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Shortage of nutrients and excess of toxic elements in soils limit the distribution of soil-sensitive tree species in temperate forests

Lorenz Walthert [a,*], Elisabeth Graf Pannatier [a], Eliane S. Meier [a,b]

[a] Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland
[b] Research Station Agroscope Reckenholz-Taenikon ART, CH-8046 Zurich, Switzerland

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ABSTRACT

A sound knowledge of the soil properties required by tree species is a prerequisite for addressing many practical and scientific issues such as forest management or the predictive mapping of tree species. To date, such knowledge has been derived mainly from laboratory experiments and from case studies in the field. The importance of soils for the distribution of tree species has, however, hardly been tested systematically with comprehensive data including climate, soil and vegetation inventories.

In our study, we analysed a comprehensive database to explore how soil and topo-climatic properties relate to the abundance of regenerating and mature beech (*Fagus sylvatica L.*), ash (*Fraxinus excelsior L.*) and sycamore (*Acer pseudoplatanus L.*) in mature forests across Switzerland.

From 806 forest plots distributed all over strong environmental gradients, we used soil and topo-climatic data as predictors and the abundances of tree species in the herb and in the tree layer as response variables. To test the explanatory power of the predictors, we conducted variation partitioning analyses with generalized linear models. Soil predictors involved nutrients, potentially toxic elements, soil aeration and water availability. The explanatory power of most soil predictors was tested in different soil layers to a depth of 1 m.

Ash and sycamore were much more sensitive to soil variables than beech. The most relevant soil variables for the competitive ability of the three species were C/N-ratio, humus form, aluminium content, base saturation, magnesium content, and soil aeration. Shortage of nutrients limited the distribution of ash and sycamore and excess of toxic elements the distribution of ash. For beech, no soil-induced distribution limits were detectable. Ash was absent if the C/N-ratio in the topsoil was greater than 20. On such sites, sycamore was absent too or reached heights of at most 15–20 m, i.e. well below the upper canopy. Ash was absent or reached a maximum height of 15 m on acidic soils including at least one soil layer with a base saturation less than 20% in the upper 1 m of the soil. The soil properties relevant for the competitive ability of ash and sycamore were more apparent for mature than for regenerating trees. In most cases, the topsoil influenced tree abundances more than the subsoil did.

1. Introduction

The distribution of plant species is not only driven by climate, but also by soil properties such as water and nutrient availability. This has been well established in forests since the beginning of the twentieth century (e.g. Hesselman, 1910; Pallmann and Haffter, 1933; Tüxen, 1954). The importance of soils for plant distribution is taken into account in the concept of bioindication (e.g. Ellenberg, 1979), where the presence of specific plant species is assumed to reflect specific soil properties. Various experiments and case studies have also shown the impacts of soil nutrients and toxic elements on the nutritional state, growth or survival of plant species (e.g. Binner et al., 2000; Cronan and Grigal, 1995; Weber-Blaschke et al., 2008, 2002).

The concept of bioindication and the findings from experiments and case studies in the field suffer from some limitations. First, the ecological indicator values used in the bioindication concept are largely subjective assessments (Coudun et al., 2006) since they are based mostly on expert opinions and only partially on measurements (e.g. Ellenberg, 1979). Second, in experiments under controlled conditions often conducted with soil solutions, the natural growth conditions cannot be simulated thoroughly, e.g. to take into account soil biota like mycorrhiza or microbial communities (Nygaard and de Wit, 2004). Moreover, the seedlings or saplings of a tree species may react differently to mature individuals

* Corresponding author. Tel.: +41 44 739 25 92; fax: +41 44 739 22 15.
E-mail address: lorenz.walthert@wsl.ch (L. Walthert).

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due to age- and size-related changes in morphology and physiology of trees (Day et al., 2002; Ryan and Yoder, 1997) and because juvenile and mature plants often differ largely in their requirements (Leuschner et al., 2009). Thus, the results of experiments might be only partly applicable to forest ecosystems (Nygaard and de Wit, 2004). Third, case studies in the field can elucidate interactions between plants and soil on a limited number of sites, but it is often unclear to what extent the results can be generalised, and they therefore usually are considered to have limited spatial validity (Hildebrand et al., 1996). Despite these limitations, the importance of soils for the distribution of tree species have rarely been tested systematically with empirical, comprehensive data from climate, soil and vegetation inventories (Coudun et al., 2006).

We analysed a database containing climate, topography, soil and vegetation data to find out, how topo-climatic and soil properties relate to the abundance of tree species across Switzerland. Specifically, we tested: (i) whether tree species vary in their sensitivity to soil, climate and topography; (ii) whether the contents, stocks or ratios of soil chemical properties explain tree abundance best; (iii) which soil depths explain tree abundance best; and (iv) whether there are soil properties that limit tree species distribution.

To answer these four questions, we selected three tree species we expected from bioindication, laboratory and field studies to differ in their response to soil nutrients and toxic aluminium (Al), namely sycamore (*Acer pseudoplatanus L.*), ash (*Fraxinus excelsior L.*) and beech (*Fagus sylvatica L.*) (e.g. Binner et al., 2000; Ellenberg and Leuschner, 2010; Leuschner et al., 2006; Weber-Blaschke et al., 2002). These species are also among the most abundant and economically most important broadleaf tree species in Switzerland (Brändli, 1996).

From previous research, we expected the following outcomes from the analyses of our dataset: (i) species sensitivity to soil and topo-climatic factors differs (Ellenberg, 1979); (ii) contents, stocks and ratios of soil chemical properties differ in how well they explain tree abundance; (iii) soil depth influences species' response to soil due to the vertical gradients of chemical and physical properties in most soil profiles; and (iv) the distribution of ash and sycamore is limited in very acidic soils with high levels of Al and correspondingly low contents of basic cations, as well as in soils with poor nitrogen (N) availability (Binner et al., 2000; Weber and Bahr, 2000; Weber-Blaschke et al., 2008, 2002). We did not expect any soil-related distribution limits for beech (Leuschner et al., 2006).

2. Material and methods

2.1. Study area

The study area encompassed all of Switzerland (circa 46–48°N and 6–10°E) in the centre of Western Europe. Geology, relief and climate are very varied with abrupt changes often within short distances. Due to this high variability, Switzerland has relatively strong environmental gradients compared to its small surface, and forest soils and sites are consequently highly diverse as well. Roughly 30% of the country (12,000 km^2) is covered with forest, half of which is located above 1000 m. Two thirds of the forest area are in public hands, the rest is privately owned. Two thirds of the forest are frequently managed, 18% infrequently and 14% remain unmanaged (Brassel and Brändli, 1999). Forest management is primarily practiced at low elevations, where selection forestry is the predominant management scheme. Thus, no large-scale clear-cutting is applied, and natural regeneration is often furthered by management activities. Fertilizing or liming to manipulate soil fertility has always been forbidden in Swiss forests.

2.2. Forest plots, species and environmental data

2.2.1. Forest plots

Species and environmental data originate from a database of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), containing data on about 1000 forest plots across Switzerland. For each plot, a floristic inventory according to Braun-Blanquet (1964) and soil data from a soil pit 1.2 m deep on average are available. Most of the plots were selected according to ecological criteria for forest sites, i.e. that species composition and stand structure should be close to those observed in natural forests.

From this dataset, we excluded about 200 plots according to two criteria. First, we only selected mature forest stands since the site requirements of the tree species in mature stands are more apparent than in juvenile stands, because competition had time to adjust the species composition according to the competitive ability of each species. We therefore removed all plots with juvenile forests (n = 37) from the dataset by excluding forests where the tallest trees were smaller than 20 m. However, mature forests on dry sites or in high altitudes with limited growth ability, i.e. with limited tree height, were not excluded. Secondly, because we aimed to clarify whether tree species abundance responded to chemical properties at different soil depths, we also excluded all plots where the roots possibly were not able to grow to a depth of at least 1 m. Thus, we excluded all plots with soil pits that were not deep enough (less than 1 m), as well as plots with soils having parent rock or a permanent anaerobic horizon (Gr-horizon) within 1 m of the soil surface. The selection procedure resulted in 806 forest plots. Beech was present in the herb layer on 461 plots and in the tree layer on 491 plots. The corresponding numbers for ash were 344/161 and for sycamore 414/160 (Fig. 1).

Our dataset reflected quite well the horizontal and altitudinal distribution of beech, ash and sycamore measured in the Swiss National Forest Inventory (Brändli, 1996). Unlike the climatic conditions of Central Europe, many of our forest plots are located in areas with a relatively humid climate (Fig. 1).

2.2.2. Species data

Species data in the 806 mature forest stands were collected by 35 authors and partly originate from the Swiss Forest Vegetation Database (Wohlgemuth, 2012). The abundance of beech, ash and sycamore in the tree layer (mature trees) and in the herb layer (regenerating trees; the maximal height of the herb layer was 1.5 m) was assessed during the vegetation survey. All the plant species occurring in an area ranging from 100 to 500 m^2 (on average 200 m^2) in the herb, shrub and tree layers were recorded using the Braun-Blanquet cover abundance scale (Braun-Blanquet, 1964; Mueller-Dombois and Ellenberg, 1974). For the tree layer, most botanists used larger reference areas than indicated on the protocols to obtain a more representative estimate of the tree species abundances in the forest stands. As part of the vegetation survey, the height of the forest stand was estimated. Height was sometimes measured on the basis of several dominant trees with a Vertex III ultrasonic instrument (Haglöf, Långsele, Sweden). The vegetation survey for most of the plots was carried out between 1987 and 2001, however, 33 relevés were completed before 1987 and another 76 between 2007 and 2010. The vegetation survey and soil sampling were carried out in the same year on 496 plots but on 209 plots the time lag between them was at most 5 years, on 68 plots at most 10 years and on 33 plots more than 10 years.

2.2.3. Environmental data

From a very large number of environmental variables (n = 87), we selected the most relevant variables for our study in two work