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Variation in leaf nitrogen and phosphorus stoichiometry in *Picea abies* across Europe: An analysis based on local observations

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ABSTRACT

Nitrogen (N) and phosphorus (P) and N:P ratio in terrestrial plants and the patterns at a large geographical scale are an important issue in ecological stoichiometry. In particular, it is essential to know that for a single species, how the N:P stoichiometry varies with climatic factors in the context of global warming. Our analysis was based on a data set including 2583 observations at 441 sites on nutritional status of Norway spruce (*Picea abies* L.) located in European counties (including Austria, Belgium, Bulgaria, Czech Rep., Finland, Germany, Ireland, Italy, Lithuania, Norway, Slovak Rep., Slovenia, United Kingdom). Our objectives are to demonstrate how leaf N and P concentration and N:P ratio in Norway spruce vary with altitude (ALT), latitude (LAT), longitude (LON), mean annual temperature (MAT) and mean annual precipitation (MAP) across Europe. The results showed that for 1-year-old needles of Norway spruce, the N and P concentration were 13.28 mg g^{-1}, 1.41 mg g^{-1} and the N:P ratio was 9.76. Leaf N displayed a convex curve pattern with increasing MAT and decreasing LAT from the boreal Europe to the Mediterranean area. The N concentration and N:P generally reached peak at about 7 °C in MAT or 53° N in LAT. The N:P ratio varied non-linearly with LAT and MAP, but linearly with MAT. Leaf N concentration and N:P ratio decreased linearly with increasing ALT in temperate European area. Across Europe, that the patterns of leaf N and N:P ratio were mainly driven by climate-related geochemistry and plant physiology, but also greatly impacted by anthropogenic N deposition.

1. Introduction

Over the past several decades, the patterns of nitrogen concentration (N), phosphorus concentration (P), and N:P ratio in terrestrial plants and their controlling factors at regional and global scales have drawn attention (Yin, 1993; Vitousek et al., 1995; Thompson et al., 1997; Oleksyn et al., 2003; Hedin, 2004; Reich and Oleksyn, 2004; Han et al., 2005). This is mainly because leaf N, P and N:P ratio are essential indicators for assessing plant nutrient status forest ecosystems (Güsewell, 2004; McGroddy et al., 2004; Ågren, 2008) and subject to climate change (Van de Waal et al., 2010). The extant nutrient status of plants is adaptation to the habitats in long term evolution. Identifying the current patterns of nutrient-climate relationship is helpful to understand how plants respond to climate change in the future.

One of important advances in this field is that a non-linear leaf N-climate relation was founded for plants at a regional or global scale. For instance, using a data set compiled from studies across North America, Yin (1993) reported the first study on the relationships between forest tree leaf N and climatic factors at a large geographical scale. The results showed that leaf N of forest trees increases from boreal to temperate regions, and then appears to decrease towards subtropical area (Yin, 1993). Based on analysis with a global data set, Reich and Oleksyn (2004) also showed a similar pattern that leaf N increased from −10 °C (mean annual temperature, MAT, °C), peaked at about 15 °C and then tended to decrease to 30 °C. This is true for all plants as a whole, some functional groups (such as grasses, herbs, shrubs and trees) as well as some genera (e.g. *Acer*, *Vaccinium*). Such patterns are due to the temperature-related plant physiological stoichiometry and biogeographical gradients in soil substrate age from tropics to temperate areas and the lower availability of nutrients in boreal biomes (colder climate and lower litter decomposition) (Reich and Oleksyn,

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2004). Here one hypothesis is such a leaf N-temperature convex curve also holds at a species level in case that it has a widespread geographical distribution (e.g. from boreal to subtropical areas).

For different kinds of plants, the patterns of variation in nutrient concentrations substantially differ in relation to climatic factors. For instance, Reich and Oleksyn (2004) reported that N and P increase with MAT in birch (*Betula*), decrease in *Calamagrostis*, but show a convex curve in maple (*Acer*). In Scots pine (*Pinus sylvestris*) needle leaf N appears to decrease with latitude (LAT) across Europe (Oleksyn et al., 2003). Han et al. (2005) using a terrestrial plant data set across China, displayed that there is a significant difference in plant P concentration due to deficit P in Chinese subtropical soils. For those plant species in large ranges of differing habitats, we could conjecture that the relationships between leaf nutrients and climatic factors differ among species due to their dissimilarities in physiology and ecology. Consequently, the response of nutritional status to climate change in plant may need to be differentiated by individual species. In the context of global change, in this sense, it is essential to identify the pattern of variation in key nutrients (e.g. N, P) along a broad climate gradient for those specific plant species distributing across larger geographical areas.

Other than temperatures, precipitation is also an important climatic factor influencing the processes of plant physiology (Liu et al., 2006). As temperature, precipitation, evapotranspiration and LAT are correlated at a global or regional scale, temperature is generally used as a surrogate in expressing the relationship between other environmental factors and ecological variables (Reich and Oleksyn, 2004). However, the variation in precipitation along a broad gradient changes not only soil moisture level, but also light availability to plants through different cloud cover. At a local scale, the nutrient physiology of plants is strongly influenced by light availability (Walter and Schurr, 2005). It is therefore needed to reveal the relation of plant nutrient concentrations with precipitation at a broad geographical scale.

Norway spruce (*Picea abies* L.) is one of the most common and important timber trees in Europe, with a distribution from the subarctic to the Mediterranean areas (Oleksyn et al., 1998; Berg et al., 2000; Liu et al., 2004, 2006; Seynave et al., 2005) and from the low to high mountains (e.g. up to more than 2000 m in altitude in northern Italy) (Stefan et al., 1997). Within such a wide geographical distribution, there is a broad gradient of MAT and mean annual precipitation (MAP, mm), providing an opportunity to examine nutritional status and stoichiometry for individual species at a regional scale (Cape et al., 1990; Ladanai and Ågren, 2004; Seynave et al., 2005; Briceno-Elizondo et al., 2006). The nutritional status of Norway spruce has been investigated at stand level, regional level, or continental level (e.g. Cape et al., 1990; Stefan et al., 1997; Vanmechelen et al., 1997; Ladanai and Ågren, 2004; Majdi and Ohrvik, 2004). Andersson et al. (1998) also considered anthropogenic N deposition and its potential impacts on tree nutritional status (Cape et al., 1990; Andersson et al., 1998), when investigating the nutritional status of Norway spruce across climatic and N deposition gradients in north Europe. However, no study has looked at the patterns of variation in leaf N, P, and N:P ratio in Norway spruce in relation to geographical (altitude, latitude, longitude) and climatic factors (MAT and MAP) across Europe.

A regional long-term monitoring network of plots was established in the 1980s to register possible biogeochemical changes in forest ecosystems and their relationships to global change across Europe (Stefan et al., 1997; Vanmechelen et al., 1997). These monitoring plots include Norway spruce, as well as other common European tree species. With a data set of N and P concentrations in 1-year-old needles of Norway spruce (IPC PCC of ICP Forest, Institute for World Forestry, Hamburg, Germany), our objectives are (1) to identify the spatial patterns of variation in leaf N, P, and N:P ratio in relation to ALT and LAT for this tree species across Europe, and (2) to explore the effects of MAT, MAP as well as other influential factors underlying the pattern of leaf nutritional status at individual species level across a boreal-subtropical climatic gradient.

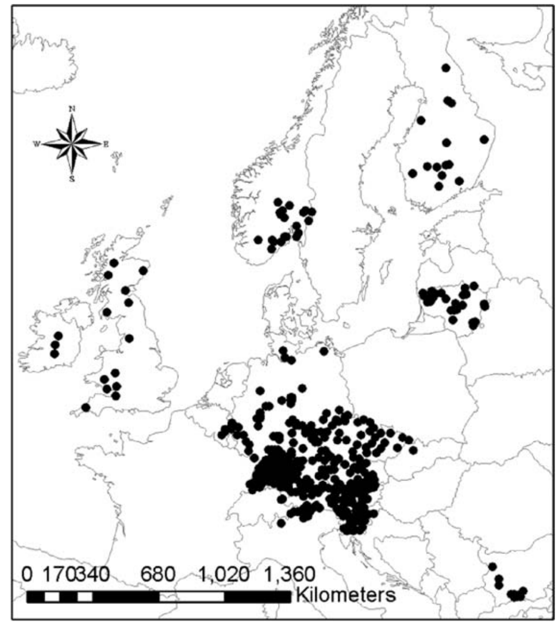

Fig. 1. Distribution map of plots used in this study.

2. Materials and methods

2.1. Data selection

We obtained a data set of N and P concentrations in current needles of Norway spruce from IPC PCC of ICP Forest, Institute for World Forestry (Hamburg, Germany). The data set comprises 2583 observations at 441 sites across 13 European countries (Fig. 1) and includes geographic information (latitudes, longitude and altitude) for each site. These sites range from 25 to 2075 m a.s.l. in altitude, 41.55° N–66.19° N in latitude and 7.95° W–30.12° E in longitude. In the lower latitude, more sites were located in the higher altitude (Fig. 2). The MAT and MAP of each site were estimated from the latitude, longitude and altitude using the Local Climate Estimator 1.0 (Grieser et al., 2002; FAO, 2001).

The data used in this study was collected through a long-term monitoring network (Monitoring Level-I) across Europe and provided information on the actual nutrient state of forest trees on

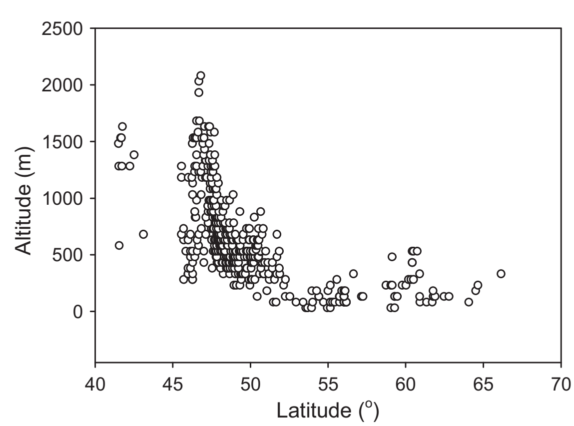

Fig. 2. Relation of latitude and altitude for the plots used in this study.