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Original Articles

Non-destructively predicting leaf area, leaf mass and specific leaf area based on a linear mixed-effect model for broadleaf species

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ABSTRACT

Based on a linear mixed-effect model, we propose here a non-destructive, rapid and reliable way for estimating leaf area, leaf mass and specific leaf area (SLA) at leaf scale for broadleaf species. For the construction of the model, the product of leaf length by width (LW) was the optimum variable to predict the leaf area of five deciduous broadleaf species in northeast China. In contrast, for species with leaf thickness (T) lower than 0.10 mm, the surface metric of a leaf (e.g., LW or width) was more suitable for predicting leaf mass; and for species with leaf thickness larger than 0.10 mm, the volume metric of a leaf (e.g., the product of length, width and thickness together, LWT) was a better predictor. The linear mixed-effect model was reasonable and accurate in predicting the leaf area and leaf mass of leaves in different seasons and positions within the canopy. The mean MAE% (mean absolute error percent) values were 6.9% (with a scope of 4.1–13.0%) for leaf area and 13.8% (9.9–20.7%) for leaf mass for the five broadleaf species. Furthermore, these models can also be used to effectively estimate SLA at leaf scale, with a mean MAE% value of 11.9% (8.2–14.1%) for the five broadleaf species. We also propose that for the SLA estimation of the five broadleaf species examined, the optimum number of sample leaves necessary for good accuracy and reasonable error was 40–60. The use of the provided method would enable researchers or managers to rapidly and effectively detect the seasonal dynamic of leaf traits (e.g., leaf area, leaf mass or SLA) of the same sample leaves in the future.

1. Introduction

Green leaves are the most important organs for the functioning of terrestrial ecosystems (Baker et al., 2015). Leaf traits are known to be strongly linked to the climate and other abiotic conditions, rendering them suitable traits for examining plant community responses to the environment (Lavorel and Garnier, 2002; Peppe et al., 2011). Leaf area strongly influences light interception, plant growth and productivity, making it a key variable in most models for simulating carbon and water cycles. Knowing the successive changes in leaf area is especially essential to predict the attributes of fruit or crop yields and quality levels (Ewert, 2004; Alton, 2016; Nelson et al., 2016). In addition, several rates of plant physiological processes (e.g., re-translocation of resources such as nutrients) are often expressed per each unit of leaf mass to characterize the physiological activity of the unit mass (Wright et al., 2004; Negi, 2006). Therefore, accurate estimations of not only leaf area but also of leaf mass, are essential to deeply understand and model ecosystem function.

Recently, non-destructive, rapid and reliable methods for estimating leaf area and leaf mass and the subsequent growth of broadleaf species have gained increasing attention (Tondjo et al., 2015; Weraduwage et al., 2015). Traditionally, broadleaf leaf area can be obtained through direct or indirect methods. Direct methods involve the use of blueprinting, conventional planimeters, scanner, or fixed camera and image analysis software programs (Granier and Tardieu, 2002). However, these direct methods involve destructive plant sampling. It is therefore impossible to conduct successive measurements of the same leaf, further damages to plant canopies, and potentially compromises other measurements or experiments (Cristofori et al., 2007). In addition, for an entire plant or part of a plant, leaf area measurements involving these direct methods are time consuming and labor intensive. A non-destructive alternative direct method that can be used to measure leaf area involves using portable scanning planimeters (Daughtry, 1990). However, these new tools are too expensive and complex for the purpose of conducting basic studies. In contrast, we can non-destructively estimate broadleaf leaf area by developing mathematical relationships (i.e., regression models) between leaf area and one or more

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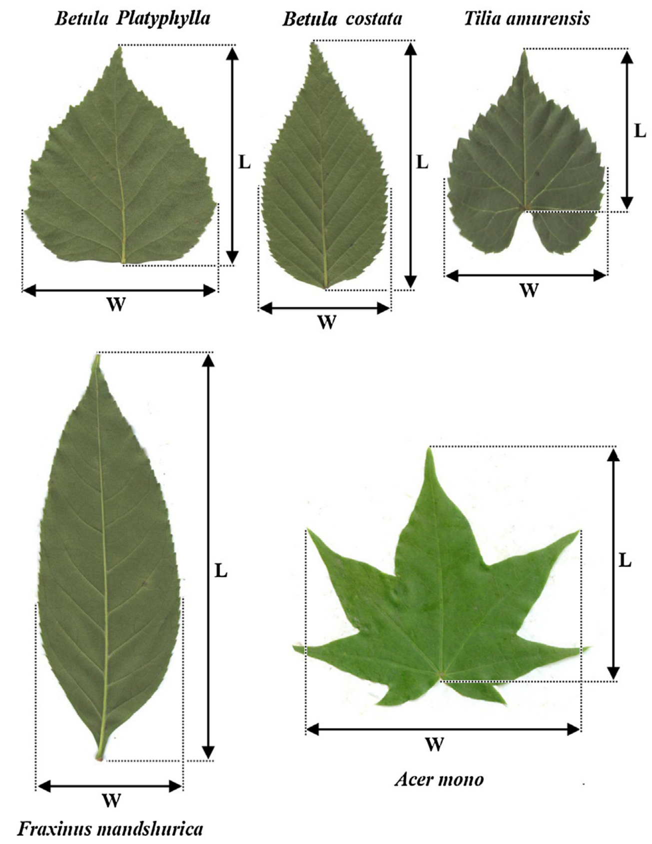

Fig. 1. Diagram of leaves showing the positions of length and width measurements for the five broadleaf species.

leaf structural parameters (e.g., length or width) (Pompelli et al., 2012; Liu et al., 2015b; Keramatlou et al., 2015), which are often considered indirect methods. In several previous studies, indirect methods, which have typically been found to be highly accurate, have been used to estimate leaf area from regression models involving leaf structural parameters, such as length (L), L^2, width (W), W^2, or some combination of these variables (e.g., the product of length and width, LW) (Cristofori et al., 2007; Meng et al., 2015). However, in most of the above listed studies, the leaf samples, used to develop these regression models between leaf area and leaf structural parameters, have often only been obtained during a certain period or from a specific canopy position.

In contrast, broadleaf leaf mass has typically been measured by sampling plants and then drying them in an oven, which is destructive and time consuming (Dwyer et al., 2014; Freschet et al., 2015). Recently, Tondjo et al. (2015) found, for teak (*Tectona grandis* Linn. f.), using an oblate leaf, that not only leaf area but also leaf mass could be measured using regression models between leaf area, leaf mass and leaf structural parameters (i.e., LW). This created a new non-destructive way to estimate broadleaf leaf mass. However, whether this method can be applied to other broadleaves with different leaf shapes has rarely been explored.

Furthermore, specific leaf area (SLA), an essential measure among these leaf traits, is relevant to understanding general plant strategy in terms of community organization (Bedecarrats and Isselin-Nondedeu, 2012), and it is often used in canopy gas-exchange models to predict the spatial and temporal variability of photosynthetic parameters (Wilson et al., 2000; Davi et al., 2007; Freschet et al., 2015). For many species, SLA varies not only with seasonal changes but also presents significant spatial variability within canopies, as has been broadly reported in several previous studies (Weiskittel et al., 2008; Nouvellon et al., 2010). To our knowledge, over large scales, SLA has often been measured via the destructive sampling of canopy plants (Osone et al., 2008). This stresses the urgent need for a non-destructive and rapid method of measuring SLA and its seasonal dynamics.

The purpose of our work was to determine regression models to non-destructively and rapidly estimating leaf area, leaf mass and SLA for different broadleaf species. To achieve this aim, five deciduous broadleaf species were selected in northeast China. We first analyzed the seasonal and canopy vertical variability of the leaves of the five species; secondly, we selected the optimal variables for predicting leaf area and leaf mass; thirdly, we developed a linear mixed-effect model linking leaf structural parameters to leaf area and leaf mass, and studied the quality of the prediction. Finally, we explored the effectiveness of the predictive models for leaf area and leaf mass in predicting SLA itself.

2. Materials and methods

2.1. Site description and experimental design

The study site is located within the Liangshui National Nature Reserve of northeastern China (47.18 N, 128.89° E). The reserve covers a 12,133 ha area, with approximately 1.88 million m^3 of growing stock and an average canopy coverage of 98%. The altitude ranges from 280 to 707 m above sea level, with an average slope of 10–15°. The mean annual air temperature is −0.3 °C, and the mean air temperature for the summer season (from June to August) is 17.5 °C. The mean annual precipitation is 676 mm, with 10–20% derived from snowfall. The area is covered by snowpack from December through April (Liu et al., 2015a).

Five deciduous broadleaf species were selected for this research: *Betula platyphylla* Sukaczev, *Betula costata* Trautv., *Tilia amurensis* Rupr., *Fraxinus mandshurica* Rupr. and *Acer mono* Maxim. This group of species includes various leaf shapes that generally represent most of the leaf shapes of broadleaf species found in this study site. For each species, three mature trees were randomly selected as samples. The diameter at breast height (DBH) of the sample trees ranged from 15.7 to 19.5 cm for the *B. platyphylla* trees, from 32.9 to 38.7 cm for the *B. costata* trees, from 27.2 to 37.0 cm for the *T. amurensis* trees, from 27.5 to 38.4 cm for the *F. mandshurica* trees and from 22.5 to 42.0 cm for the *A. mono* trees.

The leaves collected from each tree were selected from different canopy positions and in different seasons. For the canopy vertical scale, the tree canopy of each tree sampled was divided into three height levels: Top, Middle and Low. For each level, the selection of the 20 sample leaves was based on caution, ease of access and the goal of measuring leaves at a variety of positions. In this way, around 60 leaves were selected for each tree sampled. At the seasonal scale, the same sampling plan as that used for the canopy vertical scale was implemented in early June, July and September. This represented major phenological phases based on the timing of leaf-out and leaf-fall dates for all broadleaf species, i.e., the leaf growing period, stable leaf area period and leaf senescence period (Liu et al., 2015b).

For each leaf sampled, the petiole was first removed, and we then obtained the following observations: (1) length, L; (2) width, W; and (3) thickness, T. The observation details are provided in Table 1. The length was measured from the apex of the blade to the base of the petiole, and width was measured at the widest point perpendicular to the longitudinal axis of the leaf (Fig. 1). The measurements were made using a ruler (with a precision of 0.1 cm). For each sample leaf, the thickness was measured three times using a Vernier caliper (with precision of 0.01 mm), and the average value was taken as the thickness of leaf. Then, the leaf area was obtained through scanning using a BenQ-5560 image scanner