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Research Article

Above-Ground Net Primary Productivity of the Mixed Dipterocarp Forest on the Soils Derived from Volcanic Substrate in Sabah, Malaysia

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ABSTRACT

Nutrient status, structure and above-ground net primary productivity (ANPP) of a lowland mixed dipterocarp forest on the soils derived from volcanic substrates were examined in Tawau Hills Park, Sabah, northern Borneo, and compared with two mixed dipterocarp forests on soils derived from sedimentary and ultrabasic rocks within the same biogeographic region. The volcanic soils were characterised by two-orders-of-magnitude greater exchangeable Ca and Mg, and 7 to 20 fold greater inorganic N and 2 to 3 fold greater P fractions than the non-volcanic soils. Species diversity, tree density, basal area, above-ground biomass, and ANPP were all lower in the Tawau forest despite high soil fertility than in the two forests on non-volcanic soils. Above-ground biomass density (the mean mass density per unit spatial volume between the ground and the canopy top) of the Tawau forest was also much lower than the two non-volcanic forests. The Tawau forest was predominated by a single dipterocarp species, *Shorea johorensis*. We suggest that nutrient-rich soils derived from volcanic rocks favour this species, which preempts the Tawau forest with a fast population turnover, leading to impoverished species richness and sparser tree density than in the two forests on non-volcanic soils. The predominance of a single species with spatially sparse trees and low biomass density may be related to the low ANPP of the Tawau forest.

Keywords: Above-ground biomass; above-ground net primary productivity; nutrient-use efficiency; soil phosphorus; Tawau Hills Park; volcanic soils.

INTRODUCTION

The lowland tropical rainforests of Borneo are generally characterised by high species diversity and productivity (Aiba et al., 2005). They are characterised by sympatrically occurring multiple congeneric species of the family Dipterocarpaceae and called mixed dipterocarp forest (Whitmore, 1984; Richards, 1996). It is known that there are variations in species composition and structure of the mixed dipterocarp forest in Borneo and the variations are well documented in relation to soil substrate types (Baillie et al., 1987; Newbery et al., 1992; Ashton & Hall, 1992; Aiba & Kitayama, 1999). This indicates that soil nutrient availability affects species composition and structure and probably function of the mixed dipterocarp forest.

While the Soil Map of Sabah (Agricultural Research Centre, 1966) indicates that most mixed dipterocarp forests occur on deeply weathered soils derived from sedimentary rocks in Sabah, a few mixed dipterocarp forests occur on volcanic soils (Tjia et al., 1995; Takashima et al., 2004; Seino et al., 2007). Nutrient status contrasts between these soils, particularly in phosphorus (P) and cation availability. This is because these elements are primarily derived from weathering volcanic materials (i.e. volcanic ash and lava) and consequently volcanic soils are extremely rich in these elements (Crews et al., 1995; Chadwick et al., 1999). A study on the mixed dipterocarp forest on volcanic soils may add considerable knowledge on the relationship between forest ecosystems and soil nutrients by adding a new dimension of biogeochemistry on “nutrient-rich” soils to tropical forest ecology. However, the mixed dipterocarp forest on volcanic soils is not well studied in Borneo.

How P (and cations) is released from volcanic materials to terrestrial ecosystems during soil formation has been well documented along the long soil chronosequence in Hawaii (Crews et al., 1995; Chadwick et al., 1999). Briefly, P that is contained as apatite in volcanic materials is gradually dissolved as phosphate after volcanic materials are supplied to land surfaces through eruptions. Primary minerals of volcanic materials gradually change to amorphous minerals (in the order of 10^2 to 10^3 years) to secondary minerals (10^4 years) and finally to metal oxides (10^5 to 10^6 years) during soil formation. With time, phosphate is increasingly, physico-chemically bound with these derived minerals. At the same time, the concentration of total P declines due to leaching. Reflecting the interplays of gradual release of phosphate and P stabilization during soil formation, the availability of P peaks at an early stage of soil formation (i.e. 10^3 to 10^4 years after eruption), and then declines with soil ageing (Walker & Syers, 1976; Crews et al., 1995). Cations such as calcium (Ca) and magnesium (Mg) are also derived from volcanic materials and depleted with time (Chandwick et al., 1999). However, cations are externally supplied to terrestrial ecosystems through dust and rainfall while such external inputs of P are rather limited (Chadwick et al, 1999).

Reflecting the geochemical reasons described above, the ecosystem structure and productivity of the common mixed dipterocarp forests on deeply weathered soils (rich in metal oxides) are generally thought to be limited by P due to the decline of total P and stabilization by metal oxides (Kitayama et al., 2000; Kitayama & Aiba, 2002). Earlier studies investigated how species composition and productivity changed with P limitation in these forests and found that P-use efficiency increased with increasing magnitude of P deficiency (Kitayama et al., 2000; Kitayama & Aiba, 2002). P-use efficiency is defined as net primary productivity per unit P absorbed in a forest stand, suggesting that tree species with enhanced productivity per absorbed P are selected for and assembled in P-deficient mixed dipterocarp forests; this is considered an important adaptive response to P deficiency. Conversely, young volcanic soils are expected to be abundant in P and tree-species assemblage, structure and productivity must be different from those on deeply weathered soils.

In this paper, we describe the stand structure, productivity, and soil properties of the mixed dipterocarp forest on soils derived from young volcanic substrate (ca. 27,000-year-old) in Tawau, Sabah, northern Borneo. Occurrence of volcanic soils is very limited in Borneo (FAO & UNESCO, 1979; Tjia et al., 1995; Takashima et al., 2004; Seino et al., 2007), while a large area of other Sunda islands are covered by volcanic soils (Humic Andosols in the FAO classification; FAO & UNESCO, 1979). However, accounts on the structure and species composition of post-volcanic vegetation are limited to early primary succession on incipient volcanic substrates up to a few hundred years in age in this area (e.g. Whittaker et al., 1989 in Indonesia; Harrison et al. 2001in Papua New Guinea; and Marler & Del Moral, 2011, 2018 in the Philippines). Hommel (1990) reports the classification of forest types on Miocene volcanic materials in Ujung Kulon, west Java, but he concludes that the vegetation has been impacted by recent volcanic eruptions and human activities. To our knowledge, there is no account on the ecology of pristine mature forests on developed volcanic soils in the floristic region of Malesia other than Seino et al. (2007). We paid particular emphasis on soil P availability and the P use efficiency of the canopy trees.

METHODOLOGY

Study site and field observations

The study site is located at approximately 300 m asl (4˚24'N, 117˚53'E) in Tawau Hills Park (hereafter Tawau), Sabah, Malaysian Borneo. About 60% of the Tawau forest remains primary without human disturbances such as past logging. Mean annual air temperature is 23.6 ºC and mean annual rainfall is 1885 mm during 2001 to 2004 (Lakim, unpublished climate data). Tawau lies on soils derived from volcanic substrate originating from the past Quaternary eruptions of the mountains Magdalena (1320 m), Lucia (1210 m), and Maria (1090 m) within the park. The eruption occurred ca. 27,000 years ago, and the volcanic substrate consists of dacitic, andesitic, and basaltic characters (Omar & Nais, 1995; Takashima et al., 2004).

A research plot of 2 ha (100 m × 200 m) was established on a flat slope of a natural lowland forest of Tawau in 2001 (Seino et al., 2007). The plot was placed on a raised interfluve dissected by parallel small streams, thus being little affected by flooding. All living trees larger than 10.0 cm in trunk diameter at breast height at 1.3 m from the ground (trunk diameter at breast height, DBH) were measured first in November 2001 and re-measured in November 2002 and November 2003. Dead trees were checked during the tree census. Buttressed or stilt-rooted trees were measured for trunk diameter above the protrusions as “DBH” but not at 1.3 m above the ground. Multiple trunks were separately recorded for DBH. Details of the floristic composition of the research plot were described in Seino et al. (2007). Briefly, a total of 45 families, 83 genera, and 133 tree species were identified in the 2-ha research plot. The family Dipeterocarpaceae comprised approximately 60% of the total basal area (total 27.3 m^2 ha^{-1}) with 1 *Dipterocarpus* species, 1 *Dryobalanops* species, 1 *Hopea* species, 1 *Parashorea* species, 7 *Shorea* species and 1 *Vatica* species. The most dominant species was *Shorea johorenis* Foxw. with 40.6% relative abundance in basal area.

Above-ground biomass and productivity
We calculated the standing above-ground biomass (AGB, kg m^{-2}) using the allometric relationships obtained by destructive sampling of a lowland dipterocarp forest in West Kalimantan, Indonesian Borneo (Yamakura et al., 1986):

$$W_s = 0.02903(D^2H)^{0.9813}$$
$$W_b = 0.1192W_s^{1.059}$$

and

$$W_l = 0.09146(W_s + W_b)^{0.7266}$$

where W_s, W_b, and W_l (kg) are the dry mass of the trunk stem, branches, and leaves of a tree; D (cm) is DBH, and H (m) is tree height, respectively. AGB is the sum of W_s, W_b, and W_l. We also calculated AGB density (kg m^{-3}), defined as AGB/H* (cf. Kira & Shidei, 1967), where *H** is a theoretically derived maximum tree height. H* was calculated from the allometric relationship between D and H (Ogawa & Kira, 1977):

$$1/H = 1/AD + 1/H^*$$

where A (m cm^{-1}) and H* (m) are regression constants, respectively.

Basal area (BA) of each tree was derived from DBH and then total BA per ground area at the plot was calculated as the sum of all trees divided by plot area (m^2 ha^{-1}) for the initial year (2001). Wood increment was divided by initial BA and the ratio of wood increment/BA was used as an index of normalized wood increment rate.

We placed litter traps, each with a 0.5 m^2 area, made of 1 mm mesh, at 1 m above the ground at 10 m intervals along two transect lines at the plot (40 traps per plot). Trapped fine litter was collected bi-weekly, and immediately oven-dried at 70 °C for at least 3 days, before sorting by trap into leaves (including rachises of compound leaves), reproductive organs (fruits and flowers including pedicels and peduncles), twigs (≤ 2 cm girth, including bark), epiphytes (all parts combined), palms and bamboos (all parts combined) and dust (unidentifiable particles that pass through 2 mm mesh including insect detritus).

Above-ground net primary productivity (ANPP) was calculated as the AGB increment of surviving trees between the first and final censuses plus fine litterfall. No attempt was made to estimate large detritus such as fallen branches >2 cm girth. Fine litterfall (g m^{-2} yr^{-1}) was determined as the mean of the two years from March 2002 to March 2004.

In June 2003, fine roots were collected at each site with a 30-cm deep core sampler (diameter 37 mm) at ten points at 10-m intervals along a transect starting from a random point. Cores were subdivided into 0–5, 5–15, and 15–30 cm portions, gently rinsed with water to remove soil, and all live roots < 2 mm in diameter were manually collected. Roots with dark coloured tissues and rotten bark were considered dead and were discarded. Roots were oven-dried at 70 °C for 3 days, and dry weights were measured.

Soil nutrients
We collected 10 soil cores by inserting a core sampler (37-mm inner diameter) to 15-cm depth along each of the randomly placed four line transects and lumped the ten soil samples as one composite. We thus obtained four composite soil samples. The four composite samples were extracted with a 1.5N KCl solution, and extracted NO_3-N and NH_4-N were determined

colourimetrically on an auto-analyser (Futura, France). Concentrations of exchangeable Ca and Mg in the KCl solution were determined by inductively coupled plasma emission spectrometry (ICPS-7510, Shimadzu, Kyoto, Japan). Organic carbon (C) was determined on fresh soil by the Walkley-Black wet digestion method (Nelson & Sommers, 1982). Total nitrogen (N) was digested by the micro Kjeldahl procedure with concentrated sulphuric acid and determined colourimetrically. Soil pH was measured on a 1:1 fresh soil to deionised water solution. A portion of each composite was oven-dried at 105 °C for 48 hours to determine gravimetric water content.

We characterised soil P fractions using the sequential extraction of Tiessen & Moir (1993). The details of the analysis can be found in Tiessen & Moir (1993) and Kitayama et al. (2000). Briefly, this method extracts the most labile inorganic/organic P fraction to increasingly recalcitrant fractions with a sequence of weak to strong extraction agents (1M $NaHCO_3$, 0.1M NaOH, 1M HCl, and concentrated hot HCl). The residual P that cannot be extracted is finally wet-digested by H_2SO_4. However, we applied the sequence up to 1M HCl only because we needed the concentrations of the labile P fractions (Matsushima unpublished). The sum of the inorganic fractions extracted by 1M $NaHCO_3$ and 0.1M NaOH is defined as labile inorganic P. The fraction extracted by 1M HCl is calcium phosphate.

Litter and foliar nutrients

To allow for the seasonality of litterfall, the following two dried leaf litterfall samples were selected and ground: from October 2004 (relatively wet period) and July 2005 (relatively dry period).

Intact sun leaves were collected from canopy trees of the most dominant taxa of the plot, i.e., representative of four genera: *Dryobalanops, Hopea, Parashorea,* and *Shorea* of Dipterocarpaceae. In October 2004, at the plot, we shot one sunlit shoot each from the top canopies of one to five trees in each species using a catapult. We collected only fully expanded mature leaves from between the terminal and senescent whorls, and combined leaves by the individual tree. In the laboratory, leaves were wiped, measured for area using the computer software, ImageJ 1.32j, connected with an image scanner (Canon CanoScan FB1210U) within 24 hours, oven-dried at 70 °C for three days, and finely ground. Leaf mass per area (LMA, g m^{-2}) was calculated as oven-dried mass divided by area.

Each powdered litter or foliar sample was weighed in duplicate, and 0.1 g was digested in a block digester with 5.0-ml 100% concentrated H_2SO_4 and 10% H_2O_2 for 4-8 hours. Digestion was repeated until the solution became clear. Digests were filtered through Whatman 2V filter paper and made up to 50 ml with deionised water. The concentrations of P, Ca, Mg, and potassium (K) were determined by inductively coupled plasma emission spectrometry by ICPS-7510 (Shimadzu, Kyoto, Japan). An internal standard was mixed in every batch throughout to check quality of the analysis. Duplicate results were within 10% of the mean for each pair for all elements. The concentrations of N were determined on a CN analyser (JMA1000CN, J-Science, Japan).

The annual fluxes of N, P, Ca, Mg, and K that return to the soil through litterfall were determined as the annual amounts of litterfall multiplied by the mean concentration of each element. Following the method of Vitousek (1982), we calculated stand-level nutrient-use efficiency (NUE) as the ratio of annual litterfall mass to the annual flux of a respective element as litterfall.

Litter decomposition

We estimated the decomposition rates of litter at each site using the mass balance method. We regularly collected standing fine litter in 10 circular frames (each 44 cm in diameter) at 10 m intervals along a line between October 2004 and July 2005. All structured standing litter (twigs ≤ 2 cm girth, leaves, and other fractions ≥ approximately 1 cm^2) inside the frames was collected, oven-dried at 70 °C for 3 days, and weighed. At each time, we recorded the locations of frames to avoid repeated collections from the same points. We calculated the mean of five collections to represent the mean standing litter crop at the plot. The decay constant (k) was approximated as annual litterfall ($g\ m^{-2}\ yr^{-1}$) divided by mean annual standing litter crop ($g\ m^{-2}$).

Comparison with the non-volcanic mixed dipterocarp forests

To evaluate the influences of volcanic soils, we compared the results of the Tawau forest with the results obtained from the two mixed dipterocarp forests on Mount Kinabalu, Sabah, Borneo, by Kitayama et al. (2000) and Kitayama & Aiba (2002). The two forests are within the same biogeographic region but separated by approximately 200 km from Tawau. One forest occurs on the soils derived from sedimentary rock at 600 m at Poring in the Kinabalu Park (hereafter Poring), and the other on the soils derived from ultrabasic rock at 600 m at Nalumad in the Kinabalu Park (hereafter Nalumad); these forests occur at higher elevation, but they are classified as mixed dipterocarp forest. These two forests are known as nutrient deficient forests, particularly in P (Kitayama & Aiba, 2002), as will be discussed. It should be noted that our comparison is descriptive based on a single large plot without replicates.

RESULTS

Stand structure

Table 1 shows the stand properties and productivity of the Tawau forest with those of the other two non-volcanic mixed dipterocarp forests. Species diversity, basal area, and stem density of the Tawau forest were smaller than those of mixed dipterocarp forests on Mount Kinabalu. Despite large values of maximum tree height (H*) and maximum DBH, basal area and AGB of Tawau were lower than those of the other two mixed dipterocarp forests on Mount Kinabalu. Moreover, the AGB density of the Tawau forest was considerably lower than that of the other two forests. On the other hand, the wood increment/BA of the Tawau forest was higher than the other two non-volcanic forests (Table 1).

Table 1: Above-ground biomass, stand structure, and productivity of the studied and compared sites. Biomass properties include wood, leaves, and total above-ground vegetation (AGB), mean standing litter crop, and other allometric constants (A and H*, see text). Productivity includes above-ground net primary productivity (ANPP) by component ($g\ m^{-2}\ yr^{-1}$).

Site	Tawau	Poring**	Nalumad**
Biomass			
Wood biomass ($kg\ m^{-2}$)	34.03	43.20	54.80
Leaf biomass ($kg\ m^{-2}$)	0.35	0.48	0.56
Total AGB ($kg\ m^{-2}$)	34.37	43.68	55.36
Stand litter ($kg\ m^{-2}$)	0.59	0.66	0.67
ABG density ($kg\ m^{-3}$)	0.49	0.66	0.80
A ($m\ cm^{-1}$)	1.34*	1.62	1.77
H* (m)	70.6*	66.6	69.3

Stand structure*			
BA (m^2 ha^{-1})	27.3	34.0	38.8
Density (ha^{-1})	406	464	510
Max. DBH (cm)	163.3	133.8	195.7
Productivity			
Total litterfall (g m^{-2} yr^{-1})	873.55	1110.00	1113.00
Leaf litterfall (g m^{-2} yr^{-1})	594.49	726.00	619.00
Wood increment (g m^{-2} yr^{-1})	741.23	803.00	602.00
Wood increment/BA (10^4g m^{-2} yr^{-1})	27.15	23.61	15.51
ANPP (g m^{-2} yr^{-1})	1614.78	1913.00	1715.00

*; Seino et al. (2007)
**; Kitayama & Aiba (2002)

Annual litterfall rate at Tawau was 874 (g m^{-2} yr^{-1}) and annual above-ground net primary productivity (ANPP) was estimated to be 1615 (g m^{-2} yr^{-1}); both values were lower than those of the two non-volcanic forests, despite the elevation of the Tawau forest being 300 m lower (Table 2).

Table 2: Soil chemical properties, nutrient-use efficiency, and decomposition rate (*k*) of litter, chemical profiles and LMA of canopy leaves of studied and compared sites. Soil properties include pH (H_2O), inorganic N (NH_4-N and NO_3-N) and exchangeable (Ex.) cations on an oven-dry weight basis for the top 15 cm. Nutrient-use efficiency is for phosphorus (PUE), nitrogen (NUE), calcium (CaUE), magnesium (MgUE) and potassium (KUE). Soil phosphorus (P fractions include inorganic P extracted with $NaHCO_3$ (HCO_3-Pi), inorganic P extracted with NaOH (OH-Pi), inorganic P extracted with diluted HCl (Ca-Pi), organic P extracted with $NaHCO_3$ (HCO_3-Po), and organic P extracted with NaOH (OH-Po).

Site	Tawau	Poring	Nalumad
Soil chemical properties*			
pH	4.79	4.10	4.50
NH_4-N (μg g^{-1})	73.6	3.9	8.9
NO_3-N (μg g^{-1})	69.8	10.2	7.2
Ex.Ca (μg g^{-1})	2864	17	29
Ex.Mg (μg g^{-1})	527	31	84
Soil phosphorus fraction**			
HCO_3-Pi (μg g^{-1})	3.69	1.05	4.14
OH-Pi (μg g^{-1})	41.70	18.14	41.45
Ca-Pi (μg g^{-1})	10.40	2.44	15.84
HCO_3-Po (μg g^{-1})	17.40	9.94	20.01
OH-Po (μg g^{-1})	140.00	53.97	57.79
Nutrient-use efficiency***			
Ln (PUE)	7.28	8.47	8.42
Ln (NUE)	4.13	4.59	4.67
Ln (CaUE)	4.11	5.65	5.67
Ln (MgUE)	5.87	6.21	6.19
Ln (KUE)	6.12	5.85	6.19
Other value*			
Decomposition *k* (yr^{-1})	1.47	1.69	1.67
Chemical profiles and LMA of canopy leaves*			
N (%)	2.15	1.52	1.26
P (%)	0.168	0.024	0.010

N (g m^{-2})	1.39	1.93	1.77
P (mg m^{-2})	75.03	30.98	17.39
LMA (g m^{-2})	89.45	138.70	149.10

*; Values at Tawau (NH_4-N and NO_3-N) by Aoyagi et al. (2016), Poring and Nalumad by Kitayama & Aiba (2002)
**; Values at Tawau by Aoyagi et al. (2016), Poring and Nalumad by Kitayama et al. (2000)
***; Values at Poring and Nalumad by Kitayama & Aiba (2002)

Soil and foliar nutrients

All soil minerals of the Tawau forest demonstrated an extremely high concentration (Table 2). The concentration of NO_3-N and NH_4-N were both approximately 70 (μg g^{-1}), and this was one order of magnitude greater than those of the non-volcanic forests. The concentration of hydroxide-extractable organic P (OH-Po) was 140 (μg g^{-1}), and this was threefold greater than that of the non-volcanic forests. The concentration of exchangeable Ca and Mg was extremely high, 2864 and 527 (μg g^{-1}) respectively; this again was one to two orders of magnitude greater than those of the non-volcanic forests. Reflecting these high soil mineral concentrations, the nutrient-use efficiency of the Tawau forest was consistently lower for all minerals investigated than that of the two non-volcanic forests (Table 2).

Mean leaf mass per area (LMA) of the selected canopy species was 89 g m^{-2} in the Tawau forest (Table 2). The mean concentration of foliar N and P of the selected canopy species in the Tawau forest was much higher than that of the non-volcanic forests (Table 2). Noteworthy was the extremely high foliar P concentration in the Tawau forest than in the two non-volcanic forests.

DISCUSSION

The lowland tropical rainforest at Tawau (the Tawau forest) demonstrates high concentrations of soil P fractions, inorganic N and cations as our soils nutrient results indicate. Particularly, the concentration of exchangeable cations is greater by two orders of magnitude for Ca and by one order of magnitude for Mg in the Tawau forest than in the forest on soils derived from sedimentary rocks in Poring. The high concentration of soil P fractions and exchangeable cations are definitely related to the unique pedology of young Tawau soils that are derived from volcanic rocks. Ca derived from parent rocks is known to be lost relatively fast during soil formation process through leaching (Chadwick et al., 1999). The abundance of exchangeable Ca in Tawau soil indicates that minerals derived from parent material (i.e. volcanic rocks) remain in topsoil without being completely lost to leaching. Soil P is also derived from parent materials and thus the abundance of soil P also reflects the unique pedology of young Tawau soils. The high concentration of soil inorganic N is probably related to the abundance of soil P, because P enhances soil N mineralization (Kitayama & Aiba, 2002; Hall et al., 2004). Therefore, we consider that greater N availability in the Tawau forest is related also to the peculiar geology of the site.

Reflecting greater availability of soil N and P, canopy trees in the Tawau forest show remarkably high foliar N and P concentrations. P concentration in green leaves is considered to directly indicate soil P availability (Aerts, 1996); it is greater by one order of magnitude in the Tawau forest than in the two non-volcanic forests. It is known that trees enhance phosphorus-use efficiency (PUE) under greater P deficiency through such mechanisms as P resorption (Kitayama & Aiba, 2002), which is a costly process. Conversely, PUE decreases under greater P availability. Indeed, PUE of the Tawau forest demonstrates a smaller value than the other two non-volcanic forests. We suggest that the Tawau forest is characterized by abundance of soil P, while the other two forests (Poring and Nalumad) are rather P-limited. Nitrogen-use efficiency (NUE) of Tawau forest is also lower because of the greater N availability and this is again related to its unique pedology being volcanic.

The ample soil P and N availability with reduced PUE and NUE in the Tawau forest is a stark contrast to the two lowland tropical rainforests on soils derived from sedimentary and ultrabasic rocks. Soils derived from sedimentary and ultrabasic rocks widely occur in Sabah (Agricultural Research Centre, 1966). The forests on these soils may be limited by P as exemplified by the Poring and Nalumad forests in Tables 1 and 2 based on geochemical determinants of soil P concentrations. If so, the nutrient status of our Tawau forest is considered unique with a limited distribution in Sabah; this needs to be substantiated in the future by adding more data on plant and soil interactions in Sabah.

The unique nutrient status of the Tawau forest must be related to its unique floristic composition, structure and above-ground net primary productivity (ANPP). The Tawau forest is dominated by the single dipterocarp species of *Shorea johorensis* (Seino et al., 2007), which is considered as a subtype of mixed dipterocarp forest on fertile substrate (Ashton 1995). Probably, this species outcompetes other species on fertile soils and predominates the Tawau forest. Tree species diversity of the Tawau forest is relatively poor compared with the other mixed dipterocarp forests, which may be related to the predominance of a single species. On the other hand, species composition of the other mixed dipterocarp forests is characterized by greater evenness of many sympatric dipterocarp species (Whitmore, 1984; Richards, 1996). The higher dominance of a single dipterocarp species and, conversely, the lower overall species diversity are the uniqueness of the Tawau forest.

Surprisingly, both AGB and ANPP of the Tawau forest are lower than those of the two non-volcanic forests that are considered nutrient-limited (particularly by impoverished P). In addition, tree density is sparse and BA is also lower in the Tawau forest. Why are the AGB and ANPP of the Tawau forest on fertile soils lower than those of the two non-volcanic forests that are considered phosphorus-limited? We do not know the exact mechanisms, but it appears to be related to the single dominance of *Shorea johorensis.* The dimension of this species (particularly crown size) is larger and consequently stand-level tree density becomes sparser with a smaller BA value. Growth characteristics of this species is reflected in the greater wood increment/BA ratio, suggesting that *S. johorensis* can grow faster in wood biomass per unit basal area. Spatially sparse individuals of this species exhibit a high turnover rate of AGB; consequently, population of this species should turn over more quickly than the other species and preempts the Tawau forest. Aoyagi et al. (2016), who studied population dynamics, also suggest a high population turnover in the Tawau forest. However, ANPP of the Tawau forest is still lower than the other two forests due to its sparse tree density and small BA value.

The structure and ANPP of the two non-volcanic forests, which are considered nutrient limited, are contrasting to the Tawau forest. Particularly, the Nalumad forest shows a largest total AGB with a highest AGB density and a smallest wood increment/BA ratio. These values indicate that tree species in the Nalumad forest on P-impoverished soils grow more slowly and build up massive biomass.

Based on our study in Tawau, soil nutrient status determines species composition, structure and productivity of the mixed dipterocarp forests of Borneo. Nutrient (N and P) rich soils derived from volcanic rocks favour a single dominance of *S. johorensis*, which preempts the

Tawau forest with a fast population turnover, leading to impoverished species richness and sparser tree density than in the P-limited forests. The single dominance also explains the smaller AGB and ANPP. Our hypothesis explaining the linkage between soil nutrient status and forest structure/composition needs to be substantiated in future.

CONCLUSIONS

Structure and ANPP of a lowland mixed dipterocarp forest on volcanic substrate in Tawau Hill Park were compared with two dipterocarp forests on sedimentary and ultrabasic substrates within the same biogeographic region to elucidate the uniqueness of ecosystem properties on volcanic substrate. Soil P fractions in the volcanic Tawau forest were higher than in the non-volcanic forests, with elevated cation concentrations. The Tawau forest was dominated by a single Dipterocarpaceae species, *Shorea johorensis,* exhibiting low trunk density, basal area, AGB density and ANPP, but with a high wood increment per basal area. The high wood increment per basal area, coupled with the sparse tree density, suggests that individuals of *Shorea johorensis* could readily utilise these abundant soil nutrients and outcompete other dipterocarp species, enabling the maintenance of predominance through a high AGB (i.e. population) turnover rate. This contrasts with the slower wood increment per basal area, and higher AGB and ANPP in the two non-volcanic forests. There seems to be a trade-off between nutrient use efficiency, ANPP and species diversity among lowland mixed dipterocarp forests. The mechanisms underpinning the relationships of nutrient use efficiency characteristics and population dynamics merit further study to support our understanding of ecosystem function and species diversity.

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DECLARATIONS

Research permit(s). This research was conducted based on the mutual collaboration between the two parties, Sabah Parks-Japan, before the establishment of SaBC.
Ethical approval/statement. Not applicable.
Generative AI use. We declare that generative AI was not used in this study nor in the writing of this article.

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