



Tree species effects are amplified by clay content in acidic soils

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ARTICLE INFO

Keywords:

Earthworms

Soil acidity

Soil process domain

Tree species effects

Humus type

ABSTRACT

The tree species composition of many forests in western and central Europe has changed considerably over the last century, as large areas of mixed deciduous forests were replaced by conifer plantations. In this study, we aim to evaluate whether conversion of mixed broadleaved forest to Norway spruce (*Picea abies*) on the acidic soils of the Gaume forest (southern Belgium) affected soil quality in terms of soil acidity, exchangeable calcium and aluminium, humus type and earthworm communities, and determine whether this effect is mitigated or amplified by an edaphic gradient in clay content. In this ancient deciduous woodland, stands were partly converted from mixed deciduous forest to Norway spruce monocultures 30–60 years ago. A twin-plot setup was established, where we sampled pairs of adjacent deciduous and Norway spruce plots along a gradient in clay content varying between 3 and 34%. This design allowed to evaluate the effects of soil type and conversion independently. In the deciduous plots, forest type ranged from mixed oak-hornbeam forest to oak-beech forest. The first has a higher clay content, higher exchangeable calcium, mull humus type, low forest floor mass and the presence of burrowing earthworms (endogeics), while the latter is characterised by high forest floor mass and presence of only litter-dwelling earthworms (epigeics), respectively. Our results provide evidence that the natural biogeochemical gradient converges to a narrow and acid range after conversion. When comparing Norway spruce plots with adjacent broadleaved stands, topsoil pH, calcium concentrations and total earthworm biomass were significantly lower, endogeic and epi-aneic earthworms were mostly absent, and the exchangeable aluminium was significantly higher. Contrary to the current paradigm, the impact of conversion in these acidic soils is largest for the stands with the highest clay content, where the larger exchange capacity allows greater accumulation of exchangeable aluminium when pH becomes sufficiently low. These findings have important implications for forest management: for systems near a threshold in soil process domain, it is important to realise that the sites with higher CEC and more favourable pH-values are the ones that will have larger trajectories and deteriorate the most upon acidification. Hence restoring such stands into more natural deciduous or mixed forest may become increasingly difficult.

1. Introduction

Temperate forests provide a multitude of provisioning, regulating and cultural ecosystem services. Forest management practices avoiding soil degradation are a precondition for a sustainable supply of these services. One of the basic forest management decisions is the choice of overstorey tree species, as it triggers a chain of interactions between vegetation, soil chemical and physical properties and soil biological

activity (Zinke, 1962; Van Breemen, 1993; Muys, 1995; Reich et al., 2005; De Schrijver et al., 2012). The tree species composition of many forests in western and central Europe has been changed considerably since the 19th century: large areas of mixed deciduous forests were converted into conifer plantations offering faster growth of highly demanded wood products (Klimo et al., 2000. Spiecker et al., 2004). Coniferous tree species are generally considered to negatively affect site quality, as their slow-decomposing litter, high interception of

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atmospheric pollutants and higher amounts of root exudates have an acidifying effect on the forest soil (Binkley and Valentine, 1991; Ranger and Nys, 1994; Augusto et al., 2002; Vesterdal et al., 2008). Due to this acidification, the availability of macro-nutrients and so-called base cations (i.e. potassium, calcium and magnesium) decreases, while proton and aluminium concentrations may rise to toxic levels with negative effects on tree health and productivity and above- and belowground biodiversity (Nordström and Rundgren, 1974; Grossi and Brun, 1997; Wever et al., 2001; Eggleton et al., 2009; Calvaruso et al., 2011).

Soil type has been shown to modulate tree species effects, but contrasting views have emerged in literature: some studies report a greater expression of species effects on poor sites, while others obtained inconclusive or opposite results (Finzi et al., 1998; Ste-Marie et al., 2007; Augusto et al., 2015; Raulund-Rasmussen and Vejre, 1995; Forrester et al., 2013). In most of these studies, soil texture was used as the main proxy for site quality as it is relatively easy to measure or can be deduced from soil maps. Moreover, in soils with similar lithologies, clay content is a measure for the pH-independent cation exchange capacity (CEC) of a soil, and is largely unaffected by biotic drivers and management (Binkley and Fisher, 2013). These studies however fail to consider what happens if the buffer capacity provided by the exchange complex eventually runs out. Indeed, acid buffering capacity of soils is typically characterised by biogeochemical equilibria with considerable pedogenic inertia (so-called ‘buffer ranges’ or ‘soil process domains’; Ulrich and Sumner, 1991; Vitousek and Chadwick, 2013), but thresholds are steep when one buffering mechanism is exhausted and replaced by another (Chadwick and Chorover, 2001). Many temperate forests at risk for acid-induced soil deterioration have a pH range close to the threshold between the cation-exchange buffer domain and the aluminium-mediated buffer domain, corresponding to a transition from mull to moder/mor humus systems (Muys and Lust, 1992; Ponge, 2003; Andreetta et al., 2016). Studying tree species effects in forest systems near this pedogenic threshold can therefore provide vital new insights in the dynamic relationship between clay content and soil acidification upon conversion, provided that effects of tree and soil properties can be addressed independently. The latter is not straightforward as forest managers usually adapt their choice of overstory species to site fertility.

Moreover, soil biodiversity may have a much larger influence on soil quality than previously assumed (Hale et al., 2005; Lavelle et al., 2006; Mueller et al., 2015; Filser et al., 2016), as the complexity of the soil food web may dampen the effects of external drivers (Srivastava et al., 2009; Gessner et al., 2010; Morriën et al., 2017) and burrowing soil fauna actively redistribute nutrients over the soil profile (Bohlen et al., 2004; Briones, 2014; Lavelle et al., 2006). Earthworms are considered key ecosystem engineers for litter decomposition and soil bioturbation that can be strongly affected by increased acidity (Muys and Granval, 1997; Schelfhout et al., 2017). Conversion-induced ecological shifts in earthworm communities are therefore likely to affect the subsoil-topsoil-litter-layer continuum essential to forest nutrient cycles (Ponge, 2003; Ste-Marie et al., 2007; Dawud et al., 2016).

Hence, in this study, we aim to evaluate the effect of conversion to Norway spruce (*Picea abies*) on soil pH, available calcium, available aluminium, litter layer characteristics and earthworm species along a gradient in soil clay content in the ancient deciduous forest of the Gaume (southern Belgium). Although all soils of this vast forest complex are relatively sandy, a difference in marl content of the Jurassic parent material resulted in a gradient of soil clay content varying from almost 0 to over 30%. Pedogenic weathering has strongly depleted base cations in all soils: most have a pH and base saturation in the aluminium-buffer range, while only the ones with the larger clay content remain in the cation-exchange soil process domain prior to conversion (Verstraeten et al., 2013; Desie et al., 2017). Small patches of Norway spruce have been introduced in this forest ca. four decades ago, allowing a twin-plot setup with one plot in a mixed deciduous forest stand and one in an adjacent stand of Norway spruce. Twin-plots were

established along the lithological gradient, allowing to study conversion and soil effects independently.

2. Materials and methods

2.1. Study site

The study area is part of a 200 km² forest complex in southern Belgium (Gaume region, centre 49° 37' N, 5° 33' E). It is considered an ancient forest, defined as being continuously forested since at least 1777 (Hermly et al., 1999). The deciduous forest is uneven-aged and dominated by *Carpinus betulus* (percentage of total tree cover in the studied deciduous plots: 36%), *Quercus robur* (27%) and *Fagus sylvatica* (22%). In this matrix of deciduous forest, patches of 2–15 ha were clear-cut and replanted with monoculture stands of Norway spruce 30–50 years ago, creating small islands of coniferous forest in the deciduous forest matrix. The elevation of the study area ranges between 250 and 360 m above sea level, the mean annual temperature is 8.7 °C, and the mean annual precipitation of 873 mm is evenly distributed throughout the year. The site's parent material is a Jurassic calcareous sandstone (grès calcaire) with variable marl content, which is part of a cuesta landscape adjacent to the Ardennes at the northern rim of the Paris basin. Most profiles contain variable – albeit small – additions of Quaternary aeolian loess. Soil texture therefore varies from sand to loam, and mainly differences in clay content determine the intrinsic buffer capacity and CEC of the soils. Reference Soil Groups include Luvisols, Alisols and Cambisols (IUSS Working Group WRB, 2015). Soil profiles are at present completely devoid of free carbonates and have low natural weathering to replenish base saturation (Bouezmarni et al., 2009). A total of 80 plots, consisting of 40 broadleaved/Norway spruce pairs, were selected along the gradient in clay content in a stepwise approach. First, Norway spruce patches in the forest complex were identified on aerial photographs and topographical maps, avoiding stands at the outer edges of the forest and taking into account information from the soil texture map of the Service Public de Wallonie (2007) and the vegetation map of Dethioux and Vanden Berghen (1966). Complemented with field observations, Norway spruce stands were subsequently selected to have similar stand age, and to have a surrounding broadleaved matrix with similar elevation and slope orientation maximizing comparability in soil type, forest history and original tree species composition.

For each location, a twin-plot design was set out, with a square plot of 10 m × 10 m in each neighbouring stand (Fig. 1). The centre of each plot was 30 m (approximately one tree height) from the border into both the deciduous and coniferous stands to balance the trade-off between minimizing spatial variation between plots and minimizing mutual influences between stands.

2.2. Data collection

In June 2009, the percent crown cover of all species in the tree layer was recorded. Soil samples were taken at three depth intervals (0–5 cm, 10–20 cm and 25–35 cm) using a soil corer. For each depth interval, four samples were taken in each stand (one randomly in each quadrant of each plot) and pooled into a composite soil sample (Fig. 1). The soil samples were dried at 40 °C until constant mass and analysed for pH (extraction in 1 M KCl, 1:5 suspension, ion-specific electrode; ISRIC and FAO, 2002; ISO 10390:1994) at the three depths and exchangeable concentrations of Ca²⁺ and Al³⁺ (extraction in 0.1 M BaCl₂, 1:20 suspension and measurement with flame atomic absorption spectrophotometry, SpectraAA-220, Varian; Hendershot and Duquette, 1986; NEN-EN-ISO 11260:2011) for the 0–5 cm and 25–35 cm layer. The soil texture of the 10–20 cm depth interval (expressed in percentages clay, sand and loam) was determined by laser granulometry (Malvern Mastersizer S). The litter (L), fragmentation (F) and humus (H) layer of the forest floor were collected separately in four squares of 20 × 20 cm² in

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