Drainage effects on leaf traits of trees in tropical peat swamp forests in Central Kalimantan, Indonesia

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ABSTRACT

Large areas of the tropical peat swamp forests in Central Kalimantan were drained to be converted into rice fields and then abandoned. A change in the soil water level due to drainage in the forests must have had a big impact on the ecology and ecophysiology of the trees in the drained remnant forests. The leaf traits of these trees in particular may have been directly or indirectly affected by drainage because of their high sensitivity to environmental change. To understand the influence of drainage on leaf traits, we investigated leaf morphological and physiological differences between intact and drained peat swamp forests in Palangka Raya, Indonesia, using 14 species distributed over both types of forests. We compared the leaf mass per unit area (LMA), leaf toughness, leaf area- and mass-based nitrogen content (Narea and Nmass), carbon/nitrogen ratio, total phenolics, condensed tannin and lignin content and carbon isotope ratio (δ¹³C) of both types of forest trees. In the drained forest, trees had higher values in LMA, Narea, and δ¹³C than in the intact forest, suggesting that such trees adjust themselves to dry conditions to increase photosynthetic ability with high water use efficiency compared with those in intact forests. We also found an increase in condensed tannin content in drained forest trees, which may offset the drainage-induced acceleration of leaf decomposition to some extent.

Key words: δ¹³C, drainage, LMA, peat swamp forest, tannin

INTRODUCTION

Tropical peat swamp forests are important reservoirs of biodiversity, carbon and water (Osaki and Tsuji 2016; Page and Rieley 1998). However, extensive peatland areas in Southeast Asia have been degraded through deforestation, drainage and fire, leading to direct and indirect environmental and socio-economic impacts of local to global significance (Page et al. 2009). Drainage due to land-use change in particular is one of the main driving factors in accelerating carbon loss in ecosystems (Chimner et al. 2017; Furukawa et al. 2005; Jauhiainen et al. 2008). Of the 27.1 million hectares (Mha) of peatland in Southeast Asia, 12.9 Mha had been deforested and mostly (11.1 Mha) drained by 2006 (Hooijer et al. 2010). In Central Kalimantan, the land largely lying on deep peat experienced clear cutting for food production purposes, and an extensive area was drained by a 4600-km-long network of canals (Jauhiainen et al. 2008). Most of the area was abandoned because of the difficulty in controlling peat hydrology and applying physicochemical peat properties for agriculture (Osaki and Tsuji 2016; Rieley and Page 2005).

A decrease in the soil water level due to drainage must have had a great impact on tree ecology and ecophysiology in the abandoned disturbed forests. The leaf traits of trees in particular may have been affected by drainage because of their high sensitivity to environmental change, such as drought. In general, drought stress caused by soil moisture reduction is thought to induce the downsizing and thickening of leaves and an increase in leaf water use efficiency (Larcher 2003; Turner 2001). However, we still do not fully understand the impacts of drainage on leaf traits under extremely stressful conditions in the peat swamp forests, where nutrient deficiency and high acidity are observed (Nishimura et al. 2007).

It is possible that trees growing in the drained peat swamp forests increase leaf thickness and nitrogen concentrations to improve photosynthesis. Indeed, many
studies have reported that the productivity of forests and tree growth have been improved by drainage (Choi et al. 2007; Laiho et al. 2003; Macdonald and Lieffers 1990). Macdonald and Lieffers (1990) and Choi et al. (2007) reported an improvement in the nitrogen concentrations of trees growing on drained boreal peatlands. An acceleration in substrate decomposition and nitrogen mineralization after drainage is likely to increase leaf nitrogen concentrations even in the trees of tropical peat swamp forests. In addition, trees may also improve their water use efficiency after drainage in peat swamp forests, as do canopy tree leaves under dry and high light conditions in tropical rain forests (Ichie et al. 2016; Kenzo et al. 2015).

The amounts of phenolic compounds as secondary metabolites, such as total phenol, tannin, and lignin, which all affect decomposition (Horner et al. 1988), may also change due to drainage. Recently, Lim et al. (2014) and Yule et al. (2016) reported that the levels of total phenolic compounds and total tannins had decreased in the leaves of some pioneer species with progress in peatland degradation after drainage in Malaysia. Yet, we still lack information about the impact of drainage on leaf traits related to decomposition rates, including leaf phenolic compounds such as lignin, the carbon to nitrogen ratio (C/N ratio), and leaf toughness that also affect soil microbial activities (Gallardo and Merino 1993).

In this study, we tested our hypothesis that trees growing in a drained peat swamp forest change some specific leaf traits related to photosynthesis and decomposition. We compared the leaf morphological and physiological traits of intact and drained peat swamp forests in Central Kalimantan, using 14 species commonly distributed over both types of forests. The research area was chosen because it had different water levels only depending on the presence or absence of drainage in similar soil environments (Tuah et al. 2003).

**Materials and Methods**

**Study site**

The study was carried out at Setia Alam (intact and undrained peat swamp forest: 2.32°S, 113.90°E) and Kalampangan (abandoned and drained peat swamp forest: 2.35°S, 114.14°E) in the upper catchment of the River Sabangau, about 20 km southeast of Palangka Raya City in Central Kalimantan, Indonesia (see details in Hirano et al. 2007, 2012, Itoh et al. 2017). The reported annual mean air temperature and precipitation for the period 2002–2010 in the area were 26.2±0.3°C and 2540±596 mm yr⁻¹ respectively (Hirano et al. 2014). In Central Kalimantan, a large peatland area was deforested and drained in the late 1990s to develop farmland according to a national project, the Mega Rice Project. This large-scale project was revoked in 1999 mainly because of an economic crisis (Rieley and Muhamad 2002). Consequently, vast devastated peat lands were left behind. Each of the two study sites is in a different tropical peat swamp forest remaining in Block C of the Mega Rice Project (see Hirano et al. 2007, 2012; Itoh et al. 2017). Both forests are homogenous secondary, and their trees had been logged selectively until the end of the 1990s. In soil nutrient conditions there is not much difference between the two forests (Tuah et al. 2003). In Central Kalimantan, seasonal variation exists in precipitation. The study sites were burnt down because of ENSO drought in 1997 (Page et al. 2002), but the vegetation is recovering (Hirano et al. 2009).

**Sample species and measurement of leaf traits**

We selected 1–3-m tall sample trees totaling 227 individuals of 14 species commonly distributed over open areas in both drained and undrained forests in September 2006 and February 2007 (Table 1). We sampled 8 fully expanded leaves per individual from each sun-exposed crown. We measured the leaf toughness of each of the fresh leaves and oven-dried them at 60°C for 48 h. Then we transported them to our laboratory and measured other leaf traits such as leaf N and C contents, total phenolics and lignin contents and δ13C. Water use efficiency (WUE) was evaluated by using leaf-tissue δ13C signatures (Farquhar et al. 1989; Kenzo et al. 2019). The leaf toughness (leaf fracture resistance) of each collected leaf was estimated by a punch test with three analytical replications by using a digital penetrometer (model RX-1: Aikoh, Osaka, Japan) (Katabuchi et al. 2012; Nomura et al. 2000). LMA was determined as the ratio of leaf dry weight to leaf flesh area. The concentrations of C and N in the leaves were analyzed by using an NC analyzer (Sumitomo Chemical, Osaka, Japan, SUMIGRAPH NC-95). The total phenolics and condensed tannin in the leaves were extracted with 50% methanol and the concentrations were determined by the Folin-Ciocalteu (for the total phenolics) and proanthocyanidin (for condensed tannin) methods respectively (Julkunen-Tiitto 1985; Waterman and Mole 1994) by using a spectrophotometer (Hitachi, Tokyo, Japan, Model U-1800). The standards for the assays were gallic acid for the total phenolics and cyanidin chloride for condensed
Drainage effects on leaf traits of peat swamp forest trees

Tannin. Lignin concentrations were determined according to Van Soest et al. (1991). The stable carbon isotope composition of each leaf sample was determined by using an isotope ratio mass spectrometer (ThermoQuest, San Jose, CA, USA, Delta Plus System). All the carbon isotope ratios were expressed in delta notation relative to the PD Belemnite standard: \( \delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1000 \) (‰), where R_{sample} is the \( ^{13}C/^ {12}C \) ratio of the sample, and R_{standard} is the ratio of the standard (Tanaka-Oda et al. 2010). We used \( \delta^{13}C \) to evaluate the long-term water-use efficiency (WUE) of each leaf (Farquhar et al. 1989, Tanaka-Oda et al. 2010).

Statistical analysis

We performed the Welch t-test for the significance of differences in mean values for all the traits of leaves between the tree species of the intact and drained forests. The respective effects of the sites and species on the various leaf traits were assessed by two-way ANOVA. Pearson’s correlations were used to evaluate the relationship between the leaf traits. Principal component analysis (PCA) was used to summarize all the leaf traits. Differences in PCs between the two forests were assessed by the t-test. For all the statistical analyses, we used the R version 3.3.1 (R Development Core Team 2016).

RESULTS

Leaf morphological and physiological traits

There was a significant difference in LMA between intact and drained forest trees \((P<0.05, \text{Table 2}, \text{Table 3}, \text{Appendix 1})\). Drained forest trees had thicker leaves than intact forest trees. There was no significant interaction between the species and the sites (ANOVA, \(P>0.05\), Table 3).

The N_{area} values of drained forest trees were significantly higher than those of intact forest trees \((P<0.01)\), although in N_{mass} there was no significant difference between the two sites \((P>0.05, \text{Table 2}, \text{Table 3})\). All of the studied species showed the increasing tendency of N_{area} in the drained forest, while the impact of drainage on N_{mass} was species-specific (Appendix 1).

The intact and the drained forest trees also differed significantly in \( \delta^{13}C \) signatures \((P<0.001, \text{Table 2}, \text{Table 3})\). The latter showed higher \( \delta^{13}C \) values. Almost all of the 14 species showed the increasing tendency of \( \delta^{13}C \) in the drained forest, and 8 of them showed statistical significance \((P<0.05, \text{Appendix 1})\). Only one species, Cratoxylum glaucum, showed a slightly opposite tendency, but not significant.

Leaf traits affecting decomposition

Drainage did not affect many of the leaf traits controlling leaf decomposition, such as leaf toughness, C/N

| Species                  | Number | Intact | Drained |
|--------------------------|--------|--------|---------|
| Mezzettia parviflora    |        | 8      | 9       |
| Shorea sp.               |        | 9      | 8       |
| Lithocarpus dasystachyus |        | 9      | 8       |
| Calophyllum hosei        |        | 9      | 8       |
| Garinia sp.              |        | 9      | 8       |
| Cratoxylum glaucum      |        | 9      | 8       |
| Stemonurus scorpioides   |        | 8      | 8       |
| Horsfieldia crassifolia  |        | 10     | 8       |
| Syzygium sp1             |        | 10     | 8       |
| Syzygium sp2             |        | 5      | 5       |
| Combretocarpus rotundatus|        | 8      | 7       |
| Tetractomia tetrandra    |        | 8      | 8       |
| Madhuca sp.              |        | 7      | 5       |
| Tetramerista glabra      |        | 12     | 8       |

Table 1. Tree species and the number of individuals on the intact and the drained plot in the peat swamp forest.
However, a significant increase was observed in condensed tannin content in the drained forest compared to that in the intact forest ($P<0.05$, Table 2, 3). In addition, two-way
ANOVA showed that the site effect on the condensed tannin to N ratio was significant ($P<0.001$, Table 3), though the differences in species mean values were insignificant between the two forests ($P>0.05$, Table 2).

**Correlation between leaf traits**

There were various significant correlations among the investigated leaf traits (Appendix 2). A clear significant correlation was found between $N_{\text{area}}$ and $\delta^{13}\text{C}$ due to a clear increase in the two factors in the drained forest (Fig. 1A). On the other hand, a significant negative correlation was found between LMA and $N_{\text{mass}}$ in both forests (Appendix 2).

We found a clear increase in LMA, but not in $N_{\text{mass}}$, in the drained forest trees compared to the intact forest trees (Table 2); there was a significant difference in intercepts (ANCOVA, $P<0.05$), but not in slopes of the regressions between the two forests ($P>0.05$) (Fig. 1B). The principal component analysis (PCA) showed clear tendencies related to the types of leaf trait (Fig. 2). The first principal component (PC1), which mostly related to leaf traits...
DISCUSSION

The biggest impact of drainage in our study was on the improvement of the leaf traits related to photosynthetic ability (Fig. 2). Several possible reasons are suggested to explain the impact. First, the improvement of environmental conditions by drainage, such as better rooting conditions (Lieffers and Rothwell 1987; Mugasha et al. 1993) and higher nutrient availability (Choi et al. 2007; Lieffers and Macdonald 1990; Westman and Laiho 2003), might have helped the leaf traits to act favorably on photosynthesis in the drained forest. In this study, the drained forest trees had higher values of LMA and N\text{max} than the intact forest trees, both of which positively affected photosynthetic ability (Kenzo et al. 2015; Koike 1988; Evans 1989, Reich et al. 2009). Second, trees in the drained peat swamp forest might have adapted to drought stress due to drainage. Trees in drained forests are exposed to drought and high temperature conditions due to strong sunlight characteristic of tropical areas (Walter 1973; Whitmore 1998). In fact, previous reports at the same study site clearly showed that soil temperature had increased and soil water content had decreased after drainage (Sundari et al. 2012; Jauhiainen et al. 2014). It is well known that leaf thickness can contribute to desiccation tolerance, which has a positive relation to high dehydration tolerance (e.g. John et al. 2018; Kenzo et al. 2007, 2019; Niinemets 2001). High LMA also increases leaf heat capacity due to large water volume and may give drought and high temperature tolerance (Turner 2001). Because leaf toughness, which usually increases with LMA (Onoda et al. 2011), did not change in this study, trees in the drained peat swamp forest may have morphological adaptation to enhance resistance to drought stress by keeping a large volume of water in the leaves (Larcher 2003). In addition, drained forest trees had higher δ\text{13}C, indicating higher water use efficiency than intact forest trees (Inoue et al. 2015). The increase in WUE suggests that trees in drained forests maintain relatively high photosynthesis with less stomatal openness under drought conditions (Farquhar et al. 1989; Kenzo et al. 2015; Kitahashi et al. 2008). Therefore, trees in the drained peat swamp forest may have thicker leaves with higher water use efficiency to maintain higher water content corresponding to environmental stress than those growing in the intact forest.

We also found that a leaf trait related to leaf decomposability, i.e. condensed tannin content, increased significantly in the drained forest, although we need to note that other leaf traits controlling leaf decomposability, such as C/N ratio and lignin content, did not change. The improvement in environmental conditions caused by the drainage (as discussed above) may have increased tannin concentrations through the elevated photosynthetic ability of trees, because literature has reported that condensed tannins increased under better environmental conditions such as elevated CO\text{2} (Bakhvalov et al. 2009; Couture et al. 2012, 2017; Hättenschwiler and Schaffelner 2004; Traw et al. 1996) and better light and nutrient conditions (Donaldson et al. 2006; Hemming and Lindroth 1999, Osier and Lindroth 2001, 2004, 2006; Stevens et al. 2007; Yamasaki and Kikuzawa 2003). Recently, Lim et al. (2014) and Yule et al. (2016) reported the clear decreasing tendency of the total phenolic and total tannin contents in leaves of some tree species in degraded tropical peat swamp forests, which contrasts with the present results. Changes in phenolic compounds including tannin might differ according to the species and/or the microenvironmental conditions, such as groundwater level, light conditions, and herbivore pressure.

The changes in leaf traits affected by the drainage have a potential importance for nutrient dynamics in the peat swamp forests, because they may have suppressive impacts on leaf litter decomposition. It is well known that the drainage and a subsequent decrease in groundwater levels generally increase CO\text{2} release from soil through the enhancement of peat decomposition by oxidation (e.g. Furukawa et al. 2005; Melling et al. 2005; Warren et al. 2017). The increase in LMA and condensed tannin content, which was observed in our study site, may offset the drainage-induced acceleration of leaf decomposition to some extent. Plant tannins can bind soil proteins and exoenzymes and also inhibit fungal respiration and nitrification (Constabel et al. 2014). LMA tends to be associated positively with relatively higher concentrations of structural or chemical compounds that promote protection against the abiotic environment (Cornelissen 1996) and thus suppress decomposition. Kurokawa and Nakashizuka (2008) showed that LMA and condensed tannin content as well as the lignin to N ratio collectively
Drainage effects on leaf traits of peat swamp forest trees

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Appendix 1. Each species' means of all the investigated leaf traits in both intact and drained peat swamp forest trees. Bold values mean significant differences between intact and drained forest trees (t-test, P<0.05).

| Species                          | LMA (g m\(^{-2}\)) | N\(_{\text{max}}\) (mg g\(^{-1}\)) | N\(_{\text{min}}\) (g m\(^{-2}\)) | \(\delta^{13}\)C (%) | C/N ratio | Toughness (M Pa) |
|----------------------------------|---------------------|--------------------------------------|-------------------------------------|------------------------|-----------|------------------|
| Calophyllum hosei                | 255.94              | 294.88                               | 19.92                               | 49.57                  | 25.49     | 2.68             |
| Combretocarpus rotundatus        | 181.18              | 256.09                               | 18.46                               | 34.65                  | 25.86     | 3.61             |
| Cratoxylum glaucum               | 235.98              | 263.88                               | 12.25                               | 31.64                  | 25.49     | 2.89             |
| Garcinia sp.                     | 226.06              | 243.00                               | 13.17                               | 32.14                  | 25.86     | 2.98             |
| Horsfieldia crassifolia          | 240.59              | 281.33                               | 15.37                               | 33.60                  | 25.49     | 3.66             |
| Lithocarpus dasystachyus         | 300.77              | 309.15                               | 11.76                               | 32.37                  | 25.49     | 3.50             |
| Madhuca sp.                     | 352.16              | 416.95                               | 9.96                                | 32.96                  | 25.49     | 3.51             |
| Mezettia parviflora             | 173.93              | 273.92                               | 19.04                               | 33.44                  | 25.49     | 3.31             |
| Shorea sp.                      | 181.58              | 234.05                               | 15.53                               | 33.92                  | 25.49     | 2.82             |
| Stemonaurus scorpioides         | 236.38              | 265.63                               | 16.08                               | 33.56                  | 25.49     | 3.77             |
| Syzygium sp1.                   | 530.34              | 385.78                               | 9.24                                | 32.95                  | 25.49     | 3.05             |
| Syzygium sp2.                   | 271.63              | 355.60                               | 9.69                                | 34.47                  | 25.49     | 2.63             |
| Tetractomia tetrandra           | 189.90              | 281.70                               | 19.84                               | 33.93                  | 25.49     | 3.74             |
| Tetramerista glabra             | 213.47              | 212.95                               | 12.25                               | 33.16                  | 25.49     | 2.58             |

| Species                          | Total phenolics conc. (mg g\(^{-1}\)) | Condensed Tannin conc. (mg g\(^{-1}\)) | Lignin conc. (mg g\(^{-1}\)) | Total phenolics/N | Condensed tannin/N | Lignin/N |
|----------------------------------|----------------------------------------|-----------------------------------------|--------------------------------|-------------------|--------------------|----------|
| Calophyllum hosei                | 148.57                                 | 139.10                                  | 13.54                          | 22.26             | 161.64             | 33.16    |
| Combretocarpus rotundatus        | 79.90                                  | 72.71                                   | 12.89                          | 14.11             | 253.89             | 32.37    |
| Cratoxylum glaucum               | 103.32                                 | 94.10                                   | 15.69                          | 15.21             | 220.88             | 32.95    |
| Garcinia sp.                     | 80.79                                  | 64.29                                   | 9.99                           | 12.30             | 257.52             | 33.06    |
| Horsfieldia crassifolia          | 65.78                                  | 69.52                                   | 11.59                          | 11.37             | 273.06             | 33.44    |
| Lithocarpus dasystachyus         | 142.11                                 | 142.96                                  | 7.49                           | 11.50             | 258.97             | 33.56    |
| Madhuca sp.                     | 128.53                                 | 151.12                                  | 14.15                          | 13.09             | 159.72             | 33.16    |
| Mezettia parviflora             | 41.79                                  | 77.08                                   | 7.83                           | 14.28             | 201.13             | 33.06    |
| Shorea sp.                      | 82.04                                  | 82.48                                   | 8.79                           | 8.00              | 357.99             | 33.06    |
| Stemonaurus scorpioides         | 76.09                                  | 56.12                                   | 9.80                           | 9.59              | 281.89             | 33.06    |
| Syzygium sp1.                   | 110.28                                 | 119.24                                  | 8.04                           | 19.25             | 218.96             | 33.06    |
| Syzygium sp2.                   | 140.13                                 | 139.81                                  | 13.91                          | 17.82             | 44.21              | 33.06    |
| Tetractomia tetrandra           | 53.79                                  | 57.50                                   | 4.77                           | 17.39             | 279.59             | 33.06    |
| Tetramerista glabra             | 105.94                                 | 93.15                                   | 14.57                          | 20.85             | 167.42             | 33.06    |
Appendix 2. Pearson’s correlations $R$ between the leaf traits. * and ** indicate significant differences at $P<0.05$ and $P<0.01$, respectively ($t$-test).

|       | LMA | $N_{mass}$ | $N_{area}$ | $\delta ^{13}$C | Toughness | C/N | Phenolics | Tannin | Lignin | Phenolics/N | Tannin/N | Lignin/N |
|-------|-----|------------|------------|------------------|-----------|-----|-----------|--------|--------|-------------|----------|---------|
| LMA   |     |            |            |                  |           |     |           |        |        |             |          |         |
| $N_{mass}$ | $-0.67^{**}$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| $N_{area}$ | 0.32 | 0.46* | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| $\delta ^{13}$C | 0.24 | 0.13 | 0.53** | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| Toughness | 0.76** | $-0.76^{**}$ | $-0.12$ | $-0.24$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| C/N | 0.72** | $-0.98^{**}$ | $-0.41^{*}$ | $-0.17$ | 0.83** | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| Phenolics | 0.64** | $-0.87^{**}$ | $-0.35$ | $-0.18$ | 0.76** | 0.88** | $-$ | $-$ | $-$ | $-$ | $-$ | $-$ |
| Tannin | 0.34 | 0.45* | $-0.11$ | 0.30 | 0.34 | 0.42* | 0.36 | $-$ | $-$ | $-$ | $-$ | $-$ |
| Lignin | $-0.41^{*}$ | 0.61** | 0.32 | 0.19 | $-0.65^{**}$ | $-0.59^{**}$ | $-0.59^{**}$ | $-0.52^{**}$ | $-$ | $-$ | $-$ | $-$ |
| Phenolics/N | 0.69** | $-0.92^{**}$ | $-0.37$ | $-0.22$ | 0.85** | 0.95** | 0.97** | 0.39* | $-0.65^{**}$ | $-$ | $-$ | $-$ |
| Tannin/N | 0.56** | $-0.74^{**}$ | $-0.26$ | 0.11 | 0.65** | 0.74** | 0.66** | 0.90** | $-0.68^{**}$ | 0.72** | $-$ | $-$ |
| Lignin/N | 0.12 | $-0.08$ | $-0.04$ | 0.15 | $-0.15$ | 0.11 | $-0.06$ | $-0.22$ | 0.69** | $-0.06$ | $-0.17$ | $-$ |