Nutritional ecology of plants grown in a tropical peat swamp

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ABSTRACT The relationships between plant and soil in peat swamp forests in two different growth stages, primary and secondary, were examined by analyzing nutritional characteristics (e.g. N, P, K, Ca, Mg, Na, Fe, Mn, Zn, Cu, Mo, Al, B, and Si concentrations) and natural abundances of $^{15}$N (Δ$^{15}$N) and $^{13}$C (Δ$^{13}$C) of plant and soils. Fifty-two plant species from primary forests and thirty from secondary forests were randomly sampled. Plants in both forests belonged to the phylogenic groups Euasterids II, Euasterids I, Ericales, Eurosids II, Eurosids I, Eudicots, and Magnoliids, which were from a newly evolved order. The results showed that Eurosids I plants in primary forests accumulated higher P, K, Mg, Fe, and B than those in secondary forests. Other minerals did not limit plant growth at either forest type. For Eurosids I plants nutrients depended on soil K, Mg, and Fe, but for P and B they relied on their own nutrient acquisition. This is similar to other plant phylogenies in both forests whose nutrient contents reflected their own nutrient requirements rather than soil nutrients. Since the leaf Δ$^{15}$N of plants in both forests is lower than soil Δ$^{15}$N, N2-fixing microorganism activity may be high. It can be hypothesized that peat swamp forests have developed symbiotic systems with N2-fixing microorganisms, because of poor N nutrition.

Key words: peat soil, plant phylogeny, primary forest, secondary forest

INTRODUCTION

The largest areas of peatland in the world are located in the Southeast Asian coastal areas along peninsula Malaysia and Indonesian Java, Sumatra, and Borneo. Thailand is a country that contains a small area of tropical peatland (45, 264 ha), however 60% of the peatland in Thailand is found in Narathiwat Province (Suzuki and Niyomdham, 1992). Floristic composition of peat swamp forest is rich, consisting of 124 families and 470 species of plants, of which 109 families and 437 species are flowering plants, and 15 families and 33 species of fern. Yoshioka et al. (2002) reported that most of the To Daeng swamp area is a primary swamp forest. Peat swamp forests in Narathiwat Province are classified as four types: typical mixed swamp forest on thick peat layer, Macaranga-dominated swamp on thick peat layer, Melaleuca-dominated forest on thin peat layer or sandy soils, and Fagraea-dominated forest on sandy soil with a thin peat layer (Suzuki and Niyomdham, 1992). Primary forests are dominated by Syzygium pyrifolium, Gaua motleyana, Campnossperma coriaceum, Macaranga pruinosa, Calophyllum teysmannii, Neesia malayana, Endiandra macrophylla, Syzygium obatum, Sterculia bicolour, Sternourus secundiflorus, Syzygium muelleri, and Baccarea bracteata (Buyanavajchewin, 1995). Former destructive anthropogenic use of the peatlands caused the disappearance of peat swamp forest, leading to peat soil degradation and forest type changes or transformation to grassland ecosystem (Nagano et al. 1996).

Peat soil is characterized as a nutrient-poor ecosystem with very high acidity and loads of organic matter e.g. lignin (Safford and Maltby, 1998; Paavilaine and Päivänen, 1995). To Daeng peat swamp is fed by rainfall and by river run-off from mountainous areas in the west. Ueda et al. (2000) reported that this swamp water has low pH, nutrient levels and very low levels of anions and cations in the surface water, even lower than in the ground water. This kind of nutrient-limited soil retards plant growth. Therefore, plants growing on peat soil must develop some specific mechanisms, such as organic acid exudation from roots, to accumulate nutrients (Osaki et al. 2003, 1998a, and 1998b, Tuah, 2003). In general, plant species that grow and dominate
in an ecosystem are affected by various environmental parameters, so differences in plant physiology, e.g. seed germination, relative growth rate, and competition with other plant species, can also express the changes in the environmental development of an ecosystem (Berendse, 1990).

Recently, natural abundances of stable isotopes N (δ¹⁵N) and C (δ¹³C) are being used widely in research on N and C assimilation cycling in organisms and ecosystems (Robinson, 2001; O’Leary, 1981). Measurements of whole plants are inadequate because they don’t address seasonal life stage differences and are limited by time or sample size. Therefore, the relative abundance of isotopic assay, which integrates physiological processes over larger temporal and spatial scales, is required (Nilsen and Orcutt, 1996). Nitrogen dynamics are fundamental in natural ecosystems and essential for all plants. However, N cycling in plant and soil is complex. This study, therefore, aims to highlight some aspects of N cycling and other physiological mechanisms of plants growing in two growth stages of peat swamp forest.

MATERIALS AND METHODS

Study site
This study was conducted in peat swamp forests of To Daeng Peat Swamp Forest, Narathiwat Province Thailand. This site comprises of primary and secondary forests. Primary forest is at a climax stage and undisturbed, in contrast to secondary forest, which is dominated by native trees and those that grow quickly after deforestation by humans or a natural disaster.

Plant sampling, preparation, and analysis
Mature leaves were randomly sampled from primary and secondary forests. Samples were oven-dried at 80 °C to constant weight, ground into a fine powder, and weighed for subsequent chemical analysis.

Plant analysis
Samples were completely digested with a mixture of H₂SO₄ and H₂O₂ following Mizuno and Minami (1980). Leaf N was analysed using a CN analyser (SUMIGRAPH NC-1000). Concentrations of P, K, Ca, Mg, Na, Fe, Mn, Zn, Cu, Mo, Al, B, and Si were determined using inductively coupled plasma emission spectrometry (ICPS-7000, SHIMADZU). Leaf δ¹⁵N and δ¹³C were analysed using an isotope mass spectrometer (EA1108-ConfloII-delta-S system).

Soil sampling and analysis
Soil samples were collected from several points at each forest type at three depths (0–20, 20–40 and 40–60 cm), air-dried and ground prior to chemical analysis. Soils were analyzed for N content using an MT-6 CHN CORDER (YANAKO). The δ¹⁵N and δ¹³C were analysed using an isotope mass spectrometer (EA1110-DELTAplus Advantage ConFloIII System). Two grams of soil were shaken for 2 hrs, extracted with 1 N HCl and filtrated through Whatman no 42 filtrate paper. Concentrations of P, K, Ca, Mg, Na, Fe, Mn, Zn, Cu, Mo, Al, B, and Si in the extract were determined using ICPS-7000.

Data analysis
The general tendency of plant mineral element accumulation was explained and comparisons between plant phylogenies were made. Phylogenetic classification was categorized by referring to the orders and families of angiosperms and gymnosperms. This classification can be accessed at http://biodiversity.uno.edu.delta. Mineral concentration means were compared with a t-test using SPSS 10.0

RESULTS
Vegetation
Fifty-two plant species in primary forests and thirty in secondary forests were observed. These plants were classified into 7 phylogenetic groups: Ericales, Euasterids I, Euasterids II, Eudicots, Eurosids I, Eurosids II, and Magnoliids.

Primary forest comprised of Ardisia lanceolata, Diospyros lanceifolia, Dispyros siamang, and Gaurna motleyana for Ericales, Ochreauclea maingayi, Isora grandifolia, Tarenna wallichii, and Euodia roxburghiana for Euasterids I, Stemonurus secundiflorus for Euasterids II, Bhesa indica, Crudia caudata, Dialium patens, Archidendron clypearia, Parastemon urophyllus, Baccoura bracteata, Blumeodendron kurzii, Macaranga griffithiana, Macaranga pruinosa, Garcinia bancana, Cartoxylum arborescens, Calophyllum teysmannii, Gynotroches axillaries, Elaeocarpus griffithii, and Elaeocarpus macrocerus for Eurosids I, Neesia malayana, Vatica pauciflora, Sterculia bicolor, Eugenia grandis, Eugenia tumida, Eugenia spicata, Eugenia caudate, Eugenia cerasiformis, Eugenia operculata, Eugenia kunstleri, Campnosperma coriaceum, Melanockyla bracteata, Sandoricum beccarianum, Aglaia rubiginosa, Chisocheton patens, Aglaia odoratissima, and Nephelium maingayi for
| Nutritional ecology of plants growing in a primary peat swamp forest |

- **Biota:** In general, plants growing in peat swamp forests have adapted to the wet and nutrient-poor conditions of the environment. They often have adaptations such as air-filled roots,erenoids, and hydrophytes, which help them survive in these environments.

- **Nutrients:** Nutrients such as nitrogen, phosphorus, and potassium are essential for plant growth. In peat swamp forests, these nutrients are often limiting due to the nutrient-poor nature of the soil.

- **Water:** Water is also a critical resource in peat swamp forests. The high water content of the soil helps to maintain the forest's structure and supports a diverse range of plant species.

- **Habitats:** Peat swamp forests can be divided into several distinct habitats, each with its own unique species composition. These habitats include the forest floor, shrub layer, and emergent vegetation.

- **Flora:** The flora of peat swamp forests is diverse, with a wide range of plant species adapted to the wet and nutrient-poor conditions. Some common plant species include Equisetum fluviatile, Potamogeton pectinatus, and Carex rostrata.

- **Fauna:** The fauna of peat swamp forests is also diverse, with a variety of animals adapted to the wet environment. These include waterfowl, amphibians, and various freshwater invertebrates.
Table 2. Nutrient concentrations and natural abundances of stable isotope $^{13}$C (δ $^{13}$C) and $^{15}$N (δ $^{15}$N) of some native plants in a secondary peat swamp forest

| Family       | Species                        | Order              | Distance to primary forest (km) | ND15C | ND13C | P  | K  | Ca | Mg | Na | Fe | Al | Cu | Zn | Mn | Si | B  | Mo |
|--------------|--------------------------------|--------------------|---------------------------------|-------|-------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Euphorbiaceae| Polyalthia lateriflora         | Sapindales         | 18                              | 0.0   | 0.0   | 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0|
| Euphorbiaceae| Aglaia rubiginosa              | Sapindales         | 18                              | 0.0   | 0.0   | 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0|
| Euphorbiaceae| Sterculia bicolor             | Sapindales         | 18                              | 0.0   | 0.0   | 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0|
| Myrtaceae    | Campnosperma coriaceum        | Myrtaceae          | 18                              | 0.0   | 0.0   | 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0|
| Myrtaceae    | K and H                      | Myrtaceae          | 18                              | 0.0   | 0.0   | 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0| 0.0|

N (−1 to 5). Euasterids I (−1 to 1). Eurosids I (−1 to 1).Euasterids II (−1 to 3). Eurosids II (−1 to 3).
while concentrations of Na, Cu, Zn, and Mo tended to be higher in the secondary forests (Figs. 1, 2, and 3). This comparison does not include Eudicots \( (n=1) \) and Euasterids II \( (n=1) \) plants of the primary forests and Ericales \( (n=2) \) of the secondary forests, because sample sizes were small.

**Soil**

Concentrations of N, K, Ca, Mg, Na, Fe, Zn, and Mn seemed to be higher in primary forest soil than secondary forest soil, while concentrations of P, Cu, and Si were not different. Concentrations of Al were higher in secondary forest soil (Table 3).

**Fig. 1.** Concentrations of N, P, K, Ca, Mg (g kg\(^{-1}\)), and Na (mg kg\(^{-1}\)) in leaves of plants grown in primary and secondary forests. Bars in figure indicate SE. * indicates significant differences at 5% level by t-test.

\[ \delta^{15}N \text{ and } \delta^{13}C \text{ values in plants and soils} \]

**Plant**

Average leaf \( \delta^{15}N \) and \( \delta^{13}C \) in the primary forests were 0.9 and −33.3 \( \% \) for Ericales, 1.1 and −33.1 \( \% \) for Euasterids I, 1.9 and −34.0 \( \% \) for Euasterids II, 0.5 and −32.4 \( \% \) for Eurosids I, −0.1 and −33.0 \( \% \) for Eurosids II, and 0.4 and −33.6 \( \% \) for Magnoliids, respectively (Table 1 and Fig. 4). Average leaf \( \delta^{15}N \) and \( \delta^{13}C \) in secondary forests were 1.8 and −31.4 \( \% \) for Ericales, 0.2 and −30.3 \( \% \) for Euasterids I, 1.0 and −29.7 \( \% \) for Euasterids II, 0.7 and −29.8 \( \% \) for Eurosids I, 2.1 and −30.4 \( \% \) for Eurosids II, and −0.7 and −30.5 \( \% \) for
Fig. 2. Concentrations of Fe, Al, Cu, Zn and Mn (mg kg$^{-1}$) in leaves of plants grown in primary and secondary forests. Bars in figure indicate SE. * indicates significant differences at 5% level by $t$-test.

Fig. 3. Concentrations of Fe, Al, Cu, Zn and Mn (mg kg$^{-1}$) in leaves of plants grown in primary and secondary forests. Bars in figure indicate SE. * indicates significant differences at 5% level by $t$-test.
Table 3. Soil chemical properties in primary and secondary forests

<table>
<thead>
<tr>
<th>Origin</th>
<th>Depth (cm)</th>
<th>N  (g kg$^{-1}$)</th>
<th>P  (mg kg$^{-1}$)</th>
<th>K  (g kg$^{-1}$)</th>
<th>Ca (mg kg$^{-1}$)</th>
<th>Mg (mg kg$^{-1}$)</th>
<th>Na (mg kg$^{-1}$)</th>
<th>Fe (mg kg$^{-1}$)</th>
<th>Al (mg kg$^{-1}$)</th>
<th>Cu (mg kg$^{-1}$)</th>
<th>Zn (mg kg$^{-1}$)</th>
<th>Mn (mg kg$^{-1}$)</th>
<th>Si (mg kg$^{-1}$)</th>
<th>B (mg kg$^{-1}$)</th>
<th>Mo (mg kg$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary forest</td>
<td>0--20</td>
<td>18.1</td>
<td>54.2</td>
<td>0.39</td>
<td>1.67</td>
<td>0.49</td>
<td>1.17</td>
<td>1140</td>
<td>1946</td>
<td>21.1</td>
<td>13.3</td>
<td>710</td>
<td>23.1</td>
<td>6.3</td>
<td>4.3</td>
</tr>
<tr>
<td></td>
<td>20--40</td>
<td>16.8</td>
<td>28.5</td>
<td>0.24</td>
<td>1.40</td>
<td>0.41</td>
<td>1.16</td>
<td>7235</td>
<td>1999</td>
<td>8.6</td>
<td>9.5</td>
<td>568</td>
<td>14.2</td>
<td>6.8</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>40--60</td>
<td>12.7</td>
<td>22.9</td>
<td>0.16</td>
<td>n.d.</td>
<td>0.26</td>
<td>0.17</td>
<td>5548</td>
<td>2174</td>
<td>18.9</td>
<td>6.9</td>
<td>412</td>
<td>12.8</td>
<td>6.5</td>
<td>5.3</td>
</tr>
<tr>
<td>Secondary forest</td>
<td>0--20</td>
<td>11.5</td>
<td>55.6</td>
<td>0.04</td>
<td>0.67</td>
<td>0.18</td>
<td>0.38</td>
<td>3575</td>
<td>3712</td>
<td>6.6</td>
<td>1.9</td>
<td>111</td>
<td>22.9</td>
<td>6.3</td>
<td>9.8</td>
</tr>
<tr>
<td></td>
<td>20--40</td>
<td>6.8</td>
<td>44.4</td>
<td>0.07</td>
<td>0.44</td>
<td>0.13</td>
<td>0.06</td>
<td>3648</td>
<td>4315</td>
<td>27.9</td>
<td>3.0</td>
<td>85</td>
<td>47.9</td>
<td>6.4</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>40--60</td>
<td>8.2</td>
<td>37.1</td>
<td>n.d.</td>
<td>0.39</td>
<td>0.15</td>
<td>n.d.</td>
<td>6192</td>
<td>4666</td>
<td>14.9</td>
<td>1.9</td>
<td>83</td>
<td>32.9</td>
<td>6.4</td>
<td>8.9</td>
</tr>
</tbody>
</table>

Fig. 4. Natural abundances of stable isotope $^{15}$N ($\delta^{15}$N) and $^{13}$C ($\delta^{13}$C) in leaves of plants grown in primary and secondary forests. Bars in figure indicate SE.

Fig. 5. Natural abundances of stable isotope $^{15}$N ($\delta^{15}$N) and $^{13}$C ($\delta^{13}$C) in soils of primary and secondary forests
Magnoliids, respectively (Table 2 and Fig. 4).

**Soil**

Soil $\delta^{15}N$ at 0–20, 20–40, and 40–60 cm depths were 3.05, 3.72, and 4.32 % in primary forests, and, 3.17, 3.51, 2.85 % in secondary forests, respectively. Soil $\delta^{13}C$ at 0–20, 20–40, and 40–60 cm depths were −30.1, −30.0, and −30.1 % in primary forests, and, −29.9, −29.5, and −29.7 % in secondary forests, respectively (Fig. 5).

**DISCUSSION**

**Plant nutritional characteristics**

In some phylogenetic groups, such as Eurosids I or Magnoliids, differences in the status of some nutrients in plants between primary and secondary forests corresponded to that in soils (Figs. 1, 2, and 3; Table 3). In many cases, however, the differences in the soil nutrient status between two forest types did not affect the concentrations of these nutrients in the plants, suggesting that plant species growing in a tropical peat swamp have mechanisms to acquire nutrients, even under nutrient-limited conditions.

**$\delta^{13}C$ in leaves and soils**

Plants had leaf $\delta^{13}C$ values between −32.4 and −34.0 % in primary forests, and −29.7 and −31.4 % in secondary forests, indicating that all plant species are C$_3$ plants, according to Nilsen and Orcutt (1996) who reported that the $\delta^{13}C$ values of C$_3$ and C$_4$ plants ranged between −20 to −35 % and −10 to −12 %, respectively. However, different leaf $\delta^{13}C$ values could also be attributed to water availability (Van Nieuwstadt and Douglas, 2005). Since the To Daeng peat swamp is mostly permanently waterlogged (Yoshioka et al. 2002), there may be no difference in water conditions between the primary and secondary forests. Therefore, higher leaf $\delta^{13}C$ in secondary forests may be a result of higher photosynthetic activity than in primary forests, and light intensity seems to influence leaf $\delta^{13}C$ under no water stress conditions, especially, vertical depression of leaf $\delta^{13}C$ (Matsubara et al. 2000). Moreover, fast-growing plants grown in secondary forests had more exposure to sunlight than plants grown in primary forests, where plant density is higher.

**$\delta^{15}N$ in leaves and soils**

Plants had leaf $\delta^{15}N$ values between −0.1 and 1.9 % for primary forests, and −1.0 and 2.1 % for secondary forests, indicating that plants in both forest types have relationships with N-fixing microorganisms, because the small deviation of $\delta^{15}N$ from 0 % ($\delta^{15}N$ of air) in bulk in tissues of vascular plants ($\delta^{15}N$ c.a. ± 2 % relative to air) is attributed to enzymic transformations of N within plants (Yoneyama, 1995). However, leaf $\delta^{15}N$ in secondary forests was more specific to the plant’s phylogenic group than that in primary forests, indicating that plants in secondary forests had specific access to N sources. Other researchers have also reported that plant phylogeny has a strongly effect on N acquisition from soil (Högberg, 1997). Robinson (2001) demonstrated that precipitation ( $\delta^{15}N$ is c.a. −5 %) seemed to be a major N source for plants grown in an area where the annual rainfall is over 1,400 mm. However, in this study, plants showed the possibility of obtaining N from N fixation symbioses ( $\delta^{15}N$ ranged from −1.0 to 2.1%), rather than N from precipitation.

Conclusively, soil $\delta^{15}N$ ranged from 3.05 to 4.32 % in primary forests and 2.85 to 3.51 % in secondary forests. However, $\delta^{15}N$ in leaves were clearly lower than 2.8 % in both forests. Therefore, it is hypothesized that a part of N acquisition in peat swamp forests is derived from symbiotic systems with N-fixing microorganisms. Plant phylogeny strongly controlled plant N acquisition from soil, and this phenomenon could be observed more clearly in secondary succession forests than in undisturbed, primary forests.

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