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Short communication

What controls the concentration of various aliphatic lipids in soil?

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ABSTRACT

The composition of lipids in soil offers clues to the origin and stabilization of soil organic matter, but the descriptive nature of prior research makes quantitative interpretations problematic. We statistically evaluated potential predictors of the concentrations of aliphatic lipids in mineral soils beneath plantations of 11 tree species. Lipids were recovered from leaves, roots, and soils from each plantation using base hydrolysis and solvent extraction. Nearly 70% of the variation in individual soil lipid concentrations was explained by lipid concentrations in tree leaves and roots. Less variation in soil lipid concentrations was attributed to lipid properties such as functional group composition, chain length, and whether a lipid was most abundant in leaves or roots. Surprisingly, although the chemical and biological compositions of soils were highly variable for plantations of different tree species, the tree species identity had little impact on soil lipid concentrations and the effects of lipid properties were similar for all plantations.

Main text

There is considerable variability in the abundance and composition of extractable and hydrolyzable lipids in soil (Bull et al., 2000; Jansen et al., 2006; Naafs et al., 2004; Nierop et al., 2006; Otto et al., 2005; Quenea et al., 2004; Rumpel et al., 2002), but it is difficult to *quantitatively* and *causally* relate this variability to properties of lipids and soils that influence organic matter stabilization. For example, mineral soils often have relatively high concentrations of plant-derived lipids that are abundant in roots but not in leaves (Mueller et al., 2012b), but the causes of this pattern are not clear. Does this pattern arise because lipids present in roots (i.e. "root lipids") have different chemical properties, such as lipid chain length or chemical functional groups (Fig. 1) that influence lipid stabilization in soil? Or, does this pattern arise because root-derived biomolecules are preferentially stabilized in soils, regardless of their biochemical properties (Rasse et al., 2005)? Conversely, could the abundance of root-derived lipids in soils reflect an effect of soil biota, such as preferential consumption of leaf litter by anecic earthworms (Curry and Schmidt, 2006)? To address these questions and, more generally, to achieve a mechanistic understanding of soil lipid composition, studies and statistical analyses must be designed to quantify the effects of multiple factors, including lipid origin, lipid biochemistry, and various soil properties. The concentrations of individual lipids in their sources must also be accounted, otherwise selective preservation or degradation cannot be identified or quantified. Yet, such quantitative analyses have not been conducted previously.

Here, we statistically evaluate potential controls of soil lipid concentrations beneath tree plantations in central Poland (51°14.87′N, 18°06.35′E). In 2008, we sampled mineral soils (0–20 cm) in large plots of 11 temperate tree species (2–6 plots each

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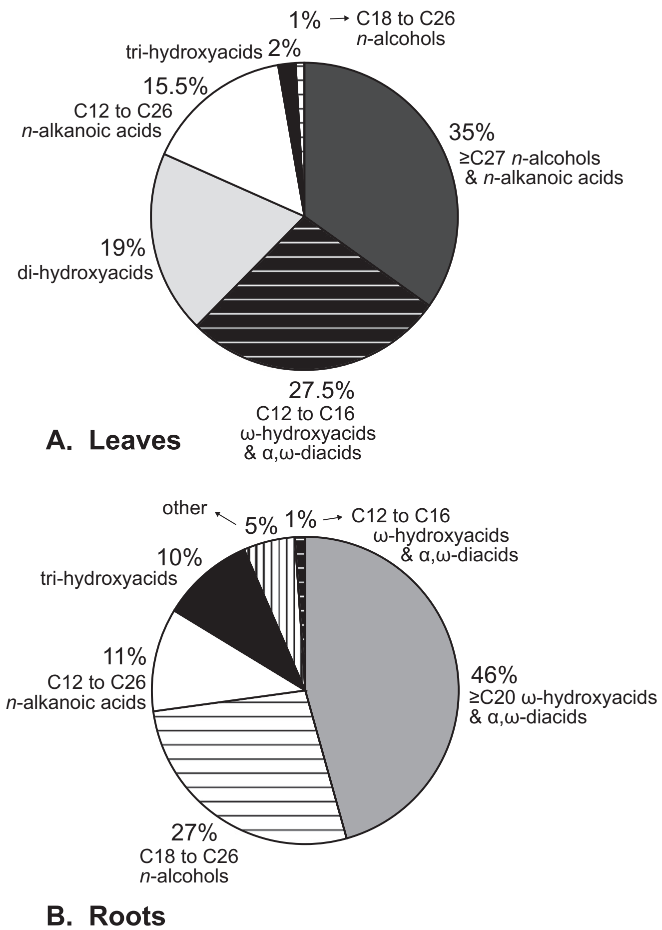

Fig. 1. The lipid chain lengths and lipid types, as defined by chemical functional groups, for aliphatic lipids that were present in soil and predominately derived from either leaves (A) or roots (B). Lipids were defined as predominately derived from leaves or from roots if they were at least 10 times more abundant in one plant organ relative to the other. Accordingly, 109 lipids were predominately in leaves and 92 lipids were predominately in roots. Each percentage is an average of data from 11 different tree species monocultures.

for *Abies alba*, *Acer platanoides*, *A. pseudoplatanus*, *Fagus sylvatica*, *Larix decidua*, *Pinus nigra*, *P. sylvestris*, *Pseudotsuga menziesii*, *Quercus robur*, *Q. rubra*, and *Tilia cordata*). Plots were planted as monocultures in 1970 and 1971 following clear-cutting of an 80-year-old *P. sylvestris* plantation and plowing to a depth of 30–60 cm. Thus, during the 118 years prior to sampling, the majority of plant inputs in a given plantation could be accounted for by *P. sylvestris* and the subsequently planted tree species. Surface soils are derived from sandy glacial outwash; with one exception, the top 20 cm of mineral soil in all plots is >70% sand and <10% clay (mostly vermiculite and kaolinite). Notably, plantations of different tree species are widely divergent with respect to soil chemistry and the composition of soil biota (Hobbie et al., 2006; Mueller et al., 2012a; Reich et al., 2005), two factors that could influence the composition of soil lipids (Bull et al., 2000; Crow et al., 2009; Nierop and Verstraten, 2003).

Lipids from soil samples (sieved to 2 mm), green leaves, and fine roots (<2 mm diameter) of each tree species were recovered in hexane and ethyl acetate extracts following hydrolysis with methanolic potassium hydroxide. Derivatized lipids were identified and quantified by GC–MS using extracted ions associated with each analyte and those of 32 external standards. Focal lipids included a range of *n*-alkanoic acids (C_{12} up to C_{30}), α,ω-diacids (C_9 up to C_{26}), *n*-alcohols (C_{12} up to C_{30}), ω-hydroxyacids (C_8 up to C_{26}), and di- and trihydroxyacids, encompassing monomers of cutin, suberin, and plant waxes (Kolattukudy, 2001). Averaged across all plantations, the total masses of quantified lipids in leaves, roots, and soils were 39.9, 35.4, and 29.0 mg g^{-1} C. Experimental and procedural details and a list of analytes were shown in Mueller et al. (2012b). Statistical analyses were performed using log-transformed lipid concentrations and type III sums of squares, such that the explanatory power of each predictor was evaluated *after* accounting for effects of the other predictors (Hector et al., 2010).

According to multiple regression (Fig. 2), nearly 70% of the variability in soil lipid concentrations could be attributed to two factors: (i) the concentrations of lipids in leaves and roots of the tree species *currently present* in each plantation and (ii) the concentrations of lipids in leaves and roots of the tree species that *previously occupied* all plots (*P. sylvestris*). In one-factor models, each of these predictors alone accounted for ca. 55% of the variability in soil lipid concentrations (Table 1; some explanatory power was shared because the two predictors were positively correlated: $P < 0.0001$, $R^2 = 0.42$, $n = 379$). Thus, some of the extractable and hydrolyzable lipids in soils are likely derived from *P. sylvestris* trees that have been absent for nearly 40 years. The very strong relationship between the concentrations of lipids in soil and in plant tissues suggests that extractable and hydrolyzable plant lipids are retained in soil by a process that operates somewhat independently of lipid chemical properties and origin (e.g. occlusion of plant litter within soil aggregates).

To assess whether other factors could account for variation in soil lipid concentrations that was not explained by leaf and root lipid concentrations, we added the following predictors to the model: the location and type of chemical functional groups (*lipid type*), the number of carbon atoms in each lipid (*chain length*), the

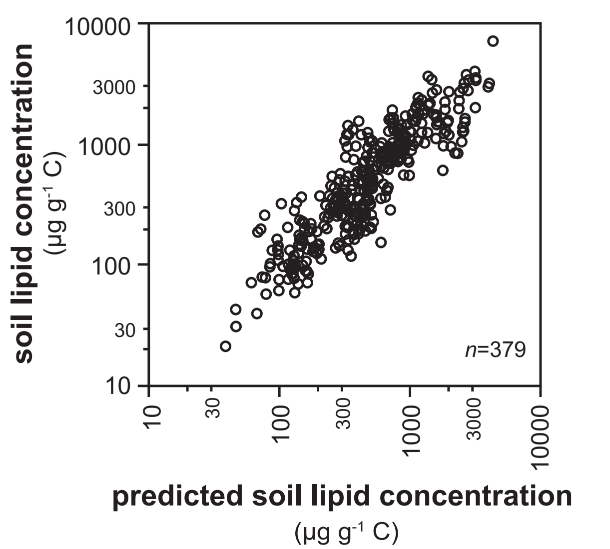

Fig. 2. Biplot of actual soil lipid concentrations (*Y*-axis) vs. soil lipid concentrations predicted by a multiple regression model that contained two factors: (i) the sum of lipid concentrations in leaves and roots of the tree species currently present in each plantation and (ii) the sum of lipid concentrations in leaves and roots of the tree species that previously occupied all plantation plots (*Pinus sylvestris*). Note the $\log_{10}$ scale on the *X* and *Y*-axes. The regression model explained 69% of the variability in untransformed soil lipid concentrations (according to a linear fit of the actual values vs. the predicted values). Each circle represents a single lipid that was observed in soil *and* in tree leaves or roots from the present *and* previous plantations. Each lipid could be represented up to 10 times, once for each tree species. Soil lipid data from the current *P. sylvestris* plantation were excluded. We also excluded data in 36 instances for which a lipid observed in soil was not quantified in plant tissues of both the current plantation species and *P. sylvestris*.