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The influence of vegetation on soil water repellency-markers and soil hydrophobicity

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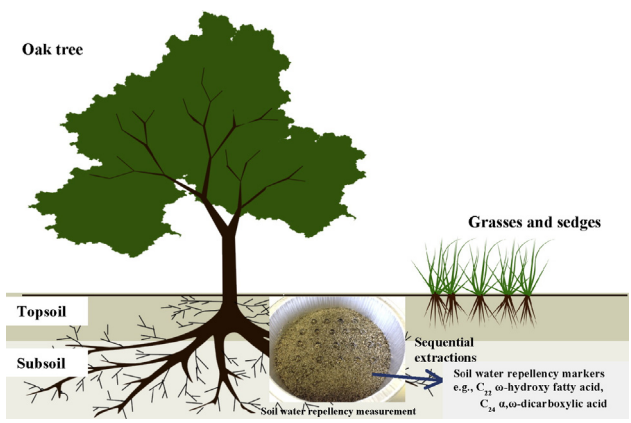
HIGHLIGHTS

- Covering plant species primarily influences soil water repellency and its markers.
- Single long-chain soil water repellency (SWR)-markers positively correlate to SWR.
- Root-derived ω-hydroxy fatty acids and α,ω-dicarboxylic acids predict SWR well.
- The corresponding biomarkers of the SWR predictors are abundant in grass roots.
- Grass roots mainly contribute to the organic matter in topsoils leading to strong SWR.

GRAPHICAL ABSTRACT



Graphical abstract shows that in an ecosystem with oak, grasses and sedges, the roots of various plant species distribute differently in the top- and subsoils. The soil water repellency was measured using water drop penetration time test. The soils were extracted sequentially and soil water repellency markers, e.g., C_{22} ω-hydroxy fatty acid and C_{24} α,ω-dicarboxylic acid, were observed mainly derived from plants.

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ABSTRACT

Soil water repellency (SWR) markers are defined as hydrophobic compounds in soil causing SWR and are mainly derived from plants. Previous studies have shown the types and abundance of SWR-markers in soils. However, how these SWR-markers are exactly related to SWR and their origin is poorly understood. This study aims to understand the relationship between SWR-markers, vegetation type and cover and SWR for a simple sandy soil ecosystem, consisting of oaks with sedge and six grass species. All the soil (at different depth) and vegetation samples were collected in the field along a 6 m transect, starting from an oak tree. Further along the transect grasses and sedges became more abundant. Free and ester-bound lipids from soils and plant leaves/roots were obtained using a sequential extraction method and identified by gas chromatography–mass spectrometry. Significant linear correlations were found between the main soil characteristics, such as total organic carbon content, and SWR. Single long-chain ($>C_{20}$) SWR-markers derived from both plant leaf waxes and roots positively related to SWR. Both ester-bound ω-hydroxy fatty acids and C_{22} and C_{24} α,ω-dicarboxylic acids were predominantly present in the grass roots, but to a lesser extent in the roots of oak and sedge. These suberin-derived ω-hydroxy fatty acids and α,ω-dicarboxylic acids characteristic of roots could well predict the SWR. Additionally, the SWR

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predictors abundantly present in the soils matched well with high concentrations of the corresponding biomarkers in the dominant vegetation species that covered the soils. Our analyses demonstrated that grass roots influenced SWR more due to their more substantial contribution of organic matter to the topsoils than oak roots. This led to a stronger SWR of the soils covered with grass than those covered with oak vegetation.

1. Introduction

As one of the common and important soil properties, soil water repellency (SWR) can limit water flow in soils and potentially trigger soil erosion (DeBano, 1981, 2000; Jungerius and De Jong, 1989; Ritsema et al., 1993; Dekker and Ritsema, 1994; Doerr et al., 2000, 2007; Zavala et al., 2009, 2014). This phenomenon occurs in different types of soils at various depths under a wide range of vegetation species, including mosses (Lichner et al., 2007), herbs (Llewellyn et al., 2004; Doerr et al., 2005), grasses (Dekker and Ritsema, 1996; Ritsema and Dekker, 1998), shrubs (Verheijen and Cammeraat, 2007) and trees (Franco et al., 1995, 2000; Mataix-Solera et al., 2007; Rodríguez-Alleres et al., 2007; Hansel et al., 2008; Atanassova and Doerr, 2010; de Blas et al., 2013). It is well known that SWR is caused by hydrophobic organic compounds in soil, which are predominantly derived from vegetation (Bisdom et al., 1993; DeBano, 2000; Horne and McIntosh, 2000; Hansel et al., 2008; de Blas et al., 2010, 2013) and to a small extent from microbes (Wallis and Horne, 1992; Rillig, 2005) and those were accordingly defined as SWR-markers by Mao et al. (2014). SWR can also be caused by amphiphilic organic compounds (cf. Doerr et al., 2000), and by the actual state of the soil ranging from water repellent to wettable which is a result of the meteorological history.

Generally, water repellent soils contain more organic matter than non-water-repellent soils (Atanassova and Doerr, 2010; Mainwaring et al., 2004, 2013). The concentration of free lipids in soils under pine and eucalyptus extractable by petroleum ether had a significant positive relation with soil hydrophobicity, while those of bound lipids did not correlate with SWR (de Blas et al., 2013). Mao et al. (2015) suggested that the linear correlation between the absolute concentrations of SWR-markers and SWR most likely followed the tendency of total organic carbon (TOC) content. A higher absolute SWR-marker concentration correlates with a higher TOC, and an increase in TOC leads to a higher soil hydrophobicity. However, only little is known about the relationships between the relative abundance of SWR-markers and water repellency, as well as the vegetation origin of these SWR-markers. Although the relative amount of microbial hydrolysed suberin-derived alcohols positively related to SWR, the insignificant relation between other major hydrophobic compounds in soil and its SWR still need to be convincingly explained (Mao et al., 2015).

The degree and distribution of soil hydrophobicity under various vegetation cover and land use vary (Doerr et al., 2005, 2007; Zavala et al., 2009; Rodríguez-Alleres and Benito, 2011, 2012; Badía et al., 2013). Since vegetation is the dominant source of the input of SWR-markers into soils (van Bergen et al., 1997; Kögel-Knabner, 2002), investigating the influence of vegetation on those compounds and SWR is essential. For instance, Rodríguez-Alleres et al. (2007) found that vegetation had more influence on the persistence of SWR under eucalyptus and pine forest than under grassland and maize crops. According to Lozano et al. (2013), the stronger persistence of SWR was found under oak, while the soil under the shrub *Cistus* was non-repellent. Badía et al. (2013) compared the soils under woody plants (pine and oak) and meadow, of which the soil under pine was most repellent, while the lowest water repellent soil was found under meadow. These studies hinted at the association of vegetation types with either soil organic compounds or water repellency; however, none of them linked SWR to their vegetation origin at the molecular level.

In Mao et al. (2015) we have tested the hypothesis that it is feasible to predict SWR using vegetation cover. However, our previous research site was probably too diverse with regard to current and past vegetation composition, which led to no or only poor correlations between vegetation and SWR. It is desired to understand whether such a poor correlation is due to the ecosystem complexity or whether the link between vegetation biomarkers and those causing SWR does inherently not exist. Therefore, we focused here on a more simple system with less vegetation variety (oak, grasses and sedge) compared to the vegetation-mixed system (algae, mosses, grasses, shrubs, trees) studied previously (Mao et al., 2014, 2015) to test this hypothesis. Within the present simple ecosystem, our study aims to investigate the effects of vegetation cover on SWR in which we aim to link SWR to SWR-markers in the soil and to link these SWR-markers to their vegetation origin (leaves/roots and species). In this paper the objectives are: i) to explore at the plot scale the possible relations between the patterns of TOC and the biomass of the vegetation cover and SWR along an oak-grass-sedge transect; ii) to understand at the molecule scale the link between vegetation biomarkers and SWR-markers and to use vegetation biomarkers to predict SWR; iii) to explore the influence of vegetation origin on SWR-markers and SWR and to use vegetation cover to predict SWR. To this end we applied a sequential extraction procedure to both soils and leaves/roots of the plant cover to obtain different compound fractions and to compare the types and abundances of typical SWR-markers with vegetation biomarkers.

2. Materials and methods

2.1. Study area

The soils and vegetation sampling was conducted in the Zuid-Kennemerland National Park of the Netherlands (52°25′09″ N, 4°35′23″ E). The sampling site is scattered with common oaks (*Quercus robur*), covered by sedge (*Carex sp.*) and different grass species (Table 1). The soils were classified as Hydrophobic Arenosols (FAO, 2015). The mineral particles in the study site are of similar mineralogical composition and the texture is: clay (<2 μm) < 0.5%; silt (2–50 μm) < 3.5% and sand (>50 μm) > 96% (Eisma, 1968).

2.2. Sampling, experimental design and pre-treatment

2.2.1. Soils

To investigate a gradient of oak and the main grass species on SWR, a 6 m long transect was laid out at the aforementioned site starting from the stem of one single oak tree in the direction of a second oak tree under the tree crown. Along this transect the soils were collected at different depths with each soil sample representing one soil horizon on 23rd of August 2013 (Table 2). The soil horizons included mineral

Table 1
Vegetation distribution and sampling. Location refers to the distance to the oak tree at which the undergrowth predominantly grows and was taken for analysis.

Vegetation	Common name	Location (m)	Type of biomass	
Quercus robur	Common oak	0	Leaves	Roots
Festuca rubra	Red fescue	2	Leaves	Roots
Poa nemoralis	Wood bluegrass	4	Leaves	Roots
Phleum pratense	Timothy-grass	5	Leaves	
Agrostis stolonifera	Creeping bentgrass	2/6	Leaves	
Holcus lanatus	Tufted grass	2/4/5/6	Leaves	Roots
Carex sp.	Carex	4	Leaves	Roots

soils only, because the litter layer was hardly present as oak leaves were only sparsely found and grass leaves decompose quickly. The determination of the soil horizons from Ah to C was based mainly on differences in soil colour (cf. Mao et al., 2014), because there was little or no soil formation in the Arenosols. Prior to further analysis, all soils were oven-dried at 30 °C for 48 h. To remove plant leaf and root fragments, the soils were passed a 1.4 mm diameter sieve after drying.

2.2.2. Vegetation/plants

Along the same transect, plant samples (leaves and roots) were collected on 7th of September 2014 (Table 1). For grasses and sedge, whole plants were retrieved from soil, and subsequently leaves and roots were separated from each other. All the plant samples were freeze-dried and stored prior to further analysis.

2.2.3. Biomass collection

Besides collecting plant material for extraction procedures, vegetation was also sampled to estimate the amount of the above-ground and below-ground biomass. To collect above-ground biomass, 10 × 10 cm frames were set in the field along our transect at distances of 0.2 m, 1.0 m, 2.0 m, 3.0 m, 4.0 m, 5.0 m and 6.0 m from the oak tree. All living plants in these frames were collected, including leaves, flowers and seeds. At each location, a 10 × 10 cm frame at soil depths between 0–10 cm and 10–30 cm were used to collect all plant roots. These soil samples were oven-dried at 30 °C for 48 h and were passed over a 1.0 mm mesh-sized sieve. The residual material that did not pass the sieve were washed under running water to remove mineral particles and to obtain the roots. Before weighing, all plant tissues were dried in the oven at 70 °C for 24 h (Adema and Grootjans, 2003; Ravindranath and Ostwald, 2008).

2.3. Soil and plant analysis

2.3.1. Soil water repellency measurement

SWR measurement was performed using the water drop penetration time (WDPT) test. The method is widely known and accepted to assess the persistence of SWR (Van't Woudt, 1959; Wessel, 1988; Dekker and Ritsema, 1994). Bisdom et al. (1993) and Dekker and Ritsema (1996) described the classifications of the hydrophobicity persistence: wettable (WDPT < 5 s), slightly water repellent (5–60s), strongly water repellent (60–600 s), severely water repellent (600–3600 s) and extremely water repellent (>3600 s). SWR was determined on the sieved and dried soil samples at room temperature. The SWR values obtained in this study comprise the average WDPT of 20 individual water droplets per sample/soil.

2.3.2. Soil characterization

Soil pH was determined from a water suspension with a 1:2.5 (w:w) soil-to-water ratio (Metson, 1956) and measured by a pH meter (Consort C830). Inorganic carbon in soils was removed using 1 M HCl (Van Wesemael, 1955), prior to total organic content (TOC) and total nitrogen content (TN) measurement. After decalcification, all soils were grinded into powder using planetary ball mills (Pulverisette®5, Fritsch). TOC and TN measurements were conducted using a CNS analyser (Fisons Instrument NA1500). The maximal error of the TOC and TN measurements was 6 and 3%, respectively.

2.3.3. SWR-marker extraction and work-up

In total 21 soil samples from different horizons were collected (Table 2). The TOC contents of 21 soil samples were normally distributed at the 95% confidence interval. The average TOC content is 16.0 mg/g soil with a standard deviation of 20.4 mg/g soil. Some of the sampled soils had similar TOC contents; therefore, based on the TOC distribution in combination with the position along the transect studied, we selected 12 soil samples from different horizons with substantially different TOC contents and SWR level for characterization of SWR-markers (Table 2).

To distinguish free and ester-bound lipids extracted from plants from the lipids extracted from soils, the terms of DCM/MeOH extractable lipids and ester-bound lipids were used to define plant lipids. Free lipids from the soils and the plant samples were obtained by Soxhlet extraction with dichloromethane/methanol (DCM/MeOH) (9:1, v:v) for 24 h to obtain the so-called D fractions from soil (Mao et al., 2014) and DCM/MeOH extractable lipids of plants, respectively (Bull et al., 2000; Nierop et al., 2005). After air-drying, the soil residues were re-extracted using isopropanol/ammonia solution (7:3, v:v, 32% ammonia solution) for 48 h. From the IPA/NH_3 extracts DCM/MeOH soluble lipids (the so-called AS fraction) and a residual DCM/MeOH insoluble part (AI fraction) were obtained. The SWR of the residual soils dramatically decreased and the majority of them became even wettable after ester-bound lipids were removed by IPA/NH_3. The AI fractions and air-dried residual leaves and roots were subsequently *trans*-methylated

Table 2
Soil profiles characteristics.

Soil label	Location[a] (m)	Soil horizon	Soil depth (cm)	pH	TOC (mg/g soil)	TN (mg/g soil)	WDPT[b] (s)	Log_{10} WDPT	Water repellency class[c]
WRO-11	0.2	Ah1	0–4	4.7	55.3	3.2	2000 ± 330	3.30 ± 0.14	Severe
WRO-10	0.2	Ah2	4–9	4.8	12.3	0.9	3100 ± 590	3.49 ± 0.17	Severe
WRO-9	0.2	B	9–14	6.5	2.4	0.4	700 ± 240	2.85 ± 0.31	Severe
WRO-3	1	Ah1	0–3.5	4.9	23.4	1.3	1800 ± 580	3.26 ± 0.29	Severe
WRO-2[d]	1	Ah2	3.5–9	5.4	9.9	0.7	1500 ± 860	3.16 ± 0.59	Severe
WRO-1	1	B	9–20	6.8	2.8	0.4	1300 ± 310	3.12 ± 0.20	Severe
WRO-14[d]	2	Ah1	0–4	5.0	58.1	3.6	5900 ± 380	3.77 ± 0.05	Extreme
WRO-15	2	Ah2	4–10	5.1	12.8	1.0	6800 ± 790	3.83 ± 0.10	Extreme
WRO-13[d]	2	B	10–19	6.8	2.7	0.4	5000 ± 610	3.69 ± 0.11	Extreme
WRO-6	3	Ah	0–8	4.6	13.6	1.1	1600 ± 490	3.19 ± 0.28	Severe
WRO-4	3	B	8–20	6.7	2.8	0.4	510 ± 58	2.71 ± 0.10	Strong
WRO-5[d]	3	C	20–27	7.2	1.6	0.4	6 ± 3	0.75 ± 0.43	Slight
WRO-16[d]	4	Ah1	0–2	5.0	79.2	5.2	3500 ± 100	3.54 ± 0.03	Severe
WRO-17[d]	4	Ah2	2–8	5.6	17.0	1.2	2200 ± 240	3.33 ± 0.10	Severe
WRO-18[d]	4	B	8–20	5.5	3.5	0.5	120 ± 45	2.09 ± 0.33	Strong
WRO-19[d]	4	C	20–30	7.4	1.6	0.4	413 ± 82	2.62 ± 0.17	Strong
WRO-8[d]	5	Ah	0–6	4.6	29.2	2.1	3400 ± 240	3.53 ± 0.06	Severe
WRO-7	5	B	6–23	6.02	4.2	0.5	3500 ± 310	3.55 ± 0.08	Severe
WRO-20[d]	6	Ah	0–6	5.4	15.2	1.2	4100 ± 570	3.62 ± 0.12	Extreme
WRO-21[d]	6	B	6–20	7.3	3.0	0.5	2200 ± 1100	3.33 ± 0.47	Severe
WRO-24[d]	6	C	20–30	7.7	1.2	0.3	3 ± 1	0.50 ± 0.21	Wettable

[a] Location refers to the distance from the starting oak tree.
[b] The average WDPT of 20 individual water droplets; the errors are standard deviations based on the measurement of these water droplets.
[c] Based on Bisdom et al. (1993).
[d] Soil horizons subjected to SWR-marker analysis.

with BF_3-MeOH at 70 °C for 16 h (Riederer et al., 1993) to release ester-bound lipids. At the end of the treatment Millipore water (0.5 ml) was added to the mixture to neutralize the residual BF_3-MeOH. Subsequently, DCM was added to extract the released lipids from the aqueous layer, which was repeated for three times.

All three fractions (D, AI and AS) from soil samples and extractable and ester-bound lipids from plant samples were re-dissolved in DCM/MeOH (9:1), passed through a Na_2SO_4-filled column to remove water and were dried using a nitrogen stream. All the D and AS fractions and DCM/MeOH extractable lipids of plants were methylated by diazomethane (CH_2N_2). Aliquots of all the fractions were eluted over a small silica gel 60 (0.063–0.2 mm diameter, 79–230 mesh) column with ethyl acetate. The aliquots were dried under a gentle nitrogen stream and were silylated using *N*,*O*-bis (trimethylsilyl) trifluoroacetamide (BSTFA) in pyridine at 60 °C for 20 min and re-dissolved in ethyl acetate to concentration of 1 mg/μl before further analysis.

2.3.4. GC and GC–MS analyses

The analysis of derivatised extracts was performed on a gas chromatography (GC) (HP 6890 Series). The GC was fitted with a flame ionisation detector (FID) and a CP-Sil 5 CB capillary column (30 m length, 0.32 mm diameter, 0.10 μm film thickness, Agilent Technologies). The carrier gas was helium with a constant pressure (100 kPa). After injection of samples, the oven was heated from an initial temperature of 70 °C to 130 °C at a rate of 20 °C/min, and then to 320 °C at 4 °C/min, and finally held at 320 °C for 20 min.

Extracts were analysed by gas chromatography–mass spectrometry (GC–MS) using a Thermo Trace GC Ultra connected to Finnigan Trace DSQ mass spectrometer with a mass range *m*/*z* 50–800 using helium as the carrier gas with a constant flow rate at 1.0 ml/min. The GC–MS used the same temperature programme as for GC-FID analysis and was equipped with the same capillary column.

The quantification of compounds was carried out by peak area integration using a known amount of squalane as an internal standard added to extracts prior to GC–MS analysis. The compounds were identified by mass spectra using a NIST library. Combined with spectral interpretation and information on retention timer and comparison with literature data where required.

2.3.5. Statistical data analysis

To determine the correlation between soil TOC content, the concentrations of SWR-markers and the persistence of SWR, simple linear regression was applied to the data of soil characteristics and SWR-markers. Due to the large number of SWR-markers, a clear link between SWR-markers and the persistence of SWR would be difficult to obtain. Therefore we have clustered the individual behaviours by using principal component analysis (PCA), to explore the possible associations among SWR-markers at both grouped and individual levels. Together with the outcome of linear regression PCA was used to analyse the relationship between SWR-markers, their plant origins and SWR.

3. Results and discussion

3.1. Plot scale

We investigated the mechanism of SWR by relating total organic carbon (TOC) content in soil to the SWR of all soils. The severity of water repellency of all the soils is between wettable to extremely water repellent. A clear relation was also found between the TOC content and the degree of SWR. For example, the severely repellent soil WRO-16 from Ah1 horizon at 4.0 m contained the highest TOC content, while the smallest TOC content was found in the soil WRO-24, which was the only wettable soil (Table 2). Log_{10} TOC had a positive relationship with SWR (log_{10} WDPT) ($r = 0.626$, $p = 0.002$) (Fig. 1). This correlation is not strong but significant ($p < 0.05$). The moderate correlation between TOC content and SWR was due to the different above- and below-ground biomass distribution and resulting in a different input of TOC to the topsoil and subsoil, respectively. Our results are in agreement with those of Scholl (1971) and Zavala et al. (2009), who also showed a significant relationship between soil organic matter (SOM) content and SWR and confirm our earlier findings (Mao et al., 2014, 2015). By contrast, no significant relation between TOC content and SWR was reported for sandy soils by Dekker and Ritsema (1994) and Doerr et al. (2005). A possible explanation for these latter observations is that, although the TOC content quantitatively represents the abundance of SOM, the composition and quality of TOC is a more important factor in determining SWR persistence (Zhang et al., 2004; Cosentino et al., 2010). Since lipids are only a fraction of TOC, other organic fractions may also influence SWR. However, the SWR dramatically decreased after lipids were extracted from soils by IPA/NH_3, and therefore we considered these extractable compounds as the main cause of SWR in the present study. The sandy soils tested in Doerr et al. (2005) were from different ecosystems with differing climate and various vegetation types. A complex system may complicate the relations between TOC content and SWR. This is the reason why we focus on a relatively simple ecosystem with only a few plant types. The primary input of organic compounds in soils is predominantly from plants, while a minor part is derived from microorganisms (Kögel-Knabner, 2002). For that reason, vegetation is closely related to the distribution of organic carbon in soils. Subsequent microbial transformation of plant residues leads to predominantly microbial-derived organic matter. By contrast, based on the composition of the SWR-markers, the contribution of microbial compounds to these markers is very small and mainly derived from plants (Mao et al., 2014). However, the role of microbes is probably vital for SWR as many SWR-markers are clearly the result of microbial reworking, i.e. microbial hydrolysis of suberin.

As above and below-ground vegetation biomass is the main source of soil organic carbon it is expected that vegetation cover may be related to TOC and the degree of SWR. Therefore, we analysed the patterns of TOC content and SWR levels in all soils along the transect (Fig. 2). For both the topsoils and the subsoils, neither the TOC nor the SWR significantly related to the distance from the oak tree, revealing that oak is not the main resource contributing to soil organic carbon. Depending on the leaf and root distribution (Materechera et al., 1992; Nepstad et al., 1994), plants will deliver organic carbon to the top- and subsoils differently. As a result, in our case, we did not find a good correlation between the TOC and SWR of the topsoils (0–10 cm depth) and the subsoils (10–30 cm depth), respectively. For our study site, the contribution of oak leaves to above-ground biomass will be neglected as, remarkably, no leaf fragments were observed on or in the topsoils. The oak leaves in the litter layer were likely quickly removed by wind, consumed by animals or decomposed by microorganisms as only few fragmented oak leaves were observed being mixed with the topsoils. Since we focused on the lipid fraction being the main cause of SWR, fluxes of organic matter input and mineralisation were not assessed. In addition, the relative input of leaves and roots to the total SOM stock is not an important variable as we use SWR-markers derived from leaves and roots to assess their impact on SWR. As a consequence, the above-ground biomass here was composed of the leaves of living grasses, sedges and some mosses only. With respect to the below-ground biomass, plant roots were found mainly in the top 10 cm soil interval, where grass and sedge roots were predominant and densely distributed. This clearly showed that the amount of root biomass is largest close to the soil surface (cf. Jeffrey, 1987). In the deeper soil interval (10–30 cm), roots from grasses and sedges were hardly observed and instead oak roots dominated. This implies that grasses and sedge contribute more to the topsoil TOC, while oak roots contribute more to the subsoil TOC.

Although it is reasonable to assume that more plant biomass contributes more organic matter to soil, the TOC of topsoils did not show correlation with either above-ground ($p = 0.62$) or below-ground ($p = 0.26$ for 0–10 cm depth, $p = 0.74$ for 10–30 cm depth) biomass

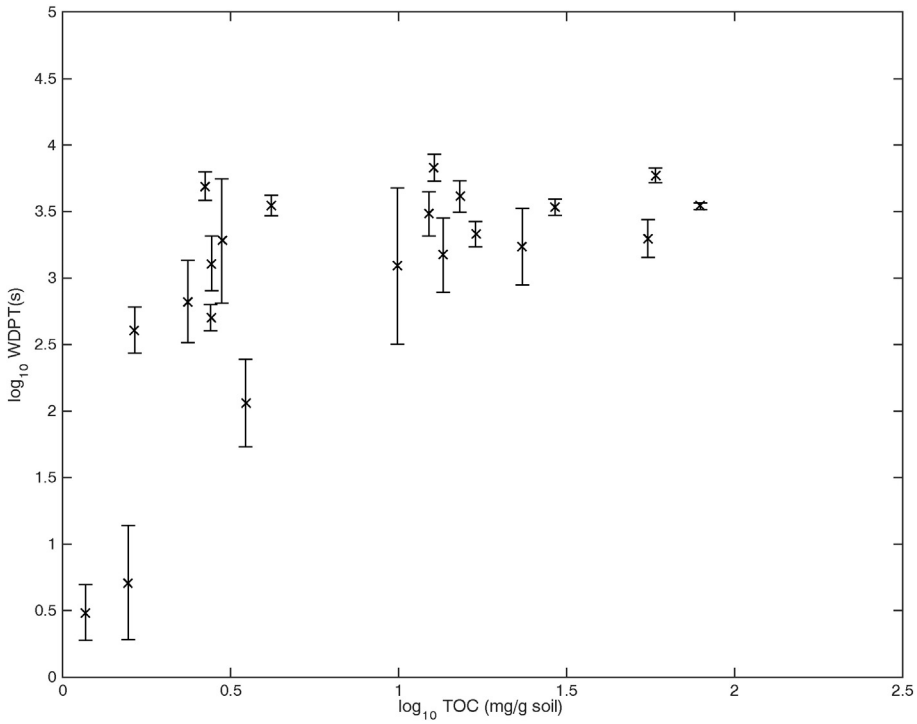

Fig. 1. WDPT as a function of TOC ($r = 0.623$, $p = 0.003$). Error bar represents standard deviation.

at the same location. A series of factors impacting plant growth or soil carbon can explain the reason of the lack of a correlation between the TOC content and above- or belowground biomass observed for the topsoils. For instance, heterogeneously distributed soil moisture and nutrients can largely affect not only plants but also the population and activities of microorganisms in soils (Lee and Jose, 2003), which are the dominant consumers of soil organic matter (Holtkamp et al., 2011). By contrast, the TOC of the B soil horizons (Table 2) had a positive significant relation with the amount of the below-ground biomass in the 0–10 cm soil interval ($r = 0.849$, $p = 0.016$). It is most likely that, rather than roots close to the surface, roots in the deeper soils have less impact from biotic and abiotic stress (Gregory, 2006). The abundance of the vegetation biomass may not be feasible to directly predict the SWR persistence as we found that neither above-ground nor below-ground biomass had a significant relation with SWR of both top- and subsoils. Therefore, we aim to understand the mechanism of SWR first from a more specific perspective by using SWR-markers. Those SWR-related hydrophobic compounds can evaluate the quality of soil organic matter (e.g. composition) and trace the role of different vegetation species on influencing SWR. Accordingly, the prediction

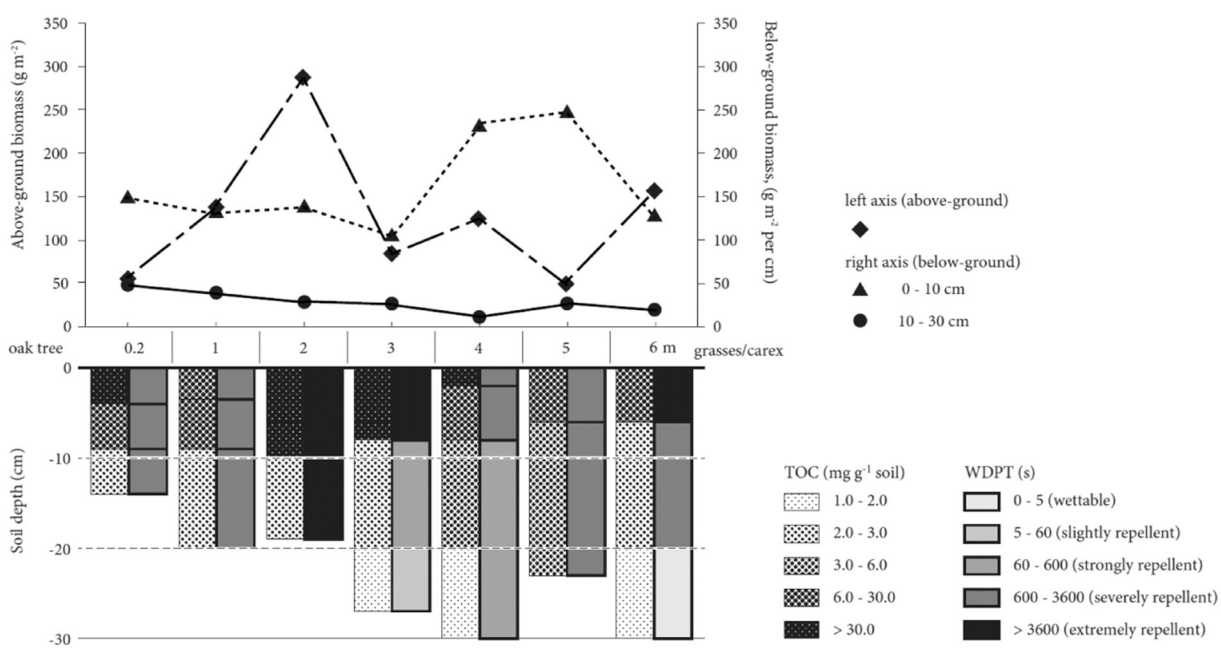

Fig. 2. Above and below ground biomass distribution (top) and soil cross-sections with TOC and WDPT (below) as a function of distance to the oak tree; the samples were collected at 0.2, 1.0, 2.0, 3.0, 4.0, 5.0 and 6.0 m from the oak tree.

and understanding of the principle of SWR needs to be extended from the vegetation level to the molecular level to quantitatively and qualitatively analyse SWR and link SWR-markers to their vegetation origin.

3.2. Molecular level

3.2.1. SWR-markers

Five main groups were found in the D fractions: (D) fatty acids, (D) alcohols, (D) alkanes, (D) ω-hydroxy fatty acids and (D) α,ω-dicarboxylic acids, of which α,ω-dicarboxylic acids were not observed earlier in such D fractions (Mao et al., 2014, 2015). Here (D), (AS), and (AI) refer to the corresponding D, AS, and AI fractions in which the specific compounds were identified, and these labels will be used in the remainder of the paper. ω-Hydroxy fatty acids and α,ω-dicarboxylic acids are likely derived from biopolymers (cutins/suberins) (Riederer et al., 1993; Franke and Schreiber, 2007; Kolattukudy, 2001), (D) C_{28} fatty acid was the most abundant fatty acid in all Ah horizons (Appendix A). Alcohols with an even-over-odd-carbon number predominance, in particular C_{24} and C_{26} alcohols, were abundant in all topsoils and in three subsoils (WRO-13, WRO-18 and WRO-19). The long-chain *n*-alkanes in the D fractions were all odd-carbon numbered. The C_{29} alkane, a typical biomarker of higher plant leaves (Bull et al., 2000; Nierop et al., 2006), dominated in most soils, except WRO-2, WRO-17, WRO-5, WRO-18 and WRO-24. For all soils, C_{24} was the most abundant ω-hydroxy fatty acid; the concentration of C_{22} ω-hydroxy fatty acid was slightly lower than C_{24} to be the second most abundant in all soils. Free α,ω-dicarboxylic acids were present mainly in the topsoils and were dominated by C_{24} except WRO-2 (Ah horizon, 1.0 m) that was dominated by C_{22}. No free α,ω-dicarboxylic acids were found in WRO-21(B horizon, 6.0 m) and all C horizons. Plant roots, which contain suberins, a potential source of α,ω-dicarboxylic acids, are predominantly present in the topsoils. Compared to subsoils, topsoils contain higher levels of organic matter and oxygen which will promote microbial activity. Consequently, (D) α,ω-dicarboxylic acids are likely to be released by microbial hydrolysis to a larger extent in the topsoils than in the subsoils.

Both AS and AI fractions contained the same four main compound groups as observed in the D fractions: fatty acids, alcohols, ω-hydroxy fatty acids and α,ω-dicarboxylic acids (Appendix B and C). Except for WRO-8 (Ah horizon), the most abundant (AS) fatty acid in all soils was C_{16}. (AS) The C_{18} alcohol dominated all soils except in the topsoil WRO-8 and WRO-14. C_{22} and C_{24} were the most abundant (AS) ω-hydroxy fatty acids in all soils. Less than half of the soils contained (AS) α,ω-dicarboxylic acids, of which either C_{22} or C_{24} predominated, except WRO-14 (Ah1 horizon, 2.0 m) that was dominated by C_{16}. For the AI fractions, the concentration of (AI) C_{22} ω-hydroxy fatty acid was the highest in all soils, except for WRO-5 and WRO-21, where C_{24} was the most abundant one. α,ω-Dicarboxylic acids were relatively more abundant in the AI fractions than in the other two fractions. As they are suberin-derived compounds the origin of AI fraction is mainly suberins. α,ω-Dicarboxylic acids were relatively more abundant in the AI fractions than in the other two fractions. C_{22} and C_{24} clearly dominated the α,ω-dicarboxylic acids in all AI fractions.

A substantial number of individual SWR-markers revealed a significant positive relation with SWR ($\log_{10}$WDPT) (Table 3). Mao et al. (2015) discussed that long-chain SWR-markers did not relate to SWR, the majority of the significant correlations were found with short-chain compounds. In the D fractions, short-chain compounds did not relate to SWR but long-chain ones did. Besides (AS) alcohols (C_{20}, C_{24} and C_{30}) and (AS) C_{20} ω-hydroxy fatty acid, more alcohols and ω-hydroxy fatty acids in the AS fractions were related to SWR. Three (AI) short-chain fatty acids (C_{16}, C_{18} and C_{21}) did not relate to SWR ($\log_{10}$ WDPT) (Table 3), whereas, by contrast, they revealed a significant correlation with SWR in Mao et al. (2015). Many more long-chain AI compounds positively, significantly related to SWR in this study than in Mao et al. (2015), of which most were fatty acids, ω-hydroxy fatty acids and α,ω-dicarboxylic acids. The concentrations of all the single even-numbered alcohols found in the AS fraction had a positive correlation with SWR, suggesting that AS alcohols are better capable of predicting SWR than other compounds, which agrees with Mao et al. (2015). (D) C_{24} alcohol did not significantly relate to SWR but was found significantly relating to SWR in our previous study (Mao et al., 2015), while, by contrast, (D) C_{26} alcohol showed the opposite result. The dominating C_{24} and C_{26} alcohols in the D fractions may represent the main contribution of the leaf waxes of oak and grasses to soil, respectively (van Bergen et al., 1997; Bull et al., 2000). The significant relation between (D) C_{26} alcohol and SWR reflects that grass leaves are contributing more to SOM and will therefore influence the persistence of SWR more than oak leaves. ω-Hydroxy fatty acids (C_{22} and C_{24}) and α,ω-dicarboxylic acids are typical suberin-derived compounds occurring in plant roots (Kolattukudy, 1981, 2001). (D) α,ω-dicarboxylic acids were not observed in D fractions of soils studied previously, but in this work their presence is due to a high abundance of plant roots, especially those of grasses. It is well-known that such roots have a high turnover rate and most likely therefore they were noticed in the D fractions. All the ω-hydroxy fatty acids (C_{22} and C_{24}) and α,ω-dicarboxylic acids found in the AI fractions had a significant positive correlation with SWR demonstrating that root-derived SWR-markers are important SWR predictors. Compared to the alcohols and ω-hydroxy fatty acids in the AI fractions, many more of them present in the AS fractions significantly related to SWR. This observation strongly confirms that plant roots induce stronger water repellency in soils than leaf waxes (Mao et al., 2014).

3.2.2. PCA of grouped and individual SWR-markers

Based on PCA (Table 4), three principal components (PCs) explained in total ca. 83% of the variance in the dataset of the main SWR-marker groups, with the first two PCs explaining in total ca. 73% of the variance. The SWR-marker groups of the D and AI fractions clustered separately (Fig. 3). The factor loading of the D fraction cluster was high positive on PC 1 and negative on PC 2. The AI fraction cluster was positive on both PC 1 and 2. In particular, the positive loading on PC 1 of (AI) α,ω-dicarboxylic acid, and on PC 2 of (AI) alcohol and (AI) ω-hydroxy fatty acid were high. The groups comprising the AS fraction scattered and contained high positive loadings on PC 1 or 2, but also negative loadings. This is a result from the mixed source of the AS group, which was composed mainly of microbial hydrolysed root lipids and a minor part was derived from leaf waxes. (D) α,ω-dicarboxylic acid, (AI) ω-hydroxy fatty acid, (AI) α,ω-dicarboxylic acid, (AS) alcohol and (AS) ω-hydroxy fatty acid had positive significant correlations with SWR (Table 5). Of these five groups, (AI) ω-hydroxy fatty acid, (AI) α,ω-dicarboxylic acid and (AS) alcohol were positive on both PC 1 and 2, while (D) α,ω-dicarboxylic acid and (AS) ω-hydroxy fatty acid were high positive on PC 1 but negative on PC 2. (AS) fatty acid was the only group negatively related to SWR but insignificantly, of which the loadings of this group on PC 1 and 2 were both negative.

Since all SWR-marker groups of the D fraction and part of groups of the AI and AS groups have a high loading on PC 1, of which the D fraction representing mainly leaf waxes and the AI and AS fractions mainly originating from roots, seem to affect both the persistence of SWR. The different loadings of the D, AI and AS fractions on PC 2 reveal likely the influence of the three fractions on SWR from either leaves (D fraction and a small part from the AS fractions) or from roots (AI fraction and most of the AS fraction).

For the PCA of the individual SWR-markers (Appendix D, Table D.1), the first two PCs reflected ca. 53% of the variance. Most short-chain SWR-markers ($<C_{22}$) had a negative loading on PC 1, whereas the loadings of longer ones ($>C_{22}$) on PC 1 were positive. In a next step, we have linked the factor loadings of individual SWR-markers on PC 1 and 2 to the significant correlations between these individual markers and SWR obtained from linear regression (Table 3). We found that the SWR-markers in the D and AI fractions, which significantly relate to SWR, had high positive loadings on component 1, which suggest that PC 1 reflects leaf-derived SWR markers, similar to the interpretation of

Table 3
Linear regressions between the relative concentrations (log (μg/g TOC)) of single SWR-markers and SWR. The single SWR-markers significantly related to SWR by Mao et al. (2015) are indicated in bold. An insignificant value is presented in italics, N.O. means not observed.

SWR-marker (D fraction)	Coef.[a]	Sig.[b]	SWR-marker (AS fraction)	Coef.	Sig.	SWR-marker (AI fraction)	Coef.	Sig.
(D) C_{16} fatty acid	*−0.111*	*0.731*				**(AI) C_{16} fatty acid**	−0.281	0.377
(D) C_{17} fatty acid	*N.O.*					**(AI) C_{18} fatty acid**	−0.228	0.476
(D) C_{18} fatty acid	*−0.181*	*0.574*				**(AI) C_{21} fatty acid**	−0.209	0.515
(D) C_{21} fatty acid	*0.420*	*0.174*						
(D) C_{15} alcohol	*N.O.*							
(D) C_{17} alcohol	*N.O.*							
(D) C_{24} alcohol	*0.526*	*0.079*						
(D) C_{20} alkane	*N.O.*							
(D) C_{23} alkane	*0.530*	*0.077*						
(D) C_{24} alkane	*N.O.*							
(D) C_{20} fatty acid	0.675	0.016	(AS) C_{32} fatty acid	−0.654	0.021	(AI) C_{20} fatty acid	0.616	0.033
(D) C_{22} fatty acid	0.643	0.024	(AS) C_{33} fatty acid	−0.645	0.023	(AI) C_{22} fatty acid	0.687	0.014
(D) C_{31} fatty acid	0.732	0.007	(AS) C_{16} alcohol	0.769	0.003	(AI) C_{26} fatty acid	0.691	0.013
(D) C_{16} alcohol[c]	−0.579	0.048	(AS) C_{18} alcohol	0.776	0.003	(AI) C_{27} fatty acid	0.722	0.008
(D) C_{18} alcohol[c]	−0.732	0.007	**(AS) C_{20} alcohol**[c]	0.624	0.030	(AI) C_{28} fatty acid	0.692	0.013
(D) C_{20} alcohol	−0.899	0.007	(AS) C_{21} alcohol	0.949	0.000	(AI) C_{29} fatty acid	0.678	0.015
(D) C_{21} alcohol	−0.590	0.044	(AS) C_{22} alcohol	0.736	0.006	(AI) C_{30} fatty acid	0.651	0.022
(D) C_{26} alcohol	0.621	0.031	**(AS) C_{24} alcohol**[c]	0.801	0.002	(AI) C_{34} fatty acid	0.782	0.003
(D) C_{28} alcohol	0.683	0.014	(AS) C_{25} alcohol	0.662	0.019	(AI) C_{18} ω-hydroxy fatty acid	0.577	0.049
(D) C_{25} alkane	0.613	0.034	(AS) C_{26} alcohol	0.740	0.006	(AI) C_{22} ω-hydroxy fatty acid	0.738	0.006
(D) C_{20} ω-hydroxy fatty acid	0.628	0.029	(AS) C_{28} alcohol	0.867	0.000	(AI) C_{24} ω-hydroxy fatty acid	0.677	0.016
(D) C_{22} α,ω-dicarboxylic acid	0.651	0.022	**(AS) C_{30} alcohol**[c]	0.646	0.023	(AI) C_{16} α,ω-dicarboxylic acid	0.671	0.017
(D) C_{24} α,ω-dicarboxylic acid	0.656	0.021	(AS) C_{16} ω-hydroxy fatty acid	0.725	0.008	(AI) C_{18} α,ω-dicarboxylic acid	0.630	0.028
			(AS) C_{20} ω-hydroxy fatty acid[c]	0.694	0.012	(AI) C_{20} α,ω-dicarboxylic acid	0.771	0.003
			(AS) C_{22} ω-hydroxy fatty acid	0.644	0.024	(AI) C_{22} α,ω-dicarboxylic acid	0.804	0.002
			(AS) C_{24} ω-hydroxy fatty acid	0.707	0.010	(AI) C_{24} α,ω-dicarboxylic acid	0.840	0.001
			(AS) C_{26} ω-hydroxy fatty acid	0.724	0.008	(AI) C_{26} α,ω-dicarboxylic acid	0.744	0.006

[a] Linear correlation coefficient.
[b] Significance.
[c] Single markers were both in this paper and Mao et al. (2015) that have a significant relation with SWR.

the PCA based on the SWR main groups. The AI compounds with a positive significant relation to SWR that showed high positive loadings on PC 2, whereas the D compounds oppositely showed negative loadings on PC 2, suggest that PC 2 reflects root-derived (AI) SWR-markers. The AS compounds did not have a clear link either with PC 1 or 2, again confirming their mixed (main) root and (minor) leaf origin.

The factor scores of the Ah horizons were all positive on PC 1, whereas the B and C horizons were all negative (Appendix D, Table D.2) confirming that the topsoils experienced more persistent SWR than the subsoils. The factor scores on PC 1 had a positive significant correlation with SWR ($r = 0.623$, $p = 0.031$), while the factor scores of the remaining components did not have any significant relation with SWR, which reveals that the main signal of PC 1 contains SWR (Appendix D, Table D.2).

Table 4
Correlation coefficients and explaining variance of the three main components with SWR-marker groups using principal component analysis (PCA).

	Component		
	1	2	3
(D) alkane	0.672	−0.468	0.140
(D) alcohol	0.827	−0.349	0.149
(D) fatty acid	0.884	−0.260	0.090
(D) ω-hydroxy acid	0.850	−0.297	−0.245
(D) α,ω-dicarboxylic acid	0.855	−0.229	−0.321
(AI) alcohol	0.355	0.800	−0.184
(AI) fatty acid	0.546	0.676	0.436
(AI) ω-hydroxy acid	0.457	0.722	−0.344
(AI) α,ω-dicarboxylic acid	0.851	0.278	0.251
(AS) alcohol	0.914	0.028	0.153
(AS) fatty acid	−0.351	−0.273	0.755
(AS) ω-hydroxy acid	0.820	−0.222	0.049
(AS) α,ω-dicarboxylic acid	0.146	0.831	0.287
% of variance	49.07	23.53	9.97
Cumulative %	49.07	72.60	82.57

3.2.3. SWR predictors

Based on the aforementioned outcomes of the simple linear regression and PCA for grouped and individual SWR-markers to more efficiently link SWR-markers to SWR and their vegetation origin, the following nine SWR-markers were defined as SWR predictors: (D) C_{26} alcohol, (D) C_{24} α,ω-dicarboxylic acid, (AS) C_{18} alcohol, (AS) C_{22} and C_{24} ω-hydroxy fatty acid, (AI) C_{22} and C_{24} ω-hydroxy fatty acid and (AI) C_{22} and C_{24} α,ω-dicarboxylic acid. These SWR predictors were dominant in their own compound groups and each individually although not strong but significantly correlated to SWR. The summed concentration (normalized on the TOC content) of SWR predictors correlated positively with the SWR persistence ($\log_{10}$ WDPT) (Fig. 4, $r = 0.856$, $p = 0.000$). This correlation was higher than for the majority of the individual SWR-markers. However, for the topsoils ($n = 6$), there was no significant correlation between the SWR predictors and SWR. The majority of these "SWR predictors" are root-derived compounds, the contribution to SWR of the topsoils is mainly from roots but still partly influenced by leaves. For the subsoils ($n = 6$), only the concentrations of (AI) C_{22} α,ω-dicarboxylic acid ($r = 0.926$, $p = 0.008$) and C_{24} α,ω-dicarboxylic acid ($r = 0.898$, $p = 0.015$) is significantly related to SWR. The correlation between the α,ω-dicarboxylic acids and SWR of the subsoils indicated that the root-derived compounds strongly link to the degree of SWR in the subsoils. Since each SWR predictor represented the most abundant SWR-marker in their corresponding compound group, they have a stronger influence on determining SWR than other SWR-markers. Thus, identifying the origin of these SWR-predictors may provide an estimate of the contribution of the covering vegetation to the organic matter responsible for SWR. (D) C_{26} alcohol has been linked to grass leaf waxes and to a lesser extent to grass roots (Jansen et al., 2006). (AI) C_{22} and C_{24} ω-hydroxy fatty acids and (AI) C_{22} and C_{24} α,ω-dicarboxylic acids are typical suberin-derived compounds from plant roots (Kolattukudy, 2001; Nierop and Verstraten, 2004). Similar to the root origin of these SWR markers in the AI fractions, (AS) C_{18} alcohol and (AS) C_{22} and C_{24} ω-hydroxy fatty acids are

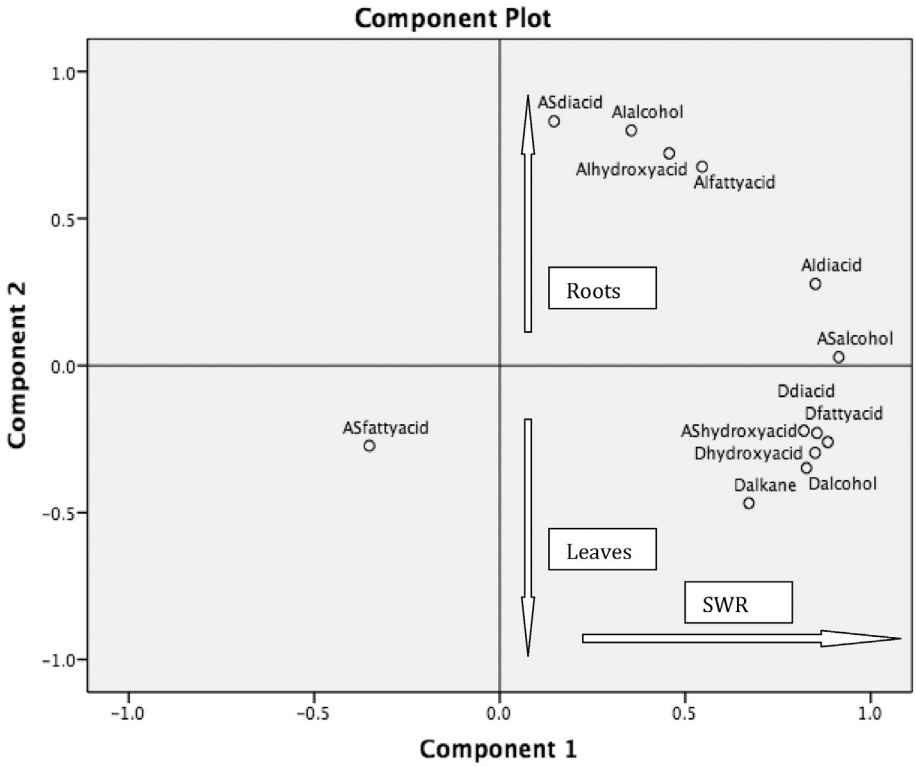

Fig. 3. PCA plot of the factor loadings of SWR-marker groups in factor 1 and 2 space. The capital letters D, AS and AI refer to the fraction, whereas the compound name is followed by small letters. E.g. 'Dhydroxyacid', 'AShydroxyacid' and 'AIhydroxyacid' refers to ω-hydroxy fatty acids in the D, AS and AI fractions, respectively.

mainly derived from suberins but were hydrolysed by soil microbes over time.

3.3. Linking molecular SWR predictors to specific vegetation

The extractable lipids of plant leaves and roots were mainly composed of three groups (Appendix E): alcohols, fatty acids and alkanes. Four main groups were identified as ester-bound building blocks of plant leaves and roots (Appendix F): alcohols, fatty acids, ω-hydroxy fatty acids and α,ω-dicarboxylic acids. The aforementioned nine SWR predictors were further classified as six biomarkers typical of leaves or roots based on their characteristics and origin: extractable C_{26} alcohol from leaves, and ester-bound C_{18} alcohol, ester-bound C_{22} and C_{24} ω-hydroxy fatty acids and ester-bound C_{22} and C_{24} α,ω-dicarboxylic acids from roots. The abundances of the six biomarkers representing SWR predictors in either leaves or roots are depicted in Fig. 5. A clear variation of the distribution and concentrations of these biomarkers in oak, sedge and six different grasses species is observed. Extractable C_{26} alcohol was the most abundant biomarker in grass leaves. The ester-bound C_{18} alcohol was the only component that was much more abundant in oak roots than in grasses or sedge, while, the other seven SWR predictors were much higher in concentration in grass or sedge roots than in oak.

Table 5
Linear regressions between the relative abundance (log (mg/g TOC)) of SWR-marker groups and SWR. The SWR-marker groups having significant correlations with SWR are indicated in bold.

SWR-group	Coef[a]	Sig.[b]
(D) alkane	0.366	0.242
(D) alcohol	0.303	0.339
(D) fatty acid	0.560	0.058
(D) ω-hydroxy fatty acid	0.484	0.111
(D) α,ω-dicarboxylic acid	0.644	0.024
(AI) alcohol	0.448	0.144
(AI) fatty acid	0.434	0.158
(AI) ω-hydroxy fatty acid	0.693	0.012
(AI) α,ω-dicarboxylic acid	0.787	0.002
(AS) alcohol	0.815	0.001
(AS) fatty acid	−0.090	0.781
(AS) ω-hydroxy fatty acid	0.730	0.007
(AS) α,ω-dicarboxylic acid	−0.118	0.715

[a] Correlations coefficient.
[b] Significance.

The link between the SWR predictors and their corresponding biomarkers in vegetation is demonstrated in Table 6. The left hand part of Table 6 shows that the locations of the profiles in which the abundant SWR predictors were observed and the dominant species of vegetation covering that location. SWR-markers, for example (D) C_{26} alcohol, can be abundant in two locations. The right hand part of Table 6 presents the biomarkers corresponding to these SWR predictors and in which species they are most abundant. The (D) C_{26} alcohol shows the highest concentration in the topsoils covered by either tufted grasses or creeping bentgrasses (Fig. 5), of which the leaves contained the highest amount of this alcohol. Compared to the leaves, tufted grass roots had the most abundant ester-bound C_{22} ω-hydroxy fatty acid and C_{22} α,ω-dicarboxylic acid. The corresponding SWR predictors of these two biomarkers were (AS) and (AI) C_{22} ω-hydroxy fatty acids and (AI) C_{22} α,ω-dicarboxylic acid, which were found in the topsoils under tufted grasses. A similar match was found for ester-bound C_{24} ω-hydroxy fatty acid that was the richest in wood bluegrass roots, which dominantly covered the topsoil with the highest (AS) and (AI) C_{24} ω-hydroxy fatty acid. The topsoils with the highest (AS) and (AI) C_{24} α,ω-dicarboxylic acid were either dominantly covered by red fescue or wood bluegrass, of which the roots contained the most abundant ester-bound C_{24} α,ω-dicarboxylic acid. Ester-bound C_{18} alcohol highly occurred in oak roots, while the soil being richest of (AS) C_{18} alcohol was the topsoil close to the oak at 1.0 m. It followed the oak roots as the oak root biomass decreased with soil depth when it was close to the stem (Spielvogel et al., 2014). However, the topsoil at 1.0 m contained the lowest amount of (AI) C_{18} alcohol. AS fraction is speculated to be mainly hydrolysed from suberins by microbes (Mao et al., 2015), therefore it

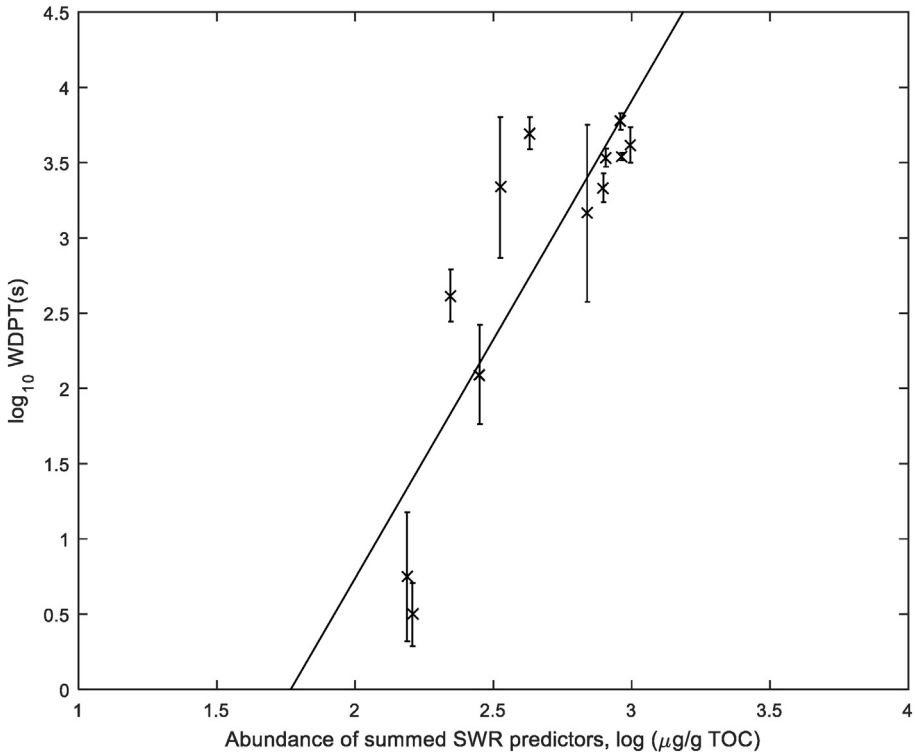

Fig. 4. WDPT as a function of SWR predictors ($r = 0.855$, $p = 0.000$). Error bars represent standard deviation.

implies that microbes in the topsoil near the oak are more active when staying closer to the oak because they benefit more from the canopy (Mordelet et al., 1993). The biomarkers indicative of the dominant covering vegetation at the location were generally found in the soils in which the corresponding SWR predictor was the richest. All observations above revealed a good match between SWR predictors and their vegetation origin and therefore indicate that the covering vegetation has a direct influence on the composition of SWR-markers and subsequently affect the SWR of the topsoils. One exception in Table 6 is SWR predictor (D) C_{24} α,ω-dicarboxylic acid. The dominant covering vegetation did not match with the species with the highest concentration of this biomarker. Comparing C_{24} α,ω-dicarboxylic acids in the D and AS fractions, although they are possibly both the result of microbial hydrolysis, (D) C_{24} α,ω-dicarboxylic acid is not protected in soil by compounds that end up in AI fractions. In short, since ester-bound long-chain (>C_{20}) ω–hydroxy fatty acids and α,ω-dicarboxylic acids are typical suberin-derived compounds (Kolattukudy, 1981, 2001) and the below-ground biomass in the topsoils was higher than in the subsoils, it is not surprising to notice that more (AI) C_{22} and C_{24} ω–hydroxy fatty acids and (AI) C_{22} and C_{24} α,ω-dicarboxylic acids appeared in the topsoils than in the subsoils. Moreover, compared to sedge and oak, the higher amounts of ester-bound ω–hydroxy fatty acids and α,ω-dicarboxylic acids in grass roots strongly implies its role as the primary source of such suberin-derived SWR-markers in the topsoils.

3.4. Link between vegetation and SWR

Plant roots proved to be the most important origin of SWR-markers to predict the degree of SWR (Mao et al., 2015). Compared with oak and sedge, grasses regardless of species type contribute relatively most SWR-markers to the topsoils. The finding is different from Rodríguez-Alleres et al. (2007) and Badía et al. (2013), who both concluded the soils under grassland or meadow showed less persistent SWR than the soils under woody trees. However, the woody trees studied in Rodríguez-Alleres et al. (2007) were pine and eucalyptus and the behaviour of these species with respect to SWR is probably not similar to oak. In addition, in Badía et al. (2013) the soils under woody plants and meadow were all fine textured, which are different from the sandy soils studied here and may therefore relate differently to SWR as soil texture is an important factor affecting SWR (DeBano, 1981; Zavala et al., 2014). Our topsoils with a dense distribution of the roots of grasses and sedge have higher TOC contents than their soils (5.1% TOC) and the positive relation between TOC and SWR may cause this higher SWR. Despite showing less influence on the SWR of the topsoils, oak roots affect the composition of SWR-markers more in the topsoil with decreasing distance to the oak tree. The SWR of the topsoils was higher than that of the underlying subsoils due to a denser spreading of grasses and sedge roots in the topsoils. Although the proportion of the roots of different grass species could not be properly identified, the dominance of the covering plants have revealed the primary contributors of SWR-markers to soil by the abundance of their corresponding biomarkers. Turfed grasses most frequently occurred at the locations where the SWR was higher than at other spots, and their roots contained indeed a relatively high amount of extractable C_{26} alcohol and ester-bound C_{22} ω–hydroxy fatty acid and C_{22} α,ω-dicarboxylic acid (Fig. 5) that are among the best SWR predictors. The highest concentrations of ester-bound C_{24} ω-hydroxy fatty acid and C_{24} α,ω-dicarboxylic acid were found in wood bluegrass roots (Fig. 5) along with the highest amount of corresponding ester-bound biomarkers in total (Fig. 6), of which the second highest amount was recorded for tufted grass roots. Roots produce more water repellent markers and therefore tufted grass and wood bluegrass contribute relatively strongly to SWR than other plant species. That fits with our observation that turfed grasses most frequently occurred at the locations where the SWR was higher than at other spots.

The abundances of SWR-markers increase as a result of the increasing biomass of vegetation cover. The SWR becomes stronger with an increasing concentration of SWR-markers. Consequently, vegetation growth generally increases the persistence of SWR. The influence of plants on SWR-markers to the top- and subsoils approximately follows the distribution of leaves and roots, respectively. Root-derived SWR-markers induce a higher SWR than leaves, although the abundance in

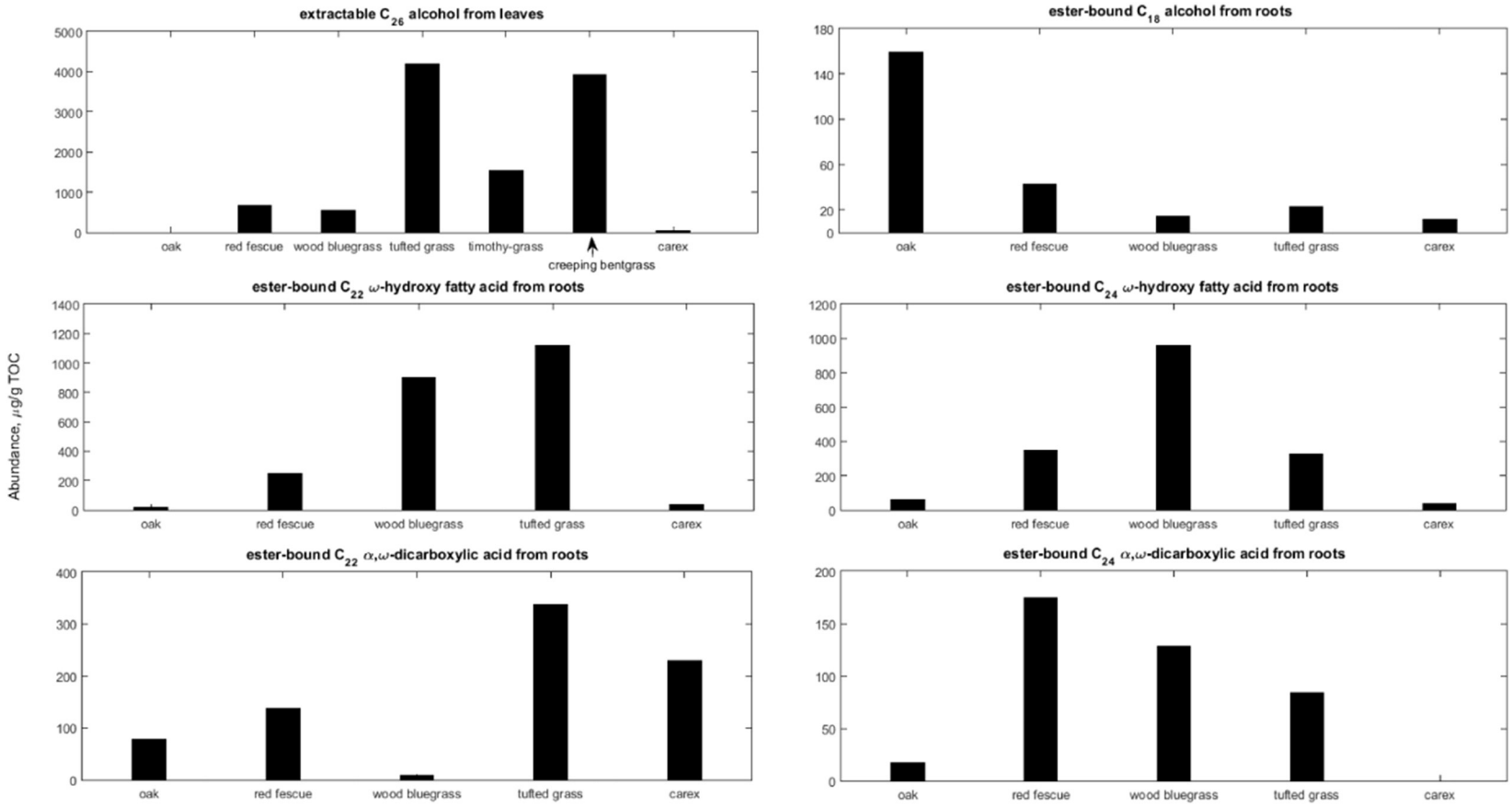

Fig. 5. The distribution and the abundance of six biomarkers (SWR predictors) in plant leaves and roots; the roots of timothy-grass and creeping bentgrass could not be identified and therefore not collected during fieldwork, for that reason they are not shown.

Table 6
The left hand part shows the most abundant SWR-markers; the right hand part indicates the main origin of these in plants and biomass types.

SWR-marker signal in soil				Biomarker in vegetation	
SWR-markers name	Profile	Location (m)	Vegetation covering	Biomarker name	Most abundantly found in species
(D) C_{26} alcohol	Topsoil	5	Tufted grass and timothy-grass	Extractable C_{26} alcohol	Leaves of tufted grass and creeping bentgrass
	Topsoil	6	Tufted grass and creeping bentgrass		
(D) C_{24} α,ω-dicarboxylic acid	Topsoil	5	Tufted grass and timothy-grass	Ester-bound C_{24} α,ω-dicarboxylic acid	Roots of red fescue and wood bluegrass
	Topsoil	6	Tufted grass and creeping bentgrass		
(AS) C_{18} alcohol	Topsoil	1	Oak	Ester-bound C_{18} alcohol	Roots of oak
(AS) C_{22} ω-hydroxy fatty acid	Topsoil	6	Tufted grass and creeping bentgrass	Ester-bound C_{22} ω-hydroxy fatty acid	Roots of turfed grass and wood bluegrass
(AS) C_{24} ω-hydroxy fatty acid	Topsoil	4	Wood bluegrass, turfed grass and carex	Ester-bound C_{24} ω-hydroxy fatty acid	Roots of wood bluegrass
(AI) C_{22} ω-hydroxy fatty acid	Topsoil	2	Red fescue, tufted grass and creeping bentgrass	Ester-bound C_{22} ω-hydroxy fatty acid	Roots of turfed grass and wood bluegrass
	Topsoil	4	Wood bluegrass, turfed grass and carex		
(AI) C_{24} ω-hydroxy fatty acid	Topsoil	2	Red fescue, tufted grass and creeping bentgrass	Ester-bound C_{24} ω-hydroxy fatty acid	Roots of wood bluegrass
	Topsoil	4	Wood bluegrass, turfed grass and carex		
(AI) C_{22} α,ω-dicarboxylic acid	Topsoil	2	Red fescue, tufted grass and creeping bentgrass	Ester-bound C_{22} α,ω-dicarboxylic acid	Roots of turfed grass and carex
(AI) C_{24} α,ω-dicarboxylic acid	Topsoil	2	Red fescue, tufted grass and creeping bentgrass	Ester-bound C_{24} α,ω-dicarboxylic acid	Roots of red fescue and wood bluegrass

soils of leaf-derived markers is larger than roots (Mao et al., 2014). Various plant species, for instance, grasses and woody plants (e.g. oak) with distinguished leaf and root characteristics contribute to SWR-markers differently resulting in a heterogeneous pattern of TOC and thus of SWR.

4. Conclusion

A higher TOC content results in a higher persistence of SWR in the sandy soils studied. SWR-markers as a primary cause of SWR, of which the D fractions originate from plant leaf waxes, while AS and AI fractions are mainly derived from plant roots. Single SWR-markers, especially long-chain compounds, show significantly positive relationships with SWR. Compared to those in ecosystems containing multiple species, SWR-markers are able to better predict SWR in an ecosystem with a more simple vegetation cover. In cases where the soil shows the highest concentration of SWR predictors, the covering species contained the most abundant biomarkers representing the SWR predictors. Therefore, based on the presence of SWR predictors and their corresponding plant biomarkers, a good match between the dominant vegetation cover species and the underlying soils was observed. The distribution of root-derived organic hydrophobic compounds follows the distribution of plant roots of various species in the top- and subsoils. The suberin-derived ω-hydroxy fatty acids (C_{22} and C_{24}) and α,ω-dicarboxylic acids (C_{22} and C_{24}) are abundantly present in the grass roots and significantly relate to SWR of all soils, which indicate that SWR-markers produced by plant roots can well predict SWR of our sandy soils. The grass roots mainly affect SWR in the topsoils. Correlations between vegetation cover and SWR of the topsoils demonstrate that the topsoils covered by more grasses than oak show a stronger SWR than soils with less grass cover. The below-ground biomass (i.e. roots) in subsoils

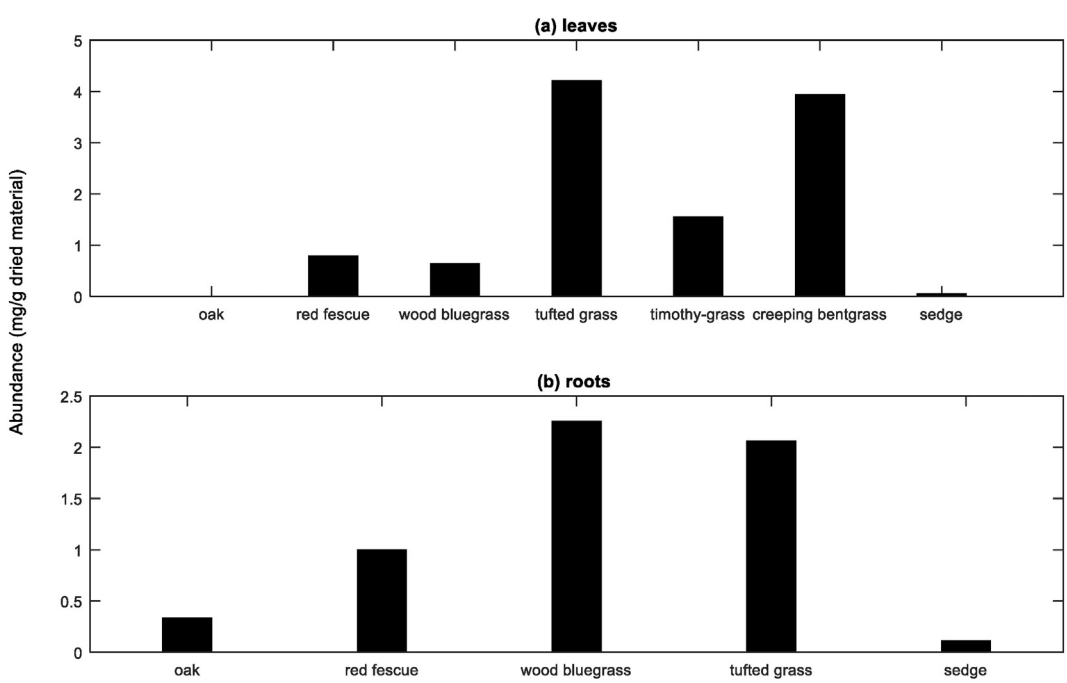

Fig. 6. The distribution of summed selected biomarkers corresponding to SWR predictors in leaves and roots.

significantly decreased with the distance from the oak. The SWR-markers originating from oak roots highly accumulate nearby the oak tree and they influence the SWR of subsoils more than other roots.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2016.05.077.

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