Leaf non-structural carbohydrates regulated by plant functional groups and climate: Evidences from a tropical to cold-temperate forest transect

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ABSTRACT

Non-structural carbohydrates (NSCs), e.g., glucose and starch, play important roles in metabolic processes of plants and represent important functional traits in plant's adaptation to external environment. To explore the variations in leaf NSCs among species and communities at a large scale and their influencing factors, we investigated the contents of leaf NSCs among 890 plant species in nine typical forests along the north–south transect of eastern China. The results showed that the contents of leaf soluble sugars, starch, and NSCs (sugars + starch) were highly variable among different plant species on the site scale, and their mean values for the 890 plant species were 45.7 mg g^{-1}, 47.5 mg g^{-1}, and 93.2 mg g^{-1}, respectively. All three metrics varied markedly across plant functional groups in the order of trees < shrubs < herbs. Weak latitudinal patterns of leaf soluble sugars, starch, and NSCs were observed from tropical to cold-temperate forests at the levels of species and plant functional groups. The contents of leaf soluble sugars, starch, and NSCs decreased with increasing temperature and precipitation which supports the growth limitation hypothesis at a large scale. In trees, leaf soluble sugars, starch, and NSCs increased with increasing photosynthetic active radiation (PAR); and were positively correlated with specific leaf area (SLA). The spatial patterns of leaf NSCs in forests along the north–south transect of eastern China and their relationships with temperature, precipitation, PAR, and SLA illustrate an important adaptation of plant communities to environmental changes at the continental scale.

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1. Introduction

Carbohydrates are the primary photosynthate and the key energy source of plant metabolism, and therefore play vital roles in plant's life processes (Volenec et al., 1996; Ogren et al., 1997; Ögren, 2000; Bouma, 2005). Carbohydrates in plants are generally classified as structural carbohydrates or non-structural carbohydrates (NSCs) (Li et al., 2002, 2008). The structural carbohydrates, such as lignin and cellulose, are primarily used for the construction of plant structural support tissues or long-term reserves (Li et al., 2002; Pan et al., 2002; Yin et al., 2009). NSCs, mainly as glucose and starch, are used in metabolic processes of photosynthesis, respiration, and production (Koch, 1996; van den Ende et al., 1999). The content of NSCs and their composition (ratio of glucose:starch) reflect the balance between carbon sources and sinks in plants (Mooney, 1972; Chapin et al., 1990; Hoch et al., 2003; Würth et al.,

2005) and indicate the adaptive strategies of plants to changing environments (Trom et al., 1989; Koch, 1996; Loewe et al., 2000). Gough et al. (2009) have demonstrated that, in temperate deciduous forests, 55% of the annual net carbon assimilation in plant canopy is firstly allocated to labile carbon production (main NSCs) rather than to structural carbon production, where labile carbon produced during late summer supported the structural growth and respiration in dormant season. The content of NSCs and their allocation ratios in leaves, roots, and stems are considered as an eco-physiological attribute to evaluate the carbon budgets and adaptive strategies of plant species (Chapin et al., 1990; Li et al., 2001; Myers and Kitajima, 2007; Poorter and Kitajima, 2007).

Many factors may influence leaf NSCs content (Volaire and Gandoin, 1996; Gaudet et al., 1999; Nanamori et al., 2004). To date, studies on factors influencing leaf NSCs have focused on nutrient elements (Nanamori et al., 2004), temperature (Gaudet et al., 1999; Gough et al., 2010), precipitation (Schellenbaum et al., 1999), and phenology (Gough et al., 2010). Less information is available regarding factors such as light intensity, leaf traits, leaf life forms (e.g., needle-leaf and broad-leaf), and plant functional groups

(PFGs, trees, shrubs, and herbs). Furthermore, most of the studies related to leaf NSCs have mainly conducted on basis of controlled experiments regarding the responses of leaf NSCs to changing environment, or focused on the variations of leaf NSCs at the individual level, or along altitudinal gradients (Mooney and Billings, 1965; Hoch et al., 2002). To date, it remains unknown the level of variation of leaf NSCs among a large number of plant species at a large scale.

Currently, two bio-physiological hypotheses have been developed from these treeline studies to explain the variation in leaf NSCs with temperature: carbon limitation hypothesis (Schulze et al., 1967; Stevens and Fox, 1991; Wardle, 1993) and direct growth limitation hypothesis (Körner, 1998). According to the carbon limitation hypothesis, leaf NSCs content is expected to decrease with decreasing temperature because of the reduced photosynthetic carbon assimilation (Stevens and Fox, 1991; Wardle, 1993). In contrast, according to the growth limitation hypothesis, if tissue formation is limited with decreasing temperature, the content of leaf NSCs should increase because of the decreased demand for structural carbon with no consideration of the limitation of nitrogen, phosphorus, and others (Körner, 1998). These two hypotheses provide contradictory predictions and have not yet to be verified using the data from forests across the latitudinal transect at a large scale.

Leaf NSCs are mainly composed of soluble sugars and starch. The soluble sugars in leaves are primarily glucose, sucrose, and fructose (Hoch et al., 2003; Würth et al., 2005). The quantity of soluble sugars may increase under conditions of low temperature and drought, because soluble sugars are not only involved in the osmotic adjustment of cells but are also signal substances that enable adaptation to changing environment (Pan et al., 2002). Starch is used as a relatively long-term energy storage in plants (Zhang et al., 2006), and it's storage in leaves is negatively related to photosynthesis (Li et al., 2008). Highly soluble sugars are beneficial for amylolysis, and their accumulation is triggered by extreme day–night temperature differences (Trethewey and Aprees, 1994). Spatial variations in leaf NSCs across multiple climatic zones have been scarcely reported, preventing the testing of the above-mentioned hypotheses in terrestrial ecosystems at a large scale.

The north–south transect of eastern China (NSTEC) as the 15th standard transect of the International Geosphere-Biosphere Programme, covering multiple climatic zones and including almost all forest types except for boreal forest in Northern Hemisphere, provide an ideal setting for investigating the geographical patterns of leaf NSCs at a large scale. Herein, we measured the contents of leaf NSCs in 890 plant species collected from nine typical forests along the NSTEC. The main objectives of the present study were: (1) to investigate the variations in leaf NSCs among species, plant functional groups, and communities at a large geographic scale, (2) to explore the spatial patterns of leaf NSCs (the content of sugars and starch, NSCs, and the allocation ratio of sugar:starch) and their influencing factors (temperature, precipitation, plant functional groups, and others), and (3) to test the above-mentioned hypotheses to better characterize the underlying physiological mechanisms for the variations in leaf NSCs.

2. Materials and methods

2.1. Site description

Nine typical forests were selected along the 3500 km north–south transect of eastern China (NSTEC), which is an unique belt of vegetation formed by the heat gradients (Fig. 1) (Zhang and Yang, 1995). The growing season of plants in the north is from approximately April to October, whereas the plants
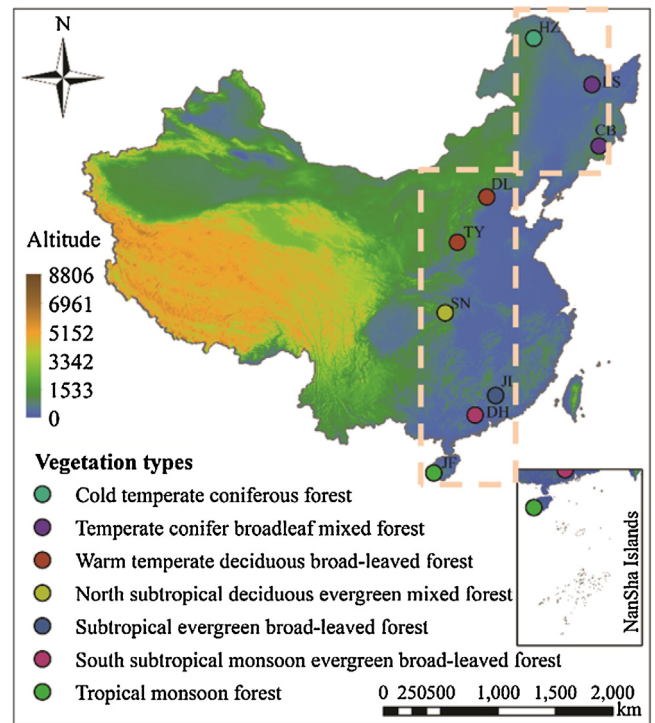

Fig. 1. The selected nine forest ecosystems along the north–south transect of eastern China (NSTEC, yellow frame). JF, Jiangfeng; DH, Dinghu; JL, Jiulian; SN, Shennong; TY, Taiyue; DL, Dongling; CB, Changbai; LS, Liangshui; HZ, Huzhong. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

in the south grow year-round. The mean annual temperature at these sites ranges from −3.67 to 23.15 °C, and the mean annual precipitation ranges from 473.0 to 2265.8 mm (Table 1).

The nine forests thus span cold-temperate, temperate, subtropical, and tropical forests. For each forest, field investigations were conducted on plots setup within the national nature reserves of China to avoid strong disturbances (e.g., fire, cutting, or plantation); these nature reserves are strongly representative of each region. Detailed information regarding the selected forests is provided in Table 1.

2.2. Field sampling

Field sampling was conducted from July 2013 to August 2013. We randomly set up four plots (30 m × 40 m) in each selected forest. Firstly, we investigated the community structure of trees, shrubs, and herbs in each plot. Subsequently, we sampled the leaves of trees, shrubs, and herbs in these plots from 10:00 a.m. to 3:00 p.m. For each tree species, we randomly selected healthy and mature trees in each plot and then sampled the leaves from the fully sunlit upper crown using a long chain saw or artificial climbing trees. For each shrub species, we collected the upper leaves; for each herb species, a mixed sample of fresh and healthy leaves was taken. Leaf samples for a given plant species were mixed together in each plot as a replicate. After field sampling, leaf samples were immediately stored in a cool box with ice, and upon transfer to the laboratory, they were minimally cleaned and stored immediately in a refrigerator (−20 °C).

In total, samples of 1112 plant species were collected in the nine forests (four replicates for each species). Since some plant species were present in more than one forests, the collected plant species comprised 890 plant species, 491 genera, and 156 families. Of the 890 plant species sampled, there were 282 tree species,