



Research article

Factors influencing the foliar elemental composition and stoichiometry in forest trees in Spain



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ARTICLE INFO

Article history:

Received 28 April 2015

Received in revised form

17 December 2015

Accepted 5 January 2016

Available online 6 January 2016

Keywords:

Calcium

C:K

C:N

C:P

Ecological stoichiometry

Growth rate hypothesis

Mean annual precipitation (MAP)

Mean annual temperature (MAT)

Mediterranean ecosystems

Magnesium

N:P

N:K

P:K

Potassium

Sulfur

Water stress

ABSTRACT

Concentrations of nutrient elements in organisms and in the abiotic environment are key factors influencing ecosystem structure and function. We studied how concentrations and stoichiometries of nitrogen (N), phosphorus (P) and potassium (K) in leaves of forest trees are related to phylogeny and to environmental factors (mean annual precipitation, mean annual temperature, forest type, and nitrogen deposition). Using data for 4691 forest plots from across Spain, we tested the following hypotheses: (i) that foliar stoichiometries of forest trees are strongly influenced by phylogeny, (ii) that climate, as an important driver of plant uptake and nutrient use efficiency, affects foliar stoichiometry, (iii) that long-term loads of N influence N, P and K concentrations and ratios in natural vegetation, and (iv) that sympatric species are differentiated according to their foliar stoichiometry, thereby reducing the intensity of resource competition.

Our analyses revealed that several factors contributed to interspecific variation in elemental composition and stoichiometry. These included phylogeny, forest type, climate, N deposition, and competitive neighborhood relationships (probably related to niche segregation effect).

These findings support the notion that foliar elemental composition reflects adaptation both to regional factors such as climate and to local factors such as competition with co-occurring species.

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1. Introduction

The elemental composition and stoichiometry of tree foliage are important topics in forest research. Foliar N:P ratios have been shown to correlate with the growth rate of plants (Elser et al., 1996, 2000a,b, 2010; Peñuelas and Sardans, 2009; Peñuelas et al., 2013a) and with the structure and function of plant communities (Peñuelas et al., 2013a; Sardans et al., 2012a; Sterner and Elser, 2002). Species with low foliar N:P ratios tend to grow rapidly and are more competitive for soil resources than species with higher N:P ratios, especially where nutrient availability is high (Elser et al.,

2001, 2003; Willby et al., 2001). In the last decade, there have been many studies of how foliar nutrient concentrations and stoichiometries (mainly N:P) vary along environmental gradients, both at regional (Santiago et al., 2004; Ordoñez et al., 2009; Sandel et al., 2010; Sardans et al., 2011) and global (Reich and Oleksyn, 2004) scales. Whereas some of these have found significant relationships between foliar N:P concentration ratios and climatic gradients (Kerkhoff et al., 2005; Reich and Oleksyn, 2004; Yuan and Chen, 2009), others have produced how contradictory results (Han et al., 2005; He et al., 2008; Lovelock et al., 2007). Overall, these studies suggest that climatic conditions do affect foliar elemental stoichiometry, but that this relationship varies regionally and may be obscured by other factors such as the distribution of plant groups, soil type, and plant growth strategy (Sardans et al., 2011, 2012a). Since climate influences plant water availability, temperature and light intensity (Carter et al., 1997; Huxman et al., 2004; Voesenek

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and Pierik, 2008; Wang et al., 2012), climatic variables such as mean annual temperature (MAT) and mean annual precipitation (MAP) can be expected to determine, at least in part, the uptake of nutrients, and thus the foliar elemental concentrations and stoichiometry. However, these will also be influenced by other features of the ecosystem, including the dominant plant growth strategies (slow versus fast growth, shade versus light tolerance, etc.), community composition and soil nutrient heterogeneity. As a consequence, we can expect to observe a spectrum of foliar elemental composition and stoichiometry even at one site.

Most studies of plant stoichiometry have considered only N and P. However, potassium (K) is the most abundant nutrient in leaves after N, and considerably more abundant than P (Sardans et al., 2006a,b; Zheng and Shangguan, 2007). Together with N and P, K plays an important role in the physiology of terrestrial plants (Cakmak, 2005). In particular, it controls the water content of leaves by controlling stomatal function, cell osmosis equilibrium and water fluxes (Babita et al., 2010; Fernandez et al., 2006; Laus et al., 2011; Milla et al., 2005; Oddo et al., 2011). Including potassium (K), therefore, should improve our understanding of the causes and consequences of plant stoichiometric shifts among species, natural gradients and competition conditions.

The concentration of K is especially significant in dry ecosystems because of its role in physiological responses of the plant to varying water availability and shifts in foliar N:P:K ratios are related to the change in response of plants to drought (Mairapetyan et al., 1999; Sardans and Peñuelas, 2007, 2008; Sardans et al., 2008b,c) in the Mediterranean forests and shrub lands. Moreover, some forests of the main biomes are K-limited (Nilsen and Abrahamsen, 2003; Olde Venterink et al., 2001; Tripler et al., 2006; Wright et al., 2011) and its concentrations and stoichiometrical relationships with N and P are important to control water use efficiency (WUE) in dry environments (Egilla et al., 2005; Graciano et al., 2005; Sardans et al., 2012a, 2012b; Welander and Ottosson, 2000). Some studies have found that a high concentration of K increases plant resistance to drought (Egilla et al., 2005; Stone and Moreira, 1996), and that stoichiometric relationships of K to N and P vary according to water availability (Peñuelas et al., 2013b; Rivas-Ubach et al., 2012; Sardans and Peñuelas, 2007; Sardans et al., 2011).

Other nutrients such as S, Mg or Ca may also limit growth in terrestrial plant communities (Baribault et al., 2012; Hailles et al., 1997; Lapenis et al., 2013; Naples and Fisk, 2010), albeit less commonly than N, P and K. Thus, in attempting to understand the factors that influence foliar elemental chemistry, there is a need for studies that also consider many more nutrients, including Ca, Mg and S.

Currently, apart from natural environmental circumstances such as climate conditions, the use of fertilizer and atmospheric deposition of N are likely to trigger shifts in the N:P ratios of terrestrial plants (Peñuelas et al., 2005, 2012, 2013a; Sardans et al., 2008a, 2011; Veresoglou et al., 2014). Estimated loads of total annual atmospheric N deposition in Spain have approached $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Avila and Rodà, 2012; Sanz et al., 2002). These levels are generally lower than those recorded in central Europe, but evidence from N concentrations of bryophytes in herbaria (Peñuelas and Filella, 2001) and a growing abundance of nitrophilous species in Spanish terrestrial ecosystems (Ariño et al., 2011) points to continuing N enrichment. In several sites of Europe, forest defoliation and dieback has been attributed to increasing N deposition (Jönsson et al., 2005; Pedersen and Bille-Hansen, 1995; Thomas et al., 2002), which has been shown to affect leaching of K, Ca, Mg and Na from soil in temperate and boreal areas of Europe and North America (Koptsik et al., 2007; Watmough et al., 2005). Meta-analysis of 107 independent studies of forest nitrogen (N) fertilization showed that the increase in N loads in temperate forest ecosystems decreased the concentrations of base cations (Ca^{2+} , Mg^{2+} , K^+ and Na^+) in soils and increased their concentrations in

soil water and stream runoff (Lucas et al., 2011). Nutrient imbalance, particularly between N and other nutrients, is related to forest defoliation and dieback in European forests (Lomský et al., 2012; Veresoglou et al., 2014) and in other world areas (Wang et al., 2009). Under N deposition, plants are able to increase their P and K uptake capacity (Rowe et al., 2008). P limitation favors higher plant phosphorus uptake through enhanced activity of soil phosphatases (Treseder and Vitousek, 2001) and root phosphatases (Gress et al., 2007; Phoenix et al., 2004) and by changing symbiotic fungi (Lilleskov et al., 2002). These mechanisms seem quantitatively insufficient to deliver enough phosphorus to alleviate P limitation (Vitousek et al., 2010), thus P becomes limiting (Turner et al., 2003; Bragazza et al., 2004) and P concentration decreases (Bragazza et al., 2004; Braun et al., 2010; Jonard et al., 2012; Lévy et al., 1996). Most studies show increase in N:P and N:K ratios under long-term N deposition in several ecosystem pools such as plants (Britton et al., 2008; Lawniczak et al., 2009; Thelin et al., 1998;) and soils (Olde Venterink et al., 2009) being N:K ratio related to changes in the plant species-specific composition and diversity of terrestrial ecosystems (Roem and Berendse, 2000). Thus, we would expect a wide effect of the gradients of N deposition on foliar elemental composition and stoichiometry of Spanish forests.

An understanding of how foliar elemental composition vary among tree species and along climatic gradients, and the different optima for elemental composition (not only N and P) among sympatric species, is relevant to forest management. These relationships should be considered in assessing the most promising species for reforestation and in managing existing forest areas. For example, some species may be more flexible than others in their stoichiometry, and better able to adapt to increasing N loads through deposition. An analysis of climatic and N-deposition data at the regional level can improve our understanding of the role of natural versus anthropogenic factors in determining plant stoichiometry and its imbalance. Correction of nutrient imbalances is a key issue for the success of afforestation, and survival and health of Spanish forests. Many of these are in arid areas where nutrient supply has a crucial influence upon the water-use efficiency of trees (Harvey and van den Driessche, 1999; Ripullone et al., 2004).

According to the biogeochemical niche hypothesis, coexisting plant species tend to use the main nutrients N, P and K (and other essential nutrients such as Ca, Mg and S) in differing proportions (Peñuelas et al., 2008, 2010; Urbina et al., 2015), and therefore occupy distinct regions in the multivariate space generated by the concentrations and ratios of macro- and micronutrients in plant tissues. Since different plant structures and metabolic processes have distinct and divergent requirements for each of the essential nutrients, the species-specific biogeochemical niches should be the result of species specialization to particular abiotic conditions. Moreover, these niches should reflect the different species-specific strategies of growth and resources uptake and the differences in soil space and time occupation. Ultimately, these differences contribute to reducing direct competition among sympatric species (Peñuelas et al., 2008, 2010; Urbina et al., 2015). Despite the existence of biogeochemical niches, however, it is also known that species exhibit varying degrees of stoichiometrical flexibility in response to environmental changes (including ontogenical and seasonal-climate changes) and competitive situations, probably under a tradeoff between flexibility and stability (homeostasis) capacity (Yu et al., 2010). Yu et al. (2011) observed that species with higher stoichiometry flexibility have higher concentrations of N and P and lower N:P ratios.

We investigated the factors influencing the stoichiometry of trees using existing data for Spanish forests. Our analysis was based upon four hypotheses. First, we predicted that the elemental stoichiometries of different forest species should be strongly determined genetically due to their long-term adaptation to specific

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