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Tree species diversity effects on productivity, soil nutrient availability and nutrient response efficiency in a temperate deciduous forest

Marcus Schmidt [a,*], Edzo Veldkamp [a], Marife D. Corre [a]

[a] Buesgen Institute – Soil Science of Tropical and Subtropical Ecosystems, Georg-August University of Goettingen, Buesgenweg 2, 37077 Goettingen, Germany

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ABSTRACT

There are contrasting reports whether and how tree diversity influences stand productivity in temperate deciduous forests. Tree species diversity may increase stand productivity in temperate forests through complementary resource use and/or facilitation if the resource considered limits productivity. In unpolluted temperate forests, net primary production is typically limited by nitrogen (N). However, in many parts of Europe high N deposition has alleviated N limitation and there is some evidence that phosphorus (P) and/or potassium (K) limitation has become more widespread. Here, we report on a study where we investigated whether complementarity and/or facilitation increase productivity in a typical German deciduous forest with tree species of beech (*Fagus sylvatica*), oak (*Quercus petraea* and *Quercus robur*), hornbeam (*Carpinus betulus*) and lime (*Tilia cordata* and *Tilia platyphyllus*). We measured biomass production and availability of soil N, P, K, calcium (Ca) and magnesium (Mg) in stands of single species (mono-species stands) and in stands with different combinations of three of the tree species above (mix-species stands). We used nutrient response efficiency (NRE) to evaluate whether a specific nutrient limits tree growth. At a stand level, above-ground net primary productivity did not differ between mono- and mix-species stands. At a tree level, using a neighborhood approach, relative growth rates of beech trees in mono-species stands were smaller than when they were in mix with lime and hornbeam whereas growth of lime trees in mono-species stands was larger than in mix with beech and oak. The NRE curve for beech showed that beech trees in mix-species stands had optimal P and K response efficiencies whereas beech trees in mono-species stands showed P and K limitations. The NRE curve for oak with exchangeable soil K showed that K levels were beyond the optimum NRE and thus K was not limiting oak growth. NRE curves for hornbeam and lime showed no significant relationships with any of the soil nutrients. Hence, nutrient limitation was species-dependent. Our results showed that using both NRE and a neighborhood approach are useful tools in quantifying the effects of individual tree species on a species' productivity between mono- and mix-species stands. Such tools provide important basis for improving management of typical mix-species, temperate forests.

1. Introduction

Species composition can alter ecosystem properties through functional traits and interactions (Hooper et al., 2005). In many experiments in grasslands where species composition was manipulated, it has been shown that biodiversity increases productivity (Loreau et al., 2001) and it was recently suggested that biodiversity in such ecosystems may be as important for productivity as the availability of growth-limiting nutrients (Tilman et al., 2012). In forest ecosystems there are, however, conflicting reports on the effects of species richness on productivity. While a positive influence has been reported in tree plantations (Piotto, 2008) as well as in boreal (Paquette and Messier, 2011) and early-successional Mediterranean (Vilà et al., 2005, 2007) forests, it has been suggested that biodiversity is less important in temperate forests growing in a stable, productive environment (Paquette and Messier, 2011). In an unmanaged temperate forest in central Germany, plots with 40% beech and the rest accounted for by ash, lime, hornbeam and maple had lower above-ground net primary production than plots with 89% beech (Jacob et al., 2010). Since beech was, however, the dominant species, such effect may not be due to the number of tree species but to beech abundance. Indeed, in the same study area, no relationship was found between tree species richness and above-ground net primary production

* Corresponding author. Tel.: +49 551 395507; fax: +49 551 3933310.
E-mail addresses: marcus.schmidt@forst.uni-goettingen.de (M. Schmidt), eveldka@gwdg.de (E. Veldkamp), mcorre@gwdg.de (M.D. Corre).

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(Seidel et al., 2013). This result is in contrast with a modeling study showing that species richness increases productivity in temperate deciduous forests (Morin et al., 2011). In summary, there are contrasting reports whether and how tree species diversity influences stand productivity in temperate deciduous forests.

There are three mechanisms through which tree species diversity can increase forest productivity: facilitation, complementary resource use and the sampling effect (Fridley, 2001). Facilitation occurs when one species positively alters the environment in favor of another (Vandermeer, 1989). A Californian oak species (*Quercus douglasii*) was able to facilitate growth of the herbal layer by providing additional nutrients, although the effect was often overlain by root interference (Callaway et al., 1991). Also, in successional post-glaciation sites in Glacier Bay, Alaska, communities of Sitka alder (*Alnus sinuata*) facilitated growth of late-succession Sitka spruce (*Picea sitchensis*) (Chapin et al., 1994). Complementarity reduces competition between species by resource partitioning (Fridley, 2001; Hooper et al., 2005). Evaluation of available data from economically-relevant temperate and boreal tree species showed that complementary functional traits, such as high and low tolerance of shade, can increase productivity by up to 30% whereas similar functional traits and ecological amplitudes increase competition and can decline stand productivity by up to 30% (Pretzsch, 2003). However, in central Germany, complementary canopy filling of stands with multiple species did not affect productivity (Seidel et al., 2013). A sampling effect addresses the greater chance of choosing highly-productive or better-adapted species or of encountering complementarity or facilitation in high versus low species-diversity communities (Fridley, 2001). Facilitation, complementary resource use as well as the sampling effect is sensitive to environmental conditions, scale of observation and human impact (Fridley, 2001). For example, in a global study, at small-scale plots high tree species number produced large biomass whereas this relationship did not hold for larger plots where environmental gradients were proposed to be more important drivers of productivity than was tree species richness (Chisholm et al., 2013).

Tree species diversity has the potential to increase productivity in a temperate forest through facilitation and/or complementary resource use if the resource considered limits productivity. In unpolluted temperate and boreal forests, net primary production is limited by nitrogen (N) (Vitousek, 1982; Hedin et al., 1995). In many parts of Germany, however, high N deposition has alleviated N limitation (e.g., Corre et al., 2003, 2007), which may have resulted in nutrient limitations other than N. Furthermore, N deposition has the potential to reduce phosphorus (P) uptake by trees through inhibiting plant-mycorrhizal association (Braun et al., 2010). This was for example reflected in German beech stands of which 23% showed P deficiency in at least one year (Ilg et al., 2009). In a review of studies examining growth of deciduous tree species with potassium (K) fertilization, 7 out of 9 studies showed positive response to increased K availability in forest soils (Tripler et al., 2006).

The efficiency with which trees convert nutrients into biomass is an important measure that determines whether or not tree species diversity can increase productivity in temperate forests. The first study that evaluated nutrient use efficiency of forests uses an index of litterfall, organic matter increment and root turnover divided by litterfall nutrient concentration (Vitousek, 1982). Later, nutrient response efficiency (biomass production divided by soil nutrient availability; Bridgham et al., 1995) was successfully tested in various ecosystems and at different scales. NRE is a suitable index to evaluate biodiversity effects on productivity since it determines, together with soil nutrient availability, whether complementary nutrient use and/or facilitation of trees affect productivity. Hence, these mechanisms will increase productivity only if differences in soil nutrient availability and nutrient response efficiencies of tree species are sufficiently large and competitive interactions are not dominant.

In the present study our objectives were to (1) determine whether tree species diversity affected productivity both at stand and tree levels, (2) assess whether tree species affected plant-available N, P, calcium (Ca), K and magnesium (Mg) in the soil, and (3) evaluate which soil nutrient elements limit productivity based on NRE curves. We hypothesized that in our study area, a deciduous forest in central Germany dominated by four species, (1) mix-species stands are more productive than mono-species stands, (2) nutrient limitation is species-dependent, and (3) mix-species stands use soil nutrient elements more efficiently than mono-species stands. We discuss the practical implications of our findings for forest management.

2. Methods

2.1. Site description

Our study was conducted in the Hainich national park, which represents the largest unmanaged deciduous forest ecosystem in central Germany. It contains tree communities typical for central Europe (Mölder et al., 2006). Our research site was an area of about 25 ha, defined as 'very close to the natural vegetation' (Nationalparkverwaltung Hainich, 2008), has an average slope of 4°, and is located near the town of Weberstedt, Thuringia, Germany (51°6′N, 10°30′E). The soil's parent material is a Triassic limestone, covered by up to 50 cm of loess. The soil is a Cambisol with texture between silt loam and silty clay loam (Appendix 1).

2.2. Stand selection

The four most common trees species in the study site were beech (*Fagus sylvatica*), oak (*Quercus petraea* and *Quercus robur*), hornbeam (*Carpinus betulus*) and lime (*Tilia cordata* and *Tilia platyphyllus*). Oak was mainly *Q. petraea* with only a few trees of *Q. robur*. Lime could not be differentiated in the field: 87% of lime trees at the site were found to be *T. cordata*, 4% *T. platyphyllus* and 9% hybrids (Rajendra, 2009). We selected stands for each of the four tree species, which we call 'mono-species stands' hereafter, and stands consisting of three out of these four species, which we call 'mix-species stands' hereafter. Each stand had between 4 and 8 trees and was replicated 6 times (4 mono- and 4 mix-species stands × 6 plots = 48 stands). The area of each stand was determined by creating Voronoi-polygons (Mead, 1966) around each tree composing a stand and calculating the total stand area using Quantum GIS (QGIS Development Team, 2012). The stand area ranged from 68 to 313 m^2. Our stand selection criteria were: (a) each stand should have similar tree species composition surrounding it, (b) all trees in a stand should have a diameter at breast height (dbh) larger than 10 cm and a well-developed crown as an indicator that they actively grew, and (c) initial field survey must show similar soil characteristics (e.g., color, field test for soil texture, slope, drainage, among others). Following stand selection, a detailed soil chemical analysis was conducted (see Section 2.4 below).

2.3. Biomass production

Stem diameter increment was measured using dendrometer bands (D1, UMS GmbH, München), which were permanently installed two months prior to the first measurement and were measured three times from July 2012 to July 2013. We expressed stem diameter growth as relative growth rate, i.e., stem diameter increment per diameter at breast height (dbh). Analysis of relative