Photosynthetic characteristics of trees in seasonally tropical dry forests in Thailand

Atsushi Ishida[1], Phanumard Ladpala [2] and Dokrak Marod [3]

[1] Center for Ecological Research, Kyoto University, Shiga 520-2113, Japan
[2] National Park, Wildlife and Plant Conservation Department, Bangkok 10900, Thailand
[3] Faculty of Forestry, Kasetsart University, Bangkok 10900, Thailand
[1] Corresponding Author E-mail: atto@ecology.kyoto-u.ac.jp

Abstract

Leaf gas exchange and ecophysiological characteristics in sun leaves in uppermost canopies of adult trees were examined in mixed deciduous forest (MDF), dry dipterocarp forest (DDF), and dry evergreen forest (DEF) in Thailand. Leaf area-based and mass-based maximum assimilation rates (A_{max}) were lower in deciduous-tree forests (DDF and MDF) than in evergreen-tree forests (DEF). Between the deciduous forests, the maximum stomatal conductance (G_{max}) in MDF were higher, and leaf mass per area (LMA) and carbon:nitrogen (C:N) ratio in MDF were lower than those in MDF. Across all species, area-based A_{max} was positively correlated to G_{max}, mass-based and N-based A_{max}, and area- and mass-based N. Mass-based A_{max} was positively correlated to G_{max}, area-based and N-based A_{max}, mass-based N, and was negatively correlated to LMA and intrinsic water use efficiency (iWUE= A_{max}/G_{max}). A_{max} at a give N was higher in MDF and DDF than in DEF, because of a low photosynthetic N use efficiency (PNUE: N-based A_{max}) in evergreens. Area-based and mass-based A_{max} were estimated from leaf traits with multiple regression analysis. Area-based A_{max} was estimated by area- and mass-based N and G_{max} (r^2=0.488), whereas mass-based A_{max} was well estimated by mass-based N, SLA (=1/LMA), and G_{max} (r^2=0.775). The high contribution of G_{max} to adequate estimation of A_{max} suggests that A_{max} and canopy gas flux are easily reduced by a decrease in precipitation and soil degradation in future.

Key Word: Carbon assimilation, Climate change, Leaf mass per area, Leaf nitrogen, Stomatal conductance, Precipitation shift

Introduction

There is a distinct dry season lasting for 4-5 months in Thailand. Although the annual precipitation and its seasonal pattern are similar, various forest types, called mixed deciduous forest (MDF), dry dipterocarp forest or drought deciduous forests (DDF), and dry evergreen forest (DEF), are found. MDF and DDF are mainly consisted of drought-deciduous trees, whereas DEF are mainly consisted of evergreen trees. DDF has thin and poor-nutrients soil and many dipterocarp trees are predominant. In contrast, MDF has rich-nutrients soil and dipterocarp trees are rare. Therefore, forest types are due to soil properties, and the forest function is dependent on species structure (Rundel and Boonpragob 1995; Ishida et al. 2006).

Canopy leaves with low mass-based photosynthetic rates and leaf nitrogen (N) concentrations and high leaf mass per area (LMA) generally have a long leaf lifespan (Reich et al. 1999; Wright et al. 2004; Ishida 2008), contributing to a slow N cycling

within forests. Leaf ecophysiological characteristics are thus major determinants of forest functions, such as carbon flux of forest canopies and nutrients cyclings within forests. Recently, meta-analysis, using a huge number of data in various areas, has become a critically important tool for understanding the linkage between forest function and environment or for estimating of changing forest structure and function under global warming in the earth.

However, to date, there are few available datasets for meta-analysis in Thailand, partially because of the long lifespans of woody plants and the difficulty of working high above the ground. For obtaining the maximum carbon assimilation (A_{max}) of trees, we have to access or collect sun leaves from the upper-most canopy of adult trees. Therefore, to make a dataset of a huge number of woody plants is often a difficult task. In the present study, we have tried to do the difficult task at various forest types in lowland (<1000 m ASL) with a distinct dry season in Thailand. In the present study, using the database, we analyze photosynthetic characteristics among forest types and discuss the effects of climate change to carbon assimilation process at the canopy leaf level.

Study sites and Methods

Three forest types were selected at two study sites: i) the Mae-Klong Watershed Research Station (14˚ 34'N, 98˚ 50'E, 160 m ASL), approximately 250 km northwest of Bangkok and ii) the Sakaerat Environmental Research Station (14˚ 29'N, 101˚ 55'E, 563 m ASL), approximately 180 km northeast of Bangkok. At Mae-Klong, there is mixed deciduous forests (MDF). At Sakaerat, there are dry dipterocarp forests (DDF) and dry evergreen forests (DEF). The top canopy heights of MDF, DEF, and DEF are approximately 30 m, 10m, and 33 m high, respectively. Because the tree density of DEF was low, sparse canopies develop. In contrast, the tree densities of MDF and DEF were relatively high, and dense canopies develop. The mean air temperature was 24-25 °C and the annual rainfall was 1200-1400 mm in 2007 at both sites. There is a distinct dry season normally from November to February at both sites (Ishida et al. 2010).

We recognized 157 tree species at MDF, 49 tree species at DDF, and 46 tree species at DEF, included woody vine and bamboo species. MDF was thus consisted of many tree species. Among these trees, A_{max}, the maximum water vapor stomatal conductance (G_{max}), LMA, and leaf N in sun leaves of adult trees were measured in 65 species (41% out of the recognized species) at MDF, 45 species (92% out of the recognized species) in DDF, and 31 species (67% out of the recognized species) in DEF during the rainy season (September to October). We collected data from one to three individual trees per a species. We carefully collected shoots from the uppermost canopies when stomata still open, using a long pole with a cutter, and immediately recut shoot in water. A fully-expanded healthy leaf was selected from the shoots, and we immediately measured A_{max} and G_{max} with an open, measurement system (LI-6400, LI-COR, Lincoln, NE, USA) at the fields. The effects of shoot cutting on leaf gas exchange rates were seldom found. The measurements were conducted under the conditions of 400 μmol mol^{-1} CO_2 in the inlet gas stream and 1500 μmol m^{-2} s^{-1} photosynthetic photon flux (PPF) with red-blue LEDs. While measurements, leaf temperature was not regulated with LI-6400. The range was 27-35 ˚C (occasionally slightly higher than air temperature at understories). After the measurements, we collected the leaves and cut disks with a borer to determine LMA and nitrogen (N) and phosphorous (P) contents within leaves. The leaf disks were oven dried (70 ˚C; 72

hr) and weighed, and total N contents were measured with an N-C analyzer (Sumigraph NC-900, Sumitomo-Kagaku, Osaka). Statistical analyses were conducted with R (ver. 3.02).

Results and Discussion

Leaf gas exchange and ecophysiological characteristics

No significant differences in area-based N and intrinsic water use efficiency (iWUE=A_{max} /G_{max}) among the study sites. In the deciduous-tree forests, the average values of area-based A_{max} were 13.2 μmol m^{-2} s^{-1} in MDF and 14.2 μmol m^{-2} s^{-1} in DDF. The average values of mass-based A_{max} were 174 nmol g^{-1} s^{-1} in MDF and 157 nmol g^{-1} s^{-1} in DDF. MDF showed the highest G_{max} and the lowest LMA among the forest types. There are no significant differences in both area- and mass-based A_{max} and photosynthetic N use efficiency (PNUE: N-based A_{max}) between the deciduous forests (MDF and DDF). In the examined trees, the number of tree species found at both sites of MDF and DDF was nine. Nevertheless, no clear trends were found between MDF and DDF among the tree species.

In evergreen forests (DDF), the average values of area- and mass-based A_{max} were 10.8 μmol m^{-2} s^{-1} and 103 nmol g^{-1} s^{-1}, respectively. DDF showed the lowest area- and mass-based A_{max} and PNUE among the forest types, indicating a low N allocation to photosystems within leaves in evergreens with a long leaf lifespan (Evans 1989, Ishida 2008).

Relationships between photosynthesis and leaf traits

Across all species, area-based N was positively correlated to area-based A_{max}, LMA and iWUE. Mass-based N was positively correlated to area- and mass-based A_{max}, G_{max}, and mass-based N, and was negatively correlated to LMA. Positive correlations between photosynthetic capacity and leaf nitrogen contents have been well known (Evans 1989). In the present study, area-based A_{max} was positively correlated to G_{max}, mass-based and N-based A_{max}, and area- and mass-based N. Mass-based A_{max} was positively correlated to G_{max}, area-based and N-based A_{max}, mass-based N, and was negatively correlated to LMA and iWUE. PNUE is an indicator of N allocation to photosystems within leaves (Evans 1989). PNUE was positively correlated to area- and mass-based A_{max}, G_{max}, and was negatively correlated to LMA, iWUE, area-based N. Nevertheless, PNUE was not correlate to mass-based N.

In the principal component analysis (PCA), Axes 1, 2, and 3 explained 45.7%, 22.2%, and 17.2% of total variations, respectively. The first three axes accounted for 85% of total variations. Axis 1 was related to leaf C and N economy, i.e., an axis from high LMA to high mass- and area-based A_{max} (Figure 1a). Axis 2 was related to area-based N. Axes 1 and 2 separated the functional groups of MDF, DDF, and DEF, but a high overlap was also found (Figure 1b). PCA shows that the deciduous trees of MDF are characterized by a high G_{max} and a low LMA, whereas the evergreens of DEF are characterized by a low photosynthetic capacity. The deciduous trees of DDF show a medium position between MDF and DEF trees.

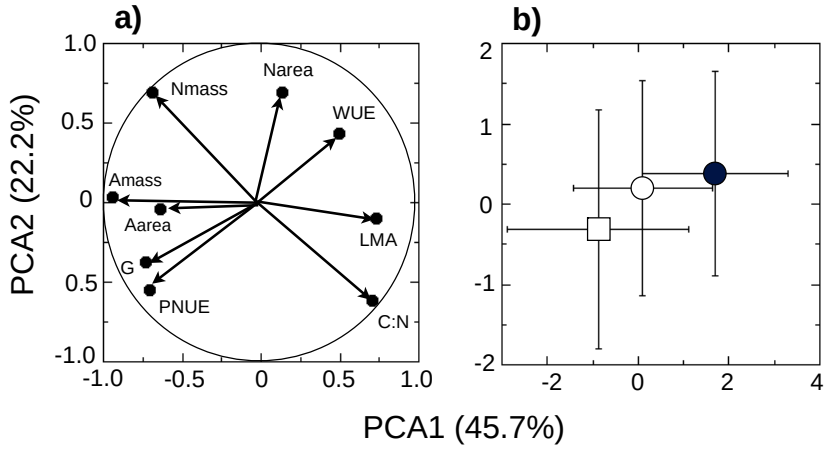

Figure 1 Principal component analysis (a) 9 leaf traits (Narea: area-based N, Nmass: mass-based N, Amass: mass-based A_{max}, Aarea: area-based A_{max}, G: G_{max}) and (b) positions (mean ± 1 SD) of woody plant species in MDF (open square), DDF (open circle), and DEF (closed circle).

Estimation of photosynthesis capacity

Convenient estimation of area-based and mass-based A_{max} is useful for evaluating carbon flux processes. We estimated A_{max} from several leaf traits with multiple regression equations. In area-based A_{max}, we obtained the equations (1, 2), as follows;

$$A_{area} = 2.274\ N_{mass} + 0.01963\ N_{area} + 6.922 \quad (r^2=0.140) \quad (1),$$

$$A_{area} = 16.00\ G_{max} + 0.8044\ N_{mass} + 0.02948\ N_{area} + 2.729 \quad (r^2=0.488) \quad (2),$$

where A_{area}, N_{mass}, N_{area}, and G_{max} are area-based A_{max} (μmol m^{-2} s^{-1}), mass-based N (mmol N g^{-1}), area-based N (mmol N m^{-2}), and the maximum stomatal conductance (mol m^{-2} s^{-1}), respectively. In mass-based A_{max}, we obtained the equations (3, 4), as follows;

$$A_{mass} = 9.269\ SLA + 62.17\ N_{mass} - 48.36 \quad (r^2=0.630) \quad (3),$$

$$A_{mass} = 8.112\ SLA + 193.1\ G_{max} + 53.93\ N_{mass} - 83.77 \quad (r^2=0.775) \quad (4),$$

where A_{mass} and SLA are mass-based A_{max} (nmol g^{-1} s^{-1}) and specific leaf area (=1/LMA; m^2 kg^{-1}), respectively.

In both equations, G_{max} contributed to a largely increase in coefficient of determination, especially in area-based A_{max} (equation 2), meaning that G_{max} is a major determinant of A_{max}. The fact predicts that a decrease in precipitation and soil degradation largely reduce G_{max} and A_{max}, as a consequently, canopy gas flux of forests. IPCC (2012) predicts precipitation shift as a result of global warming in future. Forest degradation still increased and yearly variations of precipitation becomes obvious in the world as well as Thailand. To exactly examine the effects of climate change on carbon flux and forest functions, parameters of precipitation shift and its G_{max} and A_{max} response will be needed for obtaining adequate estimation.

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