity index and soil environmental gradients. The first axes extracted by redundancy analysis had eigenvalues of 0.159 to 0.197 (Fig. 5). The spatial variation in soil moisture content was the most significant soil environmental gradient related to the Shannon diversity index and soil bacterial community profiles. Fig. 5 shows similarity between the bacterial communities in the *Acacia* plantation and the evergreen forest soils. Again, the bare ground soil bacterial community was clearly different from the others. In addition to moisture content, bulk density, pH and/or organic matter content were significant soil environmental gradients related to the variation in the community-level physiological profiles. In other words, the community-level physiological profile of the bare ground soil, having the lowest functional diversity in Sakaerat, appeared when the soil became drier, more acidic, heavier, and/or more barren because of human activities.

4 Discussion

Besides its high adaptability in degraded savanna areas (Badejo 1998), *A. auriculiformis* is known for its nitrogen-fixation property (Sprent and Parsons 2000), enriching macrofaunal composition

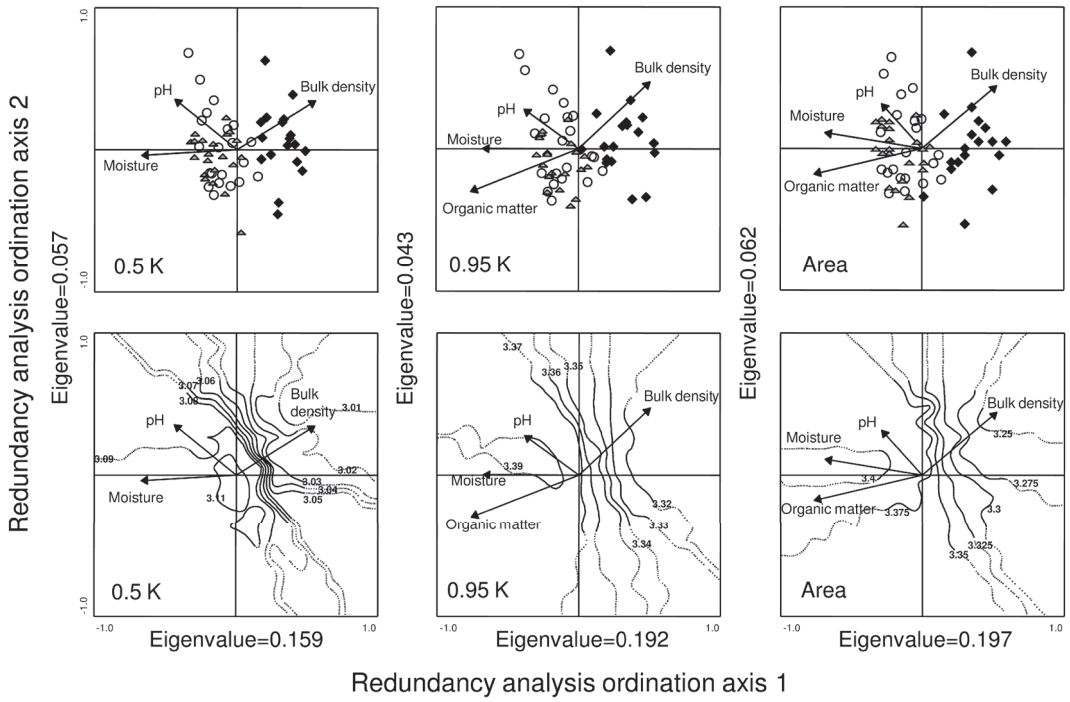

Fig. 5. Redundancy analysis ordination diagrams indicating (1) scores on the ordination axes for the soil samples (top); and (2) changes in functional diversity of soil bacterial community in the ordination plane (bottom). For the top figures, the solid diamond, the open circle and the gray triangle indicate bare ground, *Acacia* plantation and evergreen forest, respectively. For the bottom figures, the solid and the dotted contour lines indicate interpolation and extrapolation, respectively.

(Mboukou-Kimbatsa et al. 1998), low allelopathic effects (Bernhard-Reversat 1999), and pumping nutrients from the subsoil (Kang 1993). Such rehabilitative effects were also seen in our study as the above results. The *Acacia* plantation soil had largely recovered the original conditions and bacterial functions seen in the evergreen forest soil. At the same time, in the study period in 2005, the *A. auriculiformis* plantation soil seemed to still be recovering the original characteristics of the evergreen forest. This was especially indicated by the results of discriminant analysis which still clearly discriminated between the bacterial community profiles of the evergreen forest and the *Acacia* plantation soils.

A possible explanation is that slight physicochemical soil changes ($p > 0.10$) may significantly affect soil biotic variables, such as soil enzyme activity (Jha et al. 1992) and/or soil bacterial community structure (Doi and Sakurai 2003). Hence, the observed significant differences between the soil bacterial communities may be results of the amplification of physicochemical differences between the soils of the *Acacia* plot and the evergreen forest. Soil physicochemical changes have been observed relatively more often in association with land rehabilitation involving reforestation. Recently, some surveys have reported recovery of single soil biotic variables following reforestation (Doi and Ranamukhaarachchi 2009; Ren et al. 2007; Lee et al. 2006). In comparison with observation of single biotic variables, multivariate profiling of soil bacterial communities may offer more chances to find differences in soil quality.

In Sakaerat, protecting the plantation plot from fire seems to be important for succession (Sahunalu and Dhanmanonda 1995). The *A. auriculiformis* plantation soil was concluded to have

already been rehabilitated beyond the soil of the dry deciduous forest (Fig. 1) disturbed by human activities, mainly frequent running fire (Doi and Ranamukhaarachchi 2007). In North American forests, fire can accelerate succession if the dominant species are burnt and then opportunities for growth are given to suppressed native tree species (Abrams and Scott 1989). On the other hand, in a case study in Japan, fire set back succession of secondary forest dominated by Japanese red pine trees to an early stage, while pine wilt enhanced succession by promoting the growth of previously suppressed oak trees (Fujihara 1996). In Sakaerat, strong solar radiation, thus higher temperature, in addition to soil dryness (Fig. 5), was indicated to stress the native evergreen tree species (Fig. 5, Sakurai et al. 1998; Stott 1984). Recovery of moister soil and cooler microsite conditions by canopy development would be required for succession (Ren et al. 2007) while fire would destroy the chances for the native tree species, as well as the biotic life in the soil, to recover.

Once *A. auriculiformis* plantation establishes a canopy, self-thinning favors succession (Ashton et al. 2001). In 1998, among 6 tree species introduced to the Sakaerat Environmental Research Station, the *A. auriculiformis* plantation recorded the second highest species richness of plants (51), following the *Dalbergia cochinchinensis* plantation, which scored a species richness of 59, when the evergreen forest had 114 species (Kamo et al. 2002). We observed many tree species in the *A. auriculiformis* plots on the sampling days in 2005. This perceivable progress in succession is thought to contribute to the relative proximity of the *A. auriculiformis* plantation soil to the evergreen forest soil. Increasing plant community diversity can help enrich soil fertility (El-Keblawy and Ksiksi 2005) and establish the soil ecological structure (Beare et al. 1995) formed by plant roots and root exudates (Garland 1996) on which soil animals and microbes rely. These processes involved in succession were likely recovering the soil functions observed in this study.

On the other hand, we are sure that the *Acacia* plantation plots will require several more years to fully recover the original soil quality so there are no recognizable differences from the evergreen forest soil by discriminant analysis (Young 1997). Yemefack et al. (2005) recognized incomplete soil fertility recovery in a comparable rehabilitation period of 15 years after shifting cultivation in Cameroon. In the southern Yucatan peninsula of Mexico, under similar climatic conditions, 40–60 years was estimated for recovery of total aboveground biomass following shifting cultivation, based on the most optimistic estimate (Chazdon 2003). Thus, the *A. auriculiformis* plantation soil and the ecosystem were very likely to be in succession toward the climax. Therefore, even when we see similarity in multivariate profiles between soils of reforestation plots and original forest, we need to keep in mind criteria such as discriminant analysis and statistics (Doi and Ranamukhaarachchi 2007).

The fitness of introduced exotic tree species is site-specific (Ehrenfeld 2003). In the region, *A. auriculiformis* plantation looks suitable to invest for the environment, thus, in turn the society and the economy. In Sakaerat, the fitness of *A. auriculiformis* was higher than *Eucalyptus camaldulensis* and *Senna siamea*, and thinning in the *A. auriculiformis* plot encouraged growth of a native evergreen forest species, *Hopea odorata* (Sakai et al. 2009). A similar case of accelerated succession by thinning in an *A. auriculiformis* stand in Vietnam was reported by McNamara et al. (2006). In cases when the labor force for forest management is limited (Nawir et al. 2007), self-thinning is an option. Therefore, *Acacia* monoculture appeals as an alternative for rehabilitation of degraded lands in savanna regions (Lugo 1997).

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References

Abrams, M.D. & Scott, M.L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. Forest Science 35(1): 42–49.

Albrecht, S.L., Okon, Y., Lonnquist, J. & Burton,

R.H. 1981. Nitrogen fixation by corn-Azospirillum association in a temperate climate. Crop Science 21(2): 301–306.

Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P. & Gunatilleke, I.A.U.N. 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. Forest Ecology and Management 154(3): 409–430.

Badejo, M.A. 1998. Agroecological restoration of savanna ecosystems. Ecological Engineering 10(2): 209–219.

Beare, M.H., Coleman, D.C., Crossley, D.A. Jr., Hendrix, P.F. & Odum, E.P. 1995. A hierarchical approach to evaluating the significance of soil biodivresity to biogeochemical cycling. Plant and Soil 170(1) : 5–22.

Bernhard-Reversat, F. 1999. The leaching of Eucalyptus hybrids and Acacia auriculiformis leaf litter: laboratory experiments on early decomposition and ecological implications in Congolese tree plantations. Applied Soil Ecology 12(3): 251–261.

Casida, L.E. Jr., Klein, D.A. & Santoro, T. 1964. Soil dehydrogenase activity. Soil Science 98(6): 371–376.

Chazdon, R.L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6(1–2): 51–71.

Derylo, M. & Skorupska, A. 1992. Rhizobial siderophore as an iron source for clover. Physiologia Plantarum 85(1): 549–553.

Doi, R. 2005. Effects of air-drying soils on discriminating the soils with community-level physiological profiling. Journal of General and Applied Microbiology, 51(6): 379–383.

— & Ranamukhaarachchi, S.L. 2007. Soil color designation using Adobe PhotoshopTM in estimating soil fertility restoration by Acacia auriculiformis plantation on degraded land. Current Science 92(11): 1605–1610.

— & Ranamukhaarachchi, S.L. 2009. Soil dehydrogenase in a land degradation-rehabilitation gradient: observations from a savanna site with a wet/dry seasonal cycle. Revista de Biologia Tropical 57(1–2): 223–234.

— & Sakurai, K. 2003. Soil environmental factors relating to diversity of culturable soil bacterial communities in the Sakaerat Environmental Research Station, Thailand. Tropics 12(3): 185–200.

— & Sakurai, K. 2004. Principal components derived from soil physico-chemical data explained a land degradation gradient, and suggested the applicability of new indexes for estimation of soil productivity in the Sakaerat Environmental Research Station, Thailand. International Journal of Sustainable Development and World Ecology 11(3): 298–311.

Eden, M.J. & Parry, J.T. 1996. Land degradation in the tropics: environmental and policy issues. Global Development & the Environment Series. Pinter, London, UK.

Ehrenfeld, J.G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6(6): 503–523.

El-Keblawy, A. & Ksiksi, T. 2005. Artificial forests as conservation sites for the native flora of the UAE. Forest Ecology and Management 213(1): 288–296.

FAO/UNESCO 1979. Soil map of the world. IX, Southeast Asia. UNESCO, Paris.

Fisher, R. & Hirsch, P. 2008. Poverty and agrarian-forest interactions in Thailand. Geographical Research 46(1): 74–84

Fujihara, M. 1996. Development of secondary pine forests after pine wilt disease in western Japan. Journal of Vegetation Science 7(5): 729–738.

Garland, J.L. 1996. Analytical approaches to the characterization of samples of microbial communities using patterns of potential C source utilization. Soil Biology and Biochemistry 28(2): 213–221.

— & Mills, A.L. 1991. Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. Applied and Environmental Microbiology 57(8): 2351–2359.

Hackett, C.A. & Griffiths, B.S. 1997. Statistical analysis of the time-course of Biolog substrate utilization. Journal of Microbiological Methods 30(1): 183–197.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology and Management 155(1–3): 81–95.

Jia, B., Zhou, G, Wang, F., Wang, Y., Yuan, W. & Zhou, L. 2006. Partitioning root and microbial contributions to soil respiration in Leymus chinensis populations. Soil Biology and Biochemistry 38(4): 653–660.

Kaeoniam, P., Khoorat, P., Sunthornsan, W., Issareeya, M., Cherdchun, C. & Buachum, W. 1976. A study of illegal deforestation in the reserved forest area

at the Sakaerat Environmental Research Station. Environmental and Ecological Research Department, Applied Scientific Research Corporation of Thailand, Bangkok. 53 p.

Kaiser, H.F. 1960. The application of electronic computers to factor analysis. Educational and Psychological Measurement 20(1): 141–151.

Kamo, K., Vacharangkura, T., Tiyanon, S., Viriyabuncha C., Nimpila, S. & Doangsrisen, B. 2002. Plant species diversity in tropical planted forests and implication for restoration of forest ecosystems in Sakaerat, Northeastern Thailand. JARQ 36(2): 111–118.

Kang, B.T. 1993. Sustainable agroforestry systems for the tropics: concepts and examples. IITA Research Guide 26. IITA, Ibadan.

Kanzaki, M., Yoda, K. & Dhanmanonda, K. 1995. Mosaic structure and tree growth pattern in a monodomoionant tropical seasonal evergreen forest in Thailand. In: Box, E. O., Peet, R. K., Masuzawa, T., Yamada, I., Fujiwara, K., & Maycosk, P.F. (eds). Vegetation science in forestry. Kluwer Publishers, Netherlands. p. 495–513.

Köppen, W. 1931. Grundriss der Klimakunde, Walter de Gruyter, Berlin.

Krairapanond, N. & Atkinson, A. 1998. Watershed management in Thailand: concepts, problems and implementation. Regulated Rivers: Research and Management 14(6): 485–498.

Lee, Y. K., Lee, D. K., Woo, S. Y., Park, P. S., Jang, Y. H. & Abraham, E.R.G. Effect of Acacia plantations on net photosynthesis, tree species composition soil enzyme activities, and microclimate on Mt. Makiling. Photosynthetica 44(2): 299–308.

Lindstrom, J.E., Barry, R.P. & Braddock, J.F. 1998. Microbial community analysis: a kinetic approach to constructing potential C source utilization patterns. Soil Biology and Biochemistry 30(2): 231–239.

Lugo, A.E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monoculture. Forest Ecology and Management 99(1–2): 9–19.

Mboukou-Kimbatsa, I.M.C., Bernhard-Reversat, F. & Loumeto, J.J. 1998. Change in soil macrofauna and vegetation when fast-growing trees are planted on savanna soils. Forest Ecology and Management 110(1–3): 1–12.

McNamara, S., Tinh, D.G., Eriskine, P.D., Lamb, D., Yates, D. & Brown, S. 2006. Rehabilitating degraded forest land in central Vietnam with mixed native species plantings. Forest Ecology and Management 233(2–3): 358–365.

Nawir, A.A., Murniati & Rumboko, L. 2007. Forest rehabilitation in Indonesia. Center for International Forestry Research. SMK Grafka Desa Putera, Jakarta, Indonesia.

Nieto, K.F. & Frankenberg, W.T. 1989. Biosynthesis of cytokinins in soil. Soil Science Society of America Journal 53(3): 735–740

Ren, H., Li, Z., Shen, W., Yu, Z., Peng, S., Liao, C., Ding, M. & Wu, J. 2007. Changes in biodiversity and ecosystem function during the restoration of a tropical forest in south China. Science in China Series C: Life Sciences 50(2): 277–284.

Sahunalu, P. & Dhanmanonda, P. 1995. Structure and dynamics of dry dipterocarp forest, Sakaerat, northeastern Thailand. In: Box, E.O., Peet, R.K., Masuzawa, T., Yamada, I., Fujiwara, K. & Maycosk, P.F. (eds.). Vegetation science in forestry. Kluwer Publishers, Netherlands. p. 465–494.

Sakai, A., Visaratana, T., Vacharangkura, T., Thaingam, R., Tanaka, N., Ishizuka, M. & Nakamura, S. 2009. Effect of species and spacing of fast-growing nurse trees on growth of an indigenous tree, Hopea odorata Roxb., in northeast Thailand. Forest Ecology and Management 257(2): 644–652.

Sakurai, K., Tanaka, S., Ishizuka, S. & Kanzaki, M. 1998. Differences in soil properties of dry evergreen and dry deciduous forests in the Sakaerat Environmental Research Station. Tropics 8(1–2): 61–80.

Sharp, A & Nakagoshi, N. 2006. Rehabilitation of degraded forests in Thailand: policy and practice. Landscape and Ecological Engineering 2(2): 139–146.

Sprent, J.I. & Parsons, R. 2000. Nitrogen fixation in legume and non-legume trees. Field Crops Research 65(2–3): 183–196.

Staddon, W.J., Duchesne, L.C. & Trevors, J.T. 1997. Microbial divesity and community structure of postdistrubance forest soils as determined by sole-carbon-source utilization patterns. Microbial Ecology 34(2): 125–130.

Stott, P. 1984. The savanna forests of mainland southeast Asia: an ecological survey. Progress in Physical Geography 8(3): 315–335.

ter Braak, C. J. F. & Šmilauer, P. 1998. Canoco reference manual and user's guide to Canoco for windows: software for canonical community ordination

(version 4). Microcomputer Power, Ithaca, NY.
The tenth national economic and social development plan (2007–2011). 2006. National Economic and Social Development Board of Thailand, Office of the Prime Minister, Bangkok.
Wuethrich, B. 2007. Reconstructing Brazil's Atlantic rainforest. Science 315(5815): 1070–1072.
Yemefack, M., Rossiter, D.G. & Njomgang, R. 2005. Multi-scale characterization of soil variability within an agricultural landscape mosaic system in southern Cameroon. Geoderma 125(1–2): 117–143.
Young, A. 1997. Agroforestry for soil management. 2nd ed. CAB International and ICRAF, New York

Total of 52 references