



Research paper

Variation in leaf chlorophyll concentration from tropical to cold-temperate forests: Association with gross primary productivity



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ABSTRACT

Leaf chlorophyll is essential to harvest light energy to drive photosynthesis. Yet, most of studies of leaf chlorophyll concentration (Chl) have typically been limited to few species or sites, and there has been little understanding of its variation among species of contrasting environments, or across forests differing in gross primary productivity (GPP). We measured mass-based foliar Chl concentrations (Chl *a*, Chl *b*, and total Chl) for 937 species of nine Chinese forests ranging from tropical to cold-temperate regions. Total Chl varied by over ten-fold from 1.45 to 19.2 mg g⁻¹ (mean: 5.54 mg g⁻¹), and differed among plant functional groups. At the community level, total Chl decreased with increasing latitude. The ratio of Chl *a/b* decreased from trees to shrubs to herbs, consistent with adaptation to contrasting irradiance, i.e., overstory vs. understory. Total Chl was positively related to leaf N and P concentrations, as would be expected to optimize photosynthesis and carbon fixation. Across forests, GPP was positively correlated with community-averaged Chl ($r = 0.57$; $P < 0.01$), a new case of a linkage between leaf traits and ecosystem function at regional to continental scale. Our findings revealed variation in Chl from tropical to cold-temperate forests, and the linkage of leaf Chl with ecosystem function, enhancing our ability to parameterize vegetation models.

1. Introduction

Chlorophyll is an essential pigment for photosynthesis, utilizing the energy of photons for redox reactions (Mackinney, 1941; Baker, 2008). Thus, leaf chlorophyll concentration (Chl) may directly influence the photosynthetic capacity of plants to some extent (Croft et al., 2017). In past decades, many studies have focused on chlorophyll synthesis, fluorescence (Genty et al., 1989; Kooten and Snel, 1990; Maxwell and Johnson, 2000; Baker, 2008), and decomposition (Larkin et al., 2003; Pružinská et al., 2003; Zhang et al., 2006; Schelbert et al., 2009). However, most studies of Chl have been limited to specific species in a given region (Fleischer, 1935; Bojovic and Stojanovic, 2005; Luo et al., 2011; Schlemmer et al., 2013; Burzyński, 2014). Analyses across diverse species and communities may contribute to addressing a current major challenge for ecologists: how to use traits measured at organ or plant level to predict key ecosystem properties along environmental

gradients and under changing climate (Andersen et al., 2012; Garnier and Navas, 2012; Reichstein et al., 2014; Violle et al., 2014). Unfortunately, although Chl has been widely considered as an important trait there have not been data available for species across natural communities.

Leaf Chl mainly includes chlorophyll *a* (Chl *a*) and chlorophyll *b* (Chl *b*). Both pigments have a strong light absorption capacity, but differ in their absorption peaks, with Chl *a* higher in the red band and Chl *b* higher in the blue violet band (Lichtenthaler and Buschmann, 2001). Therefore, variation in the Chl *a/b* ratio may represent an adaptive strategy of leaves to different light availability across different environments. Because the spectral composition of solar light does not differ across latitudes, the Chl *a/b* of dominant trees would be expected to unchangeable with latitude. However, the vertical canopy structure of plant community results in strong variation in the light environment, with greater availability of diffuse light and less blue light in the

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understory (Ostrom, 2005). Thus, understory plants might enhance Chl *b* concentration as part of their adaptation to their light environment, resulting in a lower Chl *a/b*. Further, given that the Chl *b* is more associated with photosystem II (PSII), the Chl *a/b* ratio may also reflect the ratio of investment in photosystem I (PSI) relative to photosystem II (PSII), leading to a lower ratio in shade, because shade leaves would allocate more strongly to PSII to widen the range of utilizable light wavelengths (Boardman, 1977; Kitajima and Hogan, 2003). Additionally, canopy structure may produce the shading effect on these understory plants, resulting in the less lower Chl *a/b* in the understory. These expectations have never been tested to date across natural forests at a large scale.

The relationship of Chl to foliar nutrient concentrations also requires examination across communities. Leaf nitrogen (N) and phosphorus (P) are essential elements for plant growth. N is important for the synthesis of chlorophyll and enzymes, and inorganic P is a major metabolite in photosynthetic reactions and other energetic reactions. Studies have demonstrated that Chl and leaf N concentration are strongly correlated across and within species (Sack et al., 2003), and based on conservation of stoichiometry for metabolic reactions, one might expect Chl to correlate with leaf P concentrations too. However, such scaling relationships might be weak, given that leaf Chl is located in the chloroplast-based thylakoid-based light reactions, and mostly in the light harvesting apparatus, rather than reaction centers (Horton et al., 2003), whereas N and P are mostly allocated to stroma-based carbon reactions.

Our study was intended to contribute to the global effort to linking plant traits with ecosystem functioning, a major priority that will improve our ability to explain and predict ecosystem assembly and responses to changing environments (Garnier and Navas, 2012; Reichstein et al., 2014). A major challenge is relating properties measured at the individual or organ level to the community scale (Houborg et al., 2013; Croft et al., 2015). Given that Chl is fundamentally important to photosynthesis, we hypothesized that Chl averaged for the forest community (Chl_{Commun}) would be positively correlated with GPP. Previous studies have suggested a link between Chl and GPP (Houborg et al., 2013; Croft et al., 2015), but no studies to our knowledge have tested this relationship, or the departure from this relationship that would be expected if communities vary in their Chlorophyll production efficiency (CPE = GPP/Chl_{Commun}), i.e., the relative productivity per unit of chlorophyll.

We measured Chl for 937 common plant species within 9 Chinese forests from tropical to cold-temperate regions. Our main objectives were 1) to analyze the variation in Chl across species, plant functional groups (PFGs), and communities; 2) to determine the variation in Chl *a/b*; 3) to test the hypothesis that Chl is positively correlated with N and P across species and forests to optimize photosynthesis; and 4) to establish the relationship between Chl and GPP across forest communities at a regional scale.

2. Materials and methods

2.1. Site description

The study was conducted along the North-South Transect of Eastern China (NSTEC), representing the 15th standard transect of the International Geosphere Biosphere Programme (IGBP). The transect ranged from 18.7° N to 51.8° N in latitude and from 108.9° E to 123.0° E in longitude. We selected 9 typical forests along the NSTEC, within experimental plots set up in the National Nature Reserve to minimize human disturbance. The plots ranged from −4.40 to 20.9 °C in mean annual temperature (MAT) and from 482 to 2449 mm in mean annual precipitation (MAP), which mainly occurred in the summer (Song et al., 2016). Detailed geographical information of the region is presented in Fig. 1 and Table S1 (Song et al., 2016).

2.2. Field sampling

Field sampling was conducted from July to August 2013, the period of highest growth rate for all of the selected forests. First, we set up four representative plots (30 m × 40 m) in each forest type, to survey trees, and smaller plots within to survey shrubs (5 m × 5 m) and herbs (1 m × 1 m). We recorded the height and diameter at breast height of each individual for all trees and shrubs and collected the above-ground parts of herbs.

We chose mature, healthy trees and collected fully expanded, sun-exposed leaves from four individuals of each plant species, and each of four individuals represented a replicate. Leaf samples were collected from branches in the upper part of trees by climbing or using pole pruners and placed in a plastic self-sealing bag (Tian et al., 2016; Zhao et al., 2016).

2.3. Measurement of chlorophyll concentrations

We weighed 0.1 g of fresh leaves to extract chlorophyll using 95% ethanol, with four replicates for each plant species. The Chl (Chl *a* and Chl *b*) of the filtered solution was measured using the classical spectrophotometric method with a spectrophotometer (Pharma Spec, UV-1700, Shimadzu, Japan) (Mackinney, 1941).

According to the Lambert-Beer law the relationship between concentration and optical density is:

$$D_{665} = 83.31 C_a + 18.60 C_b \quad (1)$$

$$D_{649} = 4.54 C_a + 44.24 C_b \quad (2)$$

$$G = C_a + C_b \quad (3)$$

where D_{665} and D_{649} are the optical densities of the chlorophyll solution at wavelengths 665 nm and 649 nm; C_a , C_b , and G are the concentrations of Chl *a*, Chl *b*, and total Chl, respectively (g L^{-1}); 83.31 and 18.60 are the specific absorption of Chl *a* and Chl *b* at a wavelength of 665 nm; and 4.54 and 44.24 are the specific absorption of Chl *a* and Chl *b* at a wavelength of 649 nm.

Based on the concentration of Chl *a*, Chl *b*, and total Chl, Chl was calculated (mg g^{-1} , leaf fresh mass, FM) as:

$$\text{Chl } a \text{ concentration}(\text{mg g}^{-1}) = C_a \times 50 / (1000 \times 0.1) \quad (4)$$

$$\text{Chl } b \text{ concentration}(\text{mg g}^{-1}) = C_b \times 50 / (1000 \times 0.1) \quad (5)$$

$$\text{Chl concentration}(\text{mg g}^{-1}) = G \times 50 / (1000 \times 0.1) \quad (6)$$

2.4. Measuring leaf nitrogen and phosphorus concentrations

After collection, the leaf samples were cleaned in the laboratory to remove soil and surface particles and oven-dried at 65 °C. The samples were then ground and an elemental analyzer (Vario MAX CN Elemental Analyzer, Elementar, Hanau, Germany) was used to measure the nitrogen (N) concentration. Phosphorus (P) was measured by the ammonium molybdate method using a continuous-flow analyzer (AutoAnalyzer3 Continuous-Flow Analyzer; Bran Luebbe, Hamburg, Germany) after $\text{H}_2\text{SO}_4\text{--HClO}_4$ digestion of plant samples (Zhao et al., 2014; Zhao et al., 2016).

2.5. Calculation of forest leaf biomass

Leaf biomass for each tree species was calculated using allometric equations, using the diameter at breast height (DBH) and height. Leaf biomass for each shrub species was also calculated using allometric equations, using ground-diameter and height. All equations were obtained from the Chinese Ecosystem Research Network (CERN) database (<http://159.226.111.42/pingtai/cernc/index.jsp>) or the published literature (Wang et al., 2015). The leaf biomass of grass species was

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