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Low-temperature induced leaf elements accumulation in aquatic macrophytes across Tibetan Plateau

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ABSTRACT

The geographic patterns of leaf nutrients in different ecosystems have drawn great attention from stoichiometric ecologists. Two hypotheses, temperature–plant physiological hypothesis (TPPH) and temperature–biogeochemical hypothesis (TBH), were proposed to explain the effects of temperature on terrestrial plants nutrients concentrations and stoichiometry. However, the patterns and causes of variations in leaf C, N and P of aquatic plants in harsh environments have been less well addressed. We collected samples of 35 aquatic macrophyte species across the Tibetan Plateau. The relationships between leaf nutrients were tested and compared with previously published results from freshwater and terrestrial ecosystems and global datasets. We further examined the effects of environmental factors on leaf nutrients. The mean (and median) values of leaf C, N and P were 378.3 (385.0), 28.6 (28.6) and 2.8 (2.7) mg g^{-1}, respectively, while the mass ratios of leaf C:N and N:P were 14.4 and 11.3, respectively. The three elements were positively correlated with each other, with the exception of C and P. The power law exponent relating N and P was 0.74, higher than the expectation of 2/3, which was derived from global data set, possibly due to disproportionate accumulation of leaf P. Phylogeny and temperature primarily explained the observed variations in leaf nutrient contents along environmental gradients, whereas the properties of water and sediments had a weak influence. As temperature decreased, leaf nutrient concentrations increased, but their ratios decreased. The leaf nutrient concentrations measured in this study were higher than those from warmer regions, indicating low temperature-induced nutrient accumulation, which is consistent with TPPH. Our results suggested that the plants concentrated N and P and expedited their growth rate to offset the stress induced by low temperatures and a short growing season on the Tibetan Plateau. Alteration in species composition primarily accounted for the variation in stoichiometric patterns of aquatic macrophytes. Low temperature controlled the stoichiometric patterns directly or indirectly via affecting the species composition along sufficient environmental gradients.

1. Introduction

Plants require more than sixteen elements for their growth and survival (Ågren and Weih, 2012). Carbon (C), nitrogen (N) and phosphorus (P) are vital macronutrients that are generally limiting for plant growth (Vitousek and Howarth, 1991; Ackerly et al., 2000; Sterner and Elser, 2002; Grimm et al., 2003; Ågren, 2004; Elser et al., 2007). Functionally, P is primarily allocated to ribosomal RNA, which is used to synthesize N-rich proteins and further affects carbon harvesting (Sterner and Elser, 2002; Ågren, 2008). Therefore, the three macronutrients couple with each other in their roles in plant physiological processes (Hessen et al., 2004; Niklas et al., 2005; Reich et al., 2010; Osnas et al., 2013). Nutrient concentrations constitute a species-specific plant trait and respond weakly to local ambient nutrient concentrations (Demars and Edwards, 2007; , 2008 Frost and Hicks 2012). But in areas with sufficient climatic gradient, variations in plant nutrient concentrations and stoichiometry along environmental factors (e.g., temperature) could be observed (Reich and Oleksyn, 2004; Zhang et al., 2012). Thus, the geographic patterns of plants C, N, P concentrations and C:N:P stoichiometry across different scales have drawn great attention from stoichiometric ecologists (McGroddy et al., 2004; Reich and Oleksyn, 2004; Han et al., 2005, 2011; He et al., 2006, 2008).

As macronutrients, leaf N and P concentrations decrease, while N:P ratios increase with increasing temperature at global (McGroddy et al., 2004; Reich and Oleksyn, 2004) or regional scales (Han et al., 2005, 2011; He et al., 2006, 2008) in terrestrial ecosystems. But leaf N showed different trends in aquatic macrophytes of eastern China (Xia et al., 2014). In principle,

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energy availability coupled with the species composition and soil substrate age plays a major role in structuring the biogeographic patterns of leaf N and P by affecting physiological processes in plants or soil biogeochemical cycles (Reich and Oleksyn, 2004; Han et al., 2005; He et al., 2008). Two temperature-based hypotheses, the temperature–plant physiological hypothesis (TPPH) and the temperature–biogeochemical hypothesis (TBH), have been proposed to explain such patterns (Reich and Oleksyn, 2004). The TPPH suggests that plants require more N and P to counterbalance the depressed biochemical efficiency caused by low temperature, resulting in increased N and P concentrations in cold regions (Körner, 1999; Weih and Karlsson, 2001). In contrast, the TBH argues that low temperatures in cold regions restrict the release of nutrients from organic matter and their uptake by plants, leading to nutrient limitation (Vitousek and Howarth, 1991). Both nutrient concentrations and their ratios are hypothesized to be tightly coupled with plant growth rates. Species displaying low C:P and N:P ratios exhibit a higher growth rate (i.e., the growth rate hypothesis, GRH) (Enriquez et al., 1996; Thompson et al., 1997; Sterner and Elser, 2002; Elser et al., 2003). Based on 9356 paired observations of leaf N and P concentrations worldwide, Reich et al. (2010) suggested that the relationship between log N and log P presents a slope of approximately 2/3 for all terrestrial angiosperm and gymnosperm plants. However, since the general 2/3-power law exponent was derived from terrestrial ecosystems where the habitats were very different from aquatic ecosystems, whether it hold for aquatic plants need to be tested. Furthermore, to what extent such hypotheses explain the biogeographic gradients in leaf nutrients under the harsh environment of the Tibetan Plateau requires further studies on different life forms (He et al., 2006, 2008).

Ecological stoichiometry originated from Redfield's ratio (molar ratio: 106:16:1) in ocean systems (Elser, 2000). From then, such analysis in aquatic ecosystems has mainly focused on nutrient flows in food webs (Elser et al., 2007; van de Waal et al., 2010). Demars and Edwards (2008) analyzed the effects of habitats, biophysical zones and life forms on aquatic plant stoichiometry at local scale but with sufficient topographical and altitudinal gradients, and suggested that the variability of aquatic plant nutrient concentrations were mainly resulted from variations of taxonomy. Xia et al. (2014) investigated the stoichiometry patterns of leaf C, N and P of aquatic macrophytes in eastern China, and examined the significant roles of phylogeny, life forms and climatic parameters on determining the patterns. Some studies have attempted to fill the gaps between aquatic and terrestrial ecosystems based on a biogeographical perspective, which should be identical between the two systems in principle (Grimm et al., 2003; Elser et al., 2007; Sardans et al., 2012). However, these efforts have been hampered by the limited available studies from aquatic ecosystems (Duarte, 1992; Fernández-Aláez et al., 1999; Demars and Edwards, 2007; Xing et al., 2013). Providing data from aquatic ecosystems, especially from harsh environment regions, could enhance our knowledge of the effects of environmental changes on biogeochemical cycles in different systems (Grimm et al., 2003).

Tibetan Plateau is a special geographic unit with harsh environmental conditions and provides an ideal platform to investigate the variations of plant nutrients along environmental gradients. He et al. (2006, 2008),) analyzed the C:N:P stoichiometric patterns in alpine meadows on the Tibetan Plateau, stressing the important role of temperature in forming these patterns. In this study, we aimed to: (1) identify the distinctive patterns of leaf C, N and P in aquatic macrophytes on the Tibetan Plateau, including investigating the characteristics of leaf nutrient concentrations and stoichiometry and comparing the characteristics with previous studies on aquatic and terrestrial plants; and (2) examine the relative effects of environmental factors (temperature and local water and sediment properties), life forms, habitat types and phylogeny (genus) on the patterns.

2. Materials and methods

2.1. Study area and aquatic habitats

The field sites in this study covered almost the whole Tibetan Plateau, which is located in southwest China. The Tibetan Plateau is the highest region in the world; it has an average elevation of 4000 m and covers an area of 2,500,000 km^2 (27–40° N, 75–105° E, Fig. 1). Topographically, the average elevation of the plateau increases from the southeast to northwest.

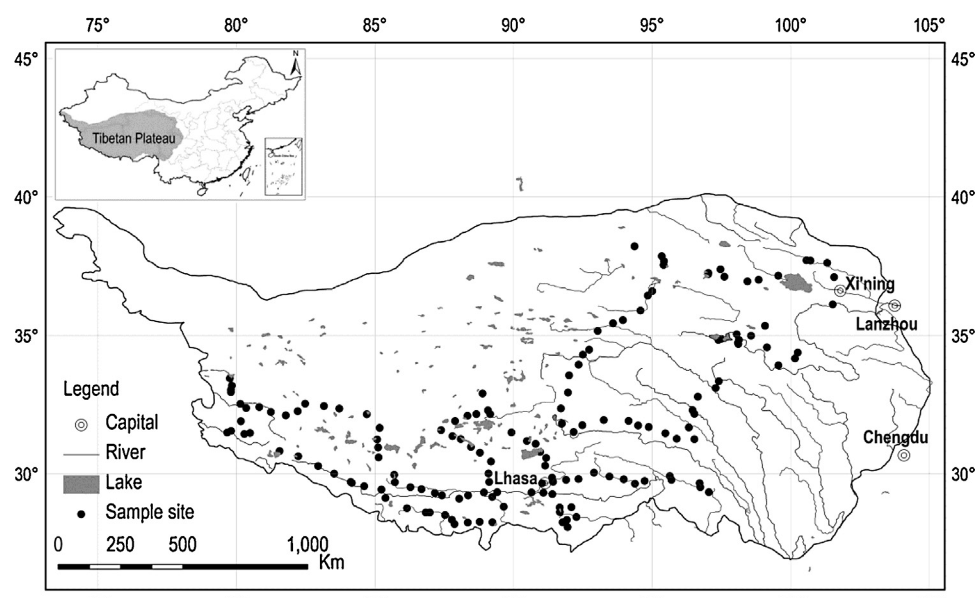

Fig. 1. Sample sites in this study. One hundred and fifty-six aquatic habitats, including rivers, marshes, lakes and other small water bodies, were selected for samples collecting across Tibetan Plateau. Small water bodies included streams, ponds, channels, and puddles.