Research paper

Land-use change under different climatic conditions: Consequences for organic matter and microbial communities in Siberian steppe soils

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\textbf{A B S T R A C T}

The Kulunda steppe is part of the greatest conversion areas of the world where 420,000 km\textsuperscript{2} grassland have been converted into cropland between 1954 and 1963. However, little is known about the recent and future impacts of land-use change (LUC) on soil organic carbon (OC) dynamics in Siberian steppe soils under various climatic conditions. By investigating grassland vs. cropland soils along a climatic gradient from forest to typical to dry steppe types of the Kulunda steppe, our study aimed to (i) quantify the change of OC stocks (0–60 cm) after LUC from grassland to cropland as function of climate, (ii) elucidate the concurrent effects on aggregate stability and different functional soil organic matter (OM) fractions (particulate vs. mineral-bound OM), and (iii) assess climate- and LUC-induced changes in the microbial community composition and the contribution of fungi to aggregate stability based on phospholipid fatty acid (PLFA) profiles. Soil OC stocks decreased from the forest steppe (grassland: 218 ± 17 Mg ha\textsuperscript{-1}) over the typical steppe (153 ± 10 Mg ha\textsuperscript{-1}) to the dry steppe (134 ± 11 Mg ha\textsuperscript{-1}). Across all climatic regimes, LUC caused similar OC losses of 31% (95% confidence interval: 17–43%) in 0–25 cm depth and a concurrent decline in aggregate stability, which was not related to the amount of fungal PLFA. Density fractionation revealed that the largest part of soil OM (>90% of total OC) was associated with minerals and <10% of C existed in particulate OM. While LUC induced smaller relative losses of mineral-associated OC than particulate OC, the absolute decline in total OC stocks was largely due to losses of OM bound to minerals. This result together with the high \textsuperscript{14}C ages of mineral-bound OM in croplands (500–2900 yrs B.P.) suggests that mineral-bound OM comprises, in addition to stable OC, also management-susceptible labile OC. The steppe type had a larger impact on microbial communities than LUC, with a larger relative abundance of gram-positive bacteria and less fungi under dry conditions. Our results imply that future drier climate conditions in the Siberian steppes will (i) result in smaller OC stocks on a biome scale but (ii) not alter the effect of LUC on soil OC, and (iii) change the microbial community composition more than the conversion from grassland to cropland.

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1. Introduction

Global soils hold a substantial proportion of the earth's carbon with about 1325 Pg organic carbon (OC) being stored in the upper first meter and almost 3000 Pg OC when deeper soil layers are included (Köchy et al., 2015). Past research found soil OC to be very sensitive to land-use changes (LUC) (Guo and Gifford, 2002; Murty et al., 2002; Poeplau et al., 2011), and its role to regulate climate
change and food security is considered to be crucial (Lal, 2004). This particularly concerns steppe soils as they are rich in organic matter (OM) and commonly under intensive agricultural use. Nowadays, about 14% of agricultural land globally consists of steppe soils, typically Chernozems and Kastanozems (FAO, 2013).

Land-use change from grassland to cropland usually involves a loss of OC due to smaller residue inputs into the soil and larger soil OM decomposition as triggered by soil tillage (Mann, 1986; Poeplau et al., 2011). Previous studies observed a break-down of soil macromolecules due to soil tillage and a subsequent release of occluded particulate OM which is then mineralized by microorganisms (reviewed by Bronnck and Lal, 2005). The formation and stabilization of macromolecules depend on the abundance and functioning of soil fungi, since their extensive hyphal network generally supports aggregate formation and stabilization (Guggenberger et al., 1999). Besides the stabilization of soil OM by occlusion within aggregates, soil OM can be chemically stabilized by its association with mineral surfaces. Mean residence times of mineral-associated OM are in the range of >100 yr, while particulate OM has a turnover of years (Kleber et al., 2015).

Research on LUC effects in steppe soils predominantly focused on American prairie soils. For this region the OC stock decline after conversion from grassland to cropland was estimated to be 24–32% for conventional soil tillage practices (Beniston et al., 2014; Doran et al., 1998; VandenBygaart et al., 2003). Some studies were conducted in steppe soils of the European part of Russia where the decrease of OC stocks after conversion from grassland to cropland ranged from 27% to more than 40% (Mikhailova et al., 2000; Rodionov et al., 1998). Apart from that, there is no study dealing with the effects of LUC on SOC in steppe soils of Siberia, despite the region belongs to the greatest agricultural production areas in the world and occupies an area greater than that in the Great Plains (Frühaufl., 2011). Moreover, little is known about the effects of LUC on soil OM under different climatic conditions, which is particularly important in the course of climate change. For south-western Siberia, Hijoka et al. (2014) predicted a temperature increase of 2–6 ºC until the late 21st century coming along with more frequent drought events, which translates into a higher degree of aridity. As this will change the environmental conditions there is an increasing demand for understanding how LUC impacts are affected by climate change. Studies on the climate-dependent effect of LUC on soil OM have not come to a clear conclusion yet. Burke et al. (1989) and Guo and Gifford (2002) found a positive relationship between relative OC loss and precipitation (until a mean annual precipitation of ca. 600 mm), but did not have an explanation for this finding. Poeplau et al. (2011) identified temperature being positively correlated to the relative soil OC loss due to LUC, but not the mean annual precipitation (MAP). Considering processes of carbon stabilization in soil, we believe that soil OC losses should be larger under dry conditions, as the formation of OM-protecting mineral-organic associations is reduced under dry conditions (Kleber et al., 2015). Thus, larger proportions of readily decomposable particulate OM are expected in arid regions, as evidenced by Ameling et al. (1998), which would lead to larger losses of soil OC upon LUC. To elucidate the effects of LUC on soil OM in Siberian steppe soils under different climatic conditions we investigated the effect of LUC from grassland to cropland in soils of the south-western Siberian Kulunda steppe along a climatic gradient. The region is part of the greatest conversion area of the world, where 420,000 km² of grassland were converted into cropland between 1954 and 1963 as part of the so-called “Virgin Lands Campaign” (Russian: “zelina”). The main objectives of our study were to (i) investigate the climate-dependent effect of LUC from grassland to cropland on soil OC stocks, (ii) account for the concurrent effects on aggregate stability and different functional soil OM fractions (particulate vs. mineral-bound OM), and (iii) determine changes in the microbial community composition along the climatic gradient and the two land use types and the contribution of fungi to aggregate stability. We approached this by quantifying soil OC stocks under different land use (grassland vs. cropland) in a paired plot design along a climatic gradient with sites in the forest, typical and dry steppe types and assessing the concurrent changes in aggregate stability and density-separated soil OM fractions. The apparent stability of particulate and mineral-bound OM was estimated based on 14C measurements. Based on phospholipid fatty acid (PLFA) profiles we elucidated the amount of bacterial and fungal PLFA and separated the microbial community into six microbial groups. We hypothesize that the response of soils to LUC depends on the climatic conditions with larger OC losses in arid regions. Moreover, we expect that the loss of OC relates to a decrease in aggregate stability which itself is associated to a reduction in the amount of fungal PLFA.

2. Material and methods

2.1. Study sites and soil sampling

The Kulunda steppe is situated in the Altai Krai region of the Russian Federation, between 51° N and 54° N and 78° E and 84° E, and belongs to the Eurasian loess belt (Fig. 1). The area is separated into three distinct steppe types: the forest steppe (FS) with a MAP of 350–450 mm, the typical steppe (TS) with a MAP of 300–350 mm and the dry steppe (DS) with a MAP of 250–300 mm. The mean annual temperature (MAT) increases from FS (MAT 1 °C) to DS (MAT 2 °C) by around 1 °C (climate data from “WorldClim” data base; Hijmans et al., 2005). As a result, aridity increases in the order FS < TS < DS and the vegetation cover changes from partially forested areas in FS to mostly grassland areas in DS with the largest biomass production in FS and the smallest one in DS. Dominant plant species in the grasslands of FS were Bromopsis inermis and Stipa capillata, while Festuca valesiaca and Bromopsis inermis dominated in grasslands of TS. Grasslands of DS were characterized by Festuca valesiaca and Artemisia frigida. The agricultural production in the entire area focuses mainly on wheat and sunflower, but also rape seed and peas are common. In FS and TS, soils were mostly classified as Chernozems, reflecting the wetter climate as compared to DS, where Kastanozems are more frequent.

For assessing the impact of LUC on soil, we used a paired plot design (Poeplau and Don, 2013). Nine sites were selected, three sites in FS, two sites in TS and four sites in DS, with a total of 21 plots (Table S1). Each site consisted of at least two plots, one reference plot, representing the soil conditions before LUC and one or more conversion plots, representing the soil conditions at a certain time after LUC. Seven sites consisted of one reference and one conversion plot, while two sites (in DS) consisted of one reference and two conversion plots (triple plot), giving a total of eleven pairs (reference and conversion plot). The grasslands chosen as reference plots were either in pristine state or in use as extensive pastures. As further criteria, soils had to be unaffected by erosion and LUC should have occurred at least 20 years ago, as several studies showed most soils establish a new equilibrium approximately after that time (e.g. Murty et al., 2002; Poeplau et al., 2011). For a LUC chronosequence in FS, we also included one plot with <20 yrs since LUC. Per plot one key profile was established for soil description and sampled according to generic horizons down to a depth of ca. 160 cm. Subhorizons (e.g. A1, A2) were treated separately in the laboratory, but the measurements were bulked according to the proportion of a subhorizon in the main horizon to obtain one value per horizon (A, AC, C). Additionally, per plot three randomly chosen soil profiles were excavated around the key profile and sampled in 0–10, 10–25 and 25–40 cm horizons.
25–60 cm depth increments (hereafter referred to as increment profiles). This gave a total of 60 horizon samples from the key profiles and 180 samples from increment profiles. The horizon samples from the key profiles were analyzed for basic soil parameters as texture, bulk density, pH, electrical conductivity, carbonate content (<CaCO3>, dithionite- and oxalate-extractable Fe, as well as particulate and mineral-associated OM contents as determined by density fractionation. The latter OM fractions were also analyzed for their 14C activities. For both, horizons from key profiles and samples from increment profiles, we determined soil OC content, total nitrogen and aggregate stability (aggregate stability only in 0–10 cm or the topmost horizon). Phospholipid fatty acid profiles were analyzed in 0–10 cm of the increment profiles.

2.2. Sample preparation and basic soil analyses

Soil samples were air-dried, gently crushed in a mortar to break down clods, and sieved to <2 mm. All visible roots and plant residues were removed and an aliquot of 5 g fine soil was dried at 105 °C to determine the residual soil water content. Soil bulk density was determined in triplicate for generic horizons of the key profile and calculated for the corresponding depths of the increment profiles. Soil pH was measured at a soil-to-water ratio of 1:2.5 (w:v), while the electrical conductivity (EC) was measured at a ratio of 1:5 (w:v). Dithionite- and oxalate-extractable Fe was measured according to the method in McKeague & Day (1966). Soil texture was determined with the standard sieve-pipette method (DIN ISO 11277, 2002) for generic horizons to a depth of 100 cm. Carbonate content was determined by the Scheibler volumetric method (Schlichting et al., 1995).

2.3. Soil organic carbon analysis

An aliquot of the <2-mm fraction was homogenized in a ball mill, treated with HCl fume to remove carbonates (Walthert et al., 2010), and analyzed for OC and total nitrogen (TN) by dry combustion in an Elementar vario MICRO cube C/N Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany).

2.4. Density fractionation and 14C analysis

We used density fractionation (modified after Golchin et al., 1994) to isolate a light fraction (LF) mostly containing particulate OM (POM) from a heavy fraction (HF) representing mineral-associated OM (MOM). As POM is generally most abundant in the topsoil, generic horizons deeper than 80 cm depth were not considered for analysis. In brief, 25 g of air-dried sample was given in duplicate in a beaker and 125 ml of sodiumpolytungstate (1.6 g cm⁻³) was added. After stirring the suspension with a glass rod, ultrasonification with an energy input of 60 J ml⁻¹ was applied for 8 min to disperse the soil. The sample was centrifuged at 3,000 g for 20 min and LF, floating on top of the suspension, was decanted on polyethersulfone filters, and washed with deionized water until the washing solution had an electrical conductivity <60 μS cm⁻¹. The procedure was repeated if the separation between LF and HF was insufficient. The HF was washed with deionized water until the electrical conductivity was <100 μS cm⁻¹ or, for samples which contained pedogenic salts, at maximum four times. The washing solutions of both fractions were collected, passed through 0.45-μm syringe filters (PVDF), and analyzed for dissolved OC (DOC) with a LiquiTOC (Elementar Analysensysteme GmbH, Hanau, Germany). This mobilized DOC accounted for 5–31% of total OC (Table S2). The isolated LF and HF were freeze-dried, weighted, and carefully homogenized in a mortar. All fractions were analyzed for OC and TN (after removal of carbonates). DOC mobilized during the washing procedure was added to the OC content of the corresponding fraction.

A subset of OM fractions was analyzed for 14C activities at the Max Planck Institute for Biogeochemistry Jena (Germany). Inorganic C was removed by 2 M HCl until pH remained <3.5. After neutralization with 2 M NaOH to pH 6, samples were freeze-dried, and measured for 14C using a 3 MV Tandetron™ AMS 14C system (Steinhof et al., 2011). 14C isotope ratios were converted to pmC (percent modern carbon) according to Steinhof (2013). Percent modern carbon is defined according to Stuiver and Polach (1977):

\[
pMC = \frac{A_{14C}}{A_{13C}} \times 100%
\]
where \( A_{SN} \) is the normalized sample activity and \( A_{abs} \) is the activity of the absolute international standard, both activities background-corrected and \( \delta^{13} \)-C-normalized. Conventional \( ^{14} \)C ages were estimated using OxCal 4.2 software (University of Oxford). The IntCal13 calibration curve (Reimer et al., 2013) was selected if pMC was < 100% while the calibration curve calculated by Hua et al. (2013) was used if pMC was > 100%.

2.5. Phospholipid fatty acid analysis

1.0–1.5 g field-moist soil was cleaned from visible roots, weighted into cryovials and stabilized in RNAlater\textsuperscript{\textregistered} to prevent sample degradation (Schnetter et al., 2012). An aliquot was dried at 105 °C to determine the soil water content. The cryovials were kept cool and frozen to \( -20 \) °C within 72 h. We used a modified method of Gunina et al. (2014) to analyze the phospholipid fatty acids (PLFAs). Briefly, the samples were transferred from the cryovials into test tubes and washed with ultrapure water to remove residual RNAlater\textsuperscript{\textregistered}. Lipids were extracted twice using a chloroform-methanol-citrate buffer (1:2:0.8 v/v/v) and separated by solid phase extraction with activated Silica gel (Sigma Aldrich, pore size 60 Å, 70–230 mesh) into glycolipids, neutral lipids, and phospholipids. Only phospholipids were used for further analysis and converted into fatty acid methyl esters (FAME) using BF\textsubscript{3} as a catalyst. FAMES were analyzed by gas chromatography using an Agilent Technologies 7890A GC system equipped with a 60 m Zebron capillary GC column (0.25 mm diameter and 0.25 μm film thickness; Phenomenex, Germany) and a flame ionization detector, using He as a carrier gas. Nonadecanoic acid (FA 19:0) was used as an internal standard. Seventeen PLFA were analyzed in total and the sum of all PLFA was used as a proxy of the microbial biomass and expressed as PLFA biomass. A principal components analysis (PCA) was conducted on data of the relative abundance of all 17 PLFA (%) to separate the microbial community into distinct microbial groups. The PCA-based classification of the PLFA into the microbial groups was in good agreement with literature data (Frostegård et al., 2011; Ruess and Chamberlain, 2010; Zelles, 1999), and we used the following markers to distinguish the microbial community: 115:0, a15:0, 116:0, 117:0, a17:0 and 18:1ω9c for gram-positive bacteria (Gram+), 16:1ω5c, 18:0ω7c and Cy19:0 for gram-negative bacteria (Gram–), 10Me16:0 for actinomycetes, 18:2ω6,9 for fungi, 20:4ω6c for protozoa, and 14:0, 15:0, 16:1ω7c, 17:0, and 18:0 for unspecific bacteria. We did not use PLFAs 18:1ω9c and 16:1ω5c as markers for fungi or arbuscular mycorrhiza, respectively, as they are also common in bacteria and, hence, had no good indicator function in arable soils (Frostegård et al., 2011). The ratio of the fungal PLFA to the bacterial PLFAs was used to estimate the fungi : bacteria ratio (Frostegård and Bååth, 1996). The ratio of PLFAs representing gram-positive bacteria and actinomycetes to those representing gram-negative bacteria was calculated to estimate the Gram+ : Gram– ratio (Wixon and Balser, 2013).

2.6. Aggregate stability

Aggregate stability was determined according to Hartge and Horn (1989) in combination of a dry- and wet sieving method. In brief, the field-moist soil was sieved to \( <8 \) mm to remove big clods and subsequently air-dried. About 120 g of the air-dry soil was placed on top of a stack of sieves with 4, 2, and 1 mm mesh size, rotated vertically 60 times, and the aggregate size fraction in each sieve was recovered and weighted. An aliquot of the air-dry soil was dried at 105 °C to determine the residual soil water content. The three isolated fractions from the dry sieving were pooled and gently wetted to 15% of their soil mass. The wetted aggregates were placed on a stack of sieves with 4, 2, 1, 0.5, and 0.2 mm mesh size, slowly submerged in water, and vertically rotated during 5 min with a frequency of 35 rpm. Each recovered aggregate size fraction was dried at 105 °C and the difference of aggregate size distributions between the dry- and the wet sieving method was calculated as difference between the masses (on a sand-free basis) of the corresponding aggregate size fractions according to Eq. (2):

\[
\Delta \text{MWD} = \frac{\sum (n_i \times d_i) - (n_i \times d_i)}{\sum n_i}
\]

where \( \Delta \text{MWD} \) is the difference of the mean weight diameter between the dry- and wet sieving method, \( d \) is the mean of an aggregate size fraction \( i \), \( n_i \) and \( n_i \) are the weights of the \( i \)th aggregate size fraction as proportion of all aggregate size fractions (%) after the dry- and wet sieving, respectively. The higher is \( \Delta \text{MWD} \) the lower is the aggregate stability (Hartge and Horn, 1989).

2.7. Calculation of organic carbon stocks

Organic C stocks (Mg ha\textsuperscript{-1}) were calculated according to Peepol and Don (2013) for all depth increments and horizons using Eq. (3):

\[
OC \text{ stock} = \sum_{i=1}^{n} \frac{FSM}{V_i} \times C_i \times D_i
\]

where \( n \) is the number of the depth increments or horizons, \( FSM \) is the fine soil mass (g), \( V \) is the volume \((\text{cm}^3)\), \( C \) is the OC content \((\% \text{ of soil mass})\) and \( D \) is the length of the depth increment or horizon \((\text{cm})\). As LUC generally implies a change in soil bulk density, OC stocks were corrected to account for different soil masses, according to Ellert and Betty (1995). The soil with the least mass was used as reference.

2.8. Statistical analyses

2.8.1. Linear mixed effects models

Data analysis was performed in R 3.1.2 (R Core Team, 2015). Linear mixed models (package lme4, Bates et al., 2012) were fitted to test for the effect of steppe type and land-use type on response variables (e.g., OC stock, aggregate stability, PLFA biomass) where possible with respect to different horizons or depth increments. We thereby accounted for the nested structure of sampling, i.e. main effects of steppe type and land-use type as well as their interaction and, where possible, the mean depth were included as fixed effects, while sites and plots within sites were included as random effects. After fitting initial models, residuals and random effect estimates were visually checked for deviations from normality, using Q-Q-normal plots. If these showed right-skewed distribution or heterogeneity of variances, models were re-fitted with log-transformed response variables. Based on the linear mixed model fit, the differences of the response variable between steppe type and land-use type classification were tested including corrections for multiple comparisons (analogous to the Tukey test), with Satterthwaite degrees of freedom, based on the R packages lsmeans (Lenth and Herve, 2015), lmerTest (Kuznetsova et al., 2015), and multcomp (Hothorn et al., 2008). To estimate the proportion of variance explained by steppe type and land-use type with respect to OC stocks, an intercept-only linear mixed effects model was fitted for each depth increment including steppe type, land-use type, sites and plots within sites as random effects and calculating the relative proportion of each component to the total variance (variance components analysis). Graphs were made using ggplot2 (Wickham, 2009) and the map of the survey area was
generated using ggmap (Kahle and Wickham, 2013) and the open source software Inkscape.

2.8.2. ADONIS and Nonmetric multidimensional scaling

After separating the microbial community into six microbial groups by PCA (see Section 2.5), Permutational Multivariate Analysis of Variance Using Distance Matrices (ADONIS; 99 permutations) was used to investigate the effect of steppe type and land-use type as well as their interaction on the microbial community composition, thereby using the Bray-Curtis dissimilarity index as distance metric. Pairwise comparisons between steppe types were tested in ADONIS by using subsets of the data with two corresponding factor levels and correcting p-values for multiple comparisons by Bonferroni correction. For graphical data presentation Nonmetric Multidimensional Scaling (NMDS) was chosen as it retains major parts of the entire variation and complexity of the data set and reflects similarities or dissimilarities within the microbial community with respect to site effects. To improve interpretation in NMDS, we chose a two-dimensional ordination which yielded a stress of 0.10. Confidence regions (95%) for the group centroids were added for steppe types and land-use types. All multivariate analysis was done in R package vegan (Oksanen et al., 2015).

3. Results

3.1. Basic soil characteristics

The soil parameters are characteristic for Chernozems and Kastanozems, with neutral to slightly alkaline pH, accumulation of carbonates in the subsoil, partial occurrence of pedogenic salts as indicated by high EC values, and low oxalate- and dithionite-extractable Fe contents as chemical weathering is limited due to the dry climate (Table 1). Comparable clay compositions in the respective horizons of grassland and cropland soils suggest same substrate at the paired plots. The thickness of the A horizons tended to decrease in the order FS > TS > DS, and was greater for grassland than for cropland soils in FS and TS. Concurrently, the OC contents were larger in grassland than in croplands, and soils of the FS had larger OC contents than those of the TS and DS (Table 1). The C : N ratios did not differ considerably between grassland and arable soils or steppe types.

3.2. Soil and organic matter properties as function of steppe type and land-use type

3.2.1. Soil organic carbon stocks

Soil OC stocks decreased significantly with decreasing MAP in the order FS > TS > DS for both land-use types (p < 0.05), while differences between TS and DS were smaller as compared to the differences to FS (Fig. 2). The conversion from grassland to cropland reduced soil OC stocks in all steppe types (p < 0.01). The relative decline of OC due to LUC was generally most pronounced in the topsoil increment (0–10 cm) and decreased when subsoil is included (0–60 cm). The proportional OC stock change was similar for FS and DS, while TS tended to have larger proportional OC losses, though statistically not significant (p = 0.54). On average, conversion from grassland to cropland decreased soil OC stocks by 37% in 0–10 cm, 31% in 0–25 cm, and 28% in 0–60 cm independently from steppe type (Fig.S1). Chronosequence data from FS showed that already after five years following grassland to cropland conversion, OC stocks declined by 29% and 22% in 0–10 and 0–25 cm, respectively, while during the following 25 years the total OC decline was much less (Fig. 3). While OC stocks in 0–10 cm depth were mainly controlled by land-use type (50% explained variance), we found that effects of steppe type and land-use type were virtually equal when considering 0–25 cm depth (each 33% explained variance, Table S3). Over the depth of 0–60 cm, OC stocks were more affected by steppe type (36% explained variance) than by land-use type (23% explained variance).

3.2.2. Organic matter fractions

Density fractionation was performed on the horizon samples in order to separate functionally different OM. The HF was the dominant OM fraction in soils of all steppe types and land-use types in all considered soil horizons (>90% of total OC, Table 2). The LF contributed <10% to the total OC pool and tended to have larger contribution under arid conditions (Table 2). Grassland to cropland
Fig. 2. Soil organic carbon stocks (Mg ha⁻¹) depending on land-use type for 0–10 cm, 0–25 cm, and 0–60 cm in different steppe types. Values are given as arithmetic mean ± standard error of the mean. Points show individual measurements and lowercase letters indicate significant differences between land-use types, tested within steppe type and depth increment (p-value, 0 < * < 0.001 < ** < 0.01 < *** < 0.05). Numbers above bars indicate the relative soil OC stock decline due to grassland to cropland conversion.

Fig. 3. Time-dependent decline of soil organic carbon stocks (%) for three depths at a chronosequence site in the forest steppe (n = 3 per depth and time interval), time intervals are 5 and 30 yrs for all three depths. Position shifting was done to avoid overlapping of error bars.

Table 2
OC content and C : N ratio of soil organic matter fractions and contribution of each fraction to the bulk soil mass and the soil OC pool depending on steppe type, horizon and land-use type. Values are given as arithmetic mean ± standard error of the mean. Abbreviations: FS = forest steppe, TS = typical steppe, DS = dry steppe.

<table>
<thead>
<tr>
<th>Steppe type</th>
<th>Horizon</th>
<th>Land-use type</th>
<th>n</th>
<th>Light fraction (LF)</th>
<th>Heavy fraction (HF)</th>
<th>% OC of total soil OC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mg OC g⁻¹ fraction</td>
<td>mg LF g⁻¹ soil</td>
<td></td>
</tr>
<tr>
<td>FS A</td>
<td>grassland</td>
<td>3</td>
<td>267.8 ± 22.0</td>
<td>18.8 ± 0.5</td>
<td>9.7 ± 1.7</td>
<td>2.5 ± 0.2</td>
</tr>
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<td></td>
<td>cropland</td>
<td>3</td>
<td>245.4 ± 19.0</td>
<td>17.6 ± 0.4</td>
<td>6.1 ± 1.3</td>
<td>1.6 ± 0.3</td>
</tr>
<tr>
<td>AC</td>
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<td>3</td>
<td>264.4 ± 6.7</td>
<td>19.6 ± 0.5</td>
<td>12.0 ± 0.5</td>
<td>0.4 ± 0.2</td>
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<tr>
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<td>266.6 ± 21.3</td>
<td>23.0 ± 1.3</td>
<td>13.8 ± 2.8</td>
<td>0.8 ± 0.2</td>
</tr>
<tr>
<td>C</td>
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<td>224.3 ± 12.5</td>
<td>11.7 ± 2.0</td>
<td>0.5 ± 0.2</td>
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<tr>
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<td>17.1 ± 1.1</td>
<td>11.0 ± 0.5</td>
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<td>9.0 ± 0.4</td>
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<td>250.3 ± 28.7</td>
<td>15.1 ± 2.0</td>
<td>5.4 ± 2.8</td>
<td>1.5 ± 0.9</td>
</tr>
<tr>
<td>AC</td>
<td>grassland</td>
<td>2</td>
<td>256.0 ± 7.6</td>
<td>16.3 ± 0.4</td>
<td>2.9 ± 0.9</td>
<td>0.8 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>2</td>
<td>282.3 ± 31.9</td>
<td>15.4 ± 2.5</td>
<td>1.5 ± 0.2</td>
<td>0.5 ± 0.1</td>
</tr>
<tr>
<td>C</td>
<td>grassland</td>
<td>2</td>
<td>258.3 ± 12.8</td>
<td>15.9 ± 1.2</td>
<td>1.6 ± 0.3</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>2</td>
<td>208.1 ± 4.5</td>
<td>11.9 ± 0.4</td>
<td>11.0 ± 0.6</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>DS A</td>
<td>grassland</td>
<td>4</td>
<td>221.4 ± 22.2</td>
<td>17.2 ± 1.0</td>
<td>10.2 ± 2.4</td>
<td>2.5 ± 0.7</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>6</td>
<td>261.7 ± 20.8</td>
<td>15.9 ± 1.0</td>
<td>6.3 ± 1.5</td>
<td>1.7 ± 0.4</td>
</tr>
<tr>
<td>AC</td>
<td>grassland</td>
<td>4</td>
<td>230.5 ± 13.7</td>
<td>17.4 ± 1.2</td>
<td>3.0 ± 0.6</td>
<td>0.7 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>6</td>
<td>213.4 ± 11.8</td>
<td>16.1 ± 1.8</td>
<td>2.2 ± 0.6</td>
<td>0.5 ± 0.1</td>
</tr>
<tr>
<td>C</td>
<td>grassland</td>
<td>4</td>
<td>212.8 ± 16.9</td>
<td>16.0 ± 0.6</td>
<td>1.8 ± 0.1</td>
<td>0.3 ± 0.0</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>6</td>
<td>223.0 ± 20.6</td>
<td>13.6 ± 0.5</td>
<td>1.6 ± 0.4</td>
<td>0.2 ± 0.0</td>
</tr>
</tbody>
</table>
3.2.3. Grassland to cropland conversion decreased the microbial PLFA biomass significantly in the topsoil (0–10 cm) of all three steppe types (p < 0.05, Table 3). The largest amounts of PLFA biomass were found in grasslands of FS with ca. 225 nmol PLFA g⁻¹ soil, while grassland soils in TS and DS had a similar level containing ca. 175 nmol PLFA g⁻¹ soil. Cropland soils had a similar PLFA biomass of ca. 115 nmol PLFA g⁻¹ soil irrespective of steppe type. The amount of PLFA biomass relative to soil OC was largest in grassland and cropland soils of DS. It decreased with increasing humidity (p < 0.05, Table 3), and the smallest values were detected in grasslands of FS and TS and croplands of FS (Table 3). Land-use change from grassland to cropland has not significantly changed the OC-based PLFA biomass in any steppe type. However, grassland soils of FS tended to have higher PLFA biomass relative to total OC than cropland soils. Fungal PLFA biomass decreased significantly due to grassland to cropland conversion in soils of FS and TS (p < 0.05), while this decrease was not significant in DS. The fungal PLFA biomass declined with increasing aridity from FS to DS, though not significant. The fungi : bacteria ratio was significantly larger in grasslands than in croplands of FS (p < 0.01), while the difference between grasslands and croplands was smaller in TS (p = 0.2) and no difference was found in DS (Table 3). Drier climate increased the Gram+ : Gram− ratio significantly in grasslands (p < 0.001), while no trend was apparent for croplands. The conversion from grassland to cropland reduced the Gram+ : Gram− ratio only in DS significantly (p < 0.05, Table 3).

Nonmetric Multidimensional Scaling showed PLFAs assigned to Gram− and fungi were slightly more abundant in FS, whereas PLFAs attributed to Gram+ and protozoa were relatively more abundant in DS (Fig. 5a). The effect of land-use type on the PLFA-based microbial community composition, on the other hand, was less clear. Only the group of unspecific bacterial PLFA tended to a larger relative abundance in croplands, while fungal PLFA tended to be slightly more abundant under grasslands (Fig. 5b). Results from ADONIS showed that steppe type (R² = 0.22, p = 0.001) had a stronger effect on the microbial community composition than land-use type (R² = 0.10, p = 0.001; Fig. 5a,b). The largest difference between the microbial communities existed between forest steppe and dry steppe (Table S4; R² = 0.25, p = 0.003), while the difference between typical steppe and dry steppe was smaller (R² = 0.15, p = 0.024) and no significant difference was evident between forest steppe and typical steppe (R² = 0.07, p = 0.381). Conversion from grassland to cropland had a different effect on microbial communities depending on steppe type, as indicated by the significant interaction between steppe type and land-use type (R² = 0.11, p = 0.01; Fig. 5c). Accordingly, LUC caused a decrease of PLFA assigned to fungi only in FS, while PLFA representing Gram+ decreased only in DS, as is also shown by the fungi : bacteria ratio and Gram+ : Gram− ratio in Table 3. It is important to note that the effect of steppe type and land-use type on the microbial community was small, as R² values range between 0.10 and 0.22.

3.2.4. Aggregate stability

Soil aggregate stability decreased significantly after conversion from grassland to cropland in all three steppe types to a similar extent (p < 0.05, Table S5). Grassland soils had a ΔMWD between 0.28 ± 0.17 (FS) and 0.40 ± 0.05 (TS), while ΔMWD values of croplands ranged between 1.37 ± 0.08 (FS) and 1.62 ± 0.17 (DS). Lower aggregate stability was related to lower OC contents (Fig. 6). In the studied soils, aggregate stability was not related to the amount of fungal PLFA (Table S6). Land-use change from grassland to cropland caused a change in the aggregate size class distribution in all steppe types, with a preferential decrease of aggregates >1 mm and a subsequent increase of aggregates <1 mm (Fig.S4).

4. Discussion

4.1. Climate-dependent effect of LUC from grassland to cropland on soil OC stocks

Soil OC stocks of the Kulunda steppe decreased from FS to DS, and thus followed a precipitation gradient (Fig. 2). As shown by

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**Table 3.** PLFA data in 0–10 cm depending on land-use type and steppe type. Values are given as arithmetic mean ± standard error of the mean. As one sample from TS grassland and two samples from DS cropland were discarded during measurement, the sample size is 57 instead of 60.

<table>
<thead>
<tr>
<th>Steppe type</th>
<th>Land-use type</th>
<th>No. plots</th>
<th>n</th>
<th>PLFA biomass nmol g⁻¹ soil</th>
<th>PLFA biomass relative to soil OC nmol g⁻¹ soil OC</th>
<th>fungal PLFA biomass nmol g⁻¹ soil</th>
<th>fungi : bacteria ratio</th>
<th>Gram+ : Gram− ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>FS</td>
<td>grassland</td>
<td>3</td>
<td>9</td>
<td>224.8 ± 41.4aA</td>
<td>4.62 ± 0.24aA</td>
<td>8.51 ± 3.22aA</td>
<td>0.037 ± 0.009aA</td>
<td>2.33 ± 0.21aA</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>3</td>
<td>9</td>
<td>114.4 ± 28.2b**A</td>
<td>3.48 ± 0.37aA</td>
<td>2.39 ± 0.94b**A</td>
<td>0.020 ± 0.003b**A</td>
<td>2.75 ± 0.25aA</td>
</tr>
<tr>
<td>TS</td>
<td>grassland</td>
<td>2</td>
<td>5</td>
<td>174.6 ± 25.8aA</td>
<td>4.56 ± 0.26aA</td>
<td>5.05 ± 0.69aA</td>
<td>0.030 ± 0.009aA</td>
<td>3.04 ± 0.36aA</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>2</td>
<td>6</td>
<td>116.8 ± 9.3b**A</td>
<td>6.05 ± 1.98aB**</td>
<td>2.56 ± 0.43B**</td>
<td>0.023 ± 0.006aA</td>
<td>2.51 ± 0.37aA</td>
</tr>
<tr>
<td>DS</td>
<td>grassland</td>
<td>4</td>
<td>12</td>
<td>178.7 ± 20.6aA</td>
<td>6.21 ± 0.37aA</td>
<td>4.39 ± 0.88aA</td>
<td>0.025 ± 0.002aA</td>
<td>3.53 ± 0.07aB**</td>
</tr>
<tr>
<td></td>
<td>cropland</td>
<td>6</td>
<td>18</td>
<td>117.6 ± 10.8b**A</td>
<td>6.15 ± 0.35aB**</td>
<td>2.88 ± 0.16aA</td>
<td>0.026 ± 0.002aA</td>
<td>3.02 ± 0.06B**</td>
</tr>
</tbody>
</table>

Lowercase letters indicate significant differences between land-use types within steppe type, and uppercase letters indicate significant differences between steppe types within land-use type (p-value, 0 < **** < 0.001 < ** < 0.01 < * < 0.05). Abbreviations: FS = forest steppe, TS = typical steppe, DS = dry steppe.
Fig. 5. Two-dimensional Nonmetric Multidimensional Scaling (NMDS), showing the effect of a) steppe type, b) land-use type and c) the interaction between steppe type and land-use type on the microbial community composition in 0–10 cm. The stress value of the NMDS is 0.10. Ellipses indicate 95% confidence regions for the group centroids. Results from ADONIS show that steppe type has a stronger effect than land-use type. Land-use change has a different effect in each steppe type as the interaction between steppe type and land-use type (Steppe x LUT) is significant. As one sample from TS grassland and two samples from DS cropland had to be discarded during measurement, the sample size n is 57 instead of 60. Abbreviations: LUT = land-use type, FS = forest steppe, TS = typical steppe, DS = dry steppe, grass = grassland, crop = cropland, Actino = actinomycetes, Gram– = gram-negative bacteria, Gram+ = gram-positive bacteria, UnspcBact = unspecific bacteria, Prot = protozoa.

Fig. 6. Relation between aggregate stability (ΔMWD) and log$_e$(soil organic carbon) (%) for topsoils in the three different steppe types. The points show arithmetic means ± standard error of the mean of each plot. The dashed lines connect all paired plots within one site. The solid line corresponds to the trend line over all plots within one steppe type.
Saparov et al. (2007) for steppe soils of Kazakhstan, there is a strong impact of plant residue input on OC stocks. Larger precipitation enhances net primary productivity and thus increases biomass input into the soil which eventually elevates soil OC stocks.

Conversion from grassland to cropland caused an average decline in the OC stock of roughly one third for the upper 25 cm, which was independent from climate (Fig. 2). For a site in FS, this decline occurred fast within the first five years, demonstrating the tremendous impact of soil disturbance (Fig. 3). The magnitude of the soil OC loss after conversion from grassland to cropland in the Kulunda steppe is in line with data from previous studies of similar soils. In North American prairies grassland to cropland conversion caused a soil OC stock decline of 24–32% (Beniston et al., 2014; Doran et al., 1998; VandenBygaart et al., 2003). In Chernozems of European Russia topsoil OC stocks decreased by 27–40% due to LUC from grassland to cropland (Mikhalina et al., 2000; Rodionov et al., 1998). Modelling results for temperate soils (MAT 0–18 °C) showed a soil OC decrease of 36 ± 5% in 0–27 cm due to conversion from grassland to cropland with ca. 80% of OC being lost within the first five years (Poepplau et al., 2011). Thus, the OC stock declines observed for Siberian steppe soils as a result of LUC were comparable to those previously reported for steppe soils of European Russia and prairie soils of North America. The aim of our study was not only to elucidate the effect of LUC on soil OC stocks, but particularly how this effect changes under different climatic conditions. In contrast to our hypothesis, we did not find larger OC losses upon LUC in drier climate (Fig. 2).

Surprisingly, the LUC-induced decline of soil OC stocks was independent from climatic conditions, though we showed that the proportion of labile POM tended to increase with drier climate (6.9 ± 0.9% of total soil OC in A horizons of grasslands in FS vs. 9.8 ± 0.9% in DS; Table 2). A possible reason is that in the Chernozems and Kastanozems under study POM comprised only a small proportion (<10%) of total OC and contributed little to the overall LUC-induced decline of OC stocks. Thus, it is not the stability of POM but rather that of mineral-associated OM, which dictates the relative loss of OC upon LUC. The stability of MOM was obviously not climate-dependent in the studied region (Fig. 4; same HF-OC stock change due to LUC in FS and DS), wherefore neither the decline of total soil OC stocks showed a climate dependence. In this regard, our results are different from what was found in previous work from other regions of the world. Burke et al. (1989) and Guo and Gifford (2002) found relative OC losses after grassland to cropland conversion positively correlated to precipitation until a MAP of 600 mm in soils from North America. On the other hand, Poepplau et al. (2011) found no correlation between precipitation and relative OC loss as a result of LUC but an attenuating effect of clay in temperate soils.

Regarding of parameters which determined the decline of soil OC due to LUC, we encountered clay content, pH and bulk density as significant environmental factors for the OC content in the studied Kulunda soils (Section S1; Table S8). This is in agreement with previous work (e.g. Schimel et al., 1994) and supports conclusions about the primary importance of these variables on soil OC contents along climate and land use gradients.

In summary, our results suggest that drier climate in the course of climate change is not expected to change the magnitude of LUC on soil OC levels in the soils under study.

4.2. Protection of soil OM on mineral surfaces and within aggregates

Particulate OM is supposed to be a labile fraction with fast turnover rates whereas mineral-associated OM is considered more stable with slower turnover rates (Kleber et al., 2015; von Lützow et al., 2006). In steppe soils, POM is believed to play an important quantitative role in terms of soil OM dynamics as it contributes substantially to total OC (>20%) in Chernozems of Canada (Plante et al., 2010), European Russia (Breulmann et al., 2014; Kalinina et al., 2011), or China (Steffens et al., 2010). However, astonishingly, in soils of the Siberian Kulunda steppe POM was of minor relevance as it accounted for maximally 10% of total OC (Table 2). Land-use change from grassland to cropland reduced particulate OC relatively more than mineral-associated OC, which is in line with previous reports from soils of the temperate zone (Poepplau and Don, 2013). However, due to its small contribution to total OC, the absolute contribution of particulate OC to the total OC stock decline was small. About 80–90% of lost OC has been associated with minerals (Fig. S2). In fact, a considerable part (20–50%, see Fig. 4) of mineral-associated OC is vulnerable to soil-management and possibly part of a labile OM pool. Thus, OC bound to minerals in the soils under study is not necessarily stabilized against decomposition by microorganisms. Weaker mineral-organic associations may result from the higher soil pH, absence of reactive minerals, or generally weaker bondings of OM to minerals (e.g. OM held by “Ca2+ bridges”; Mikutta et al., 2007; Kleber et al., 2015). However, 14C ages from mineral-bound OC of 500–2900 years B.P. in cropland soils also show that a considerable part of this fraction remained protected from decomposition. This suggests that mineral-associated OC is a heterogeneous fraction, which at the same time comprises labile and stable OC components, with the labile forms being also vulnerable to LUC.

Besides the protection of OC on mineral surfaces, aggregates are known to protect OM against microbial decomposition over decadal or even centennial time scales due to the physical separation of the aggregate-occluded organic substrate from the microbial community (Stockmann et al., 2013; von Lützow et al., 2008). Particularly in agro-ecosystems, aggregate stability was found to be a major determinant for OC contents (Bromnick and Lal, 2005). Like reported in studies from other regions (e.g., Follett et al., 2015; Six et al., 1998), aggregate stability decreased significantly due to LUC from grassland to cropland also in the soils under study and this effect did not depend on the climatic conditions (Table S5). The reduction of aggregate stability is possibly related to a decreased OM input in agricultural systems, as the input of fresh OM would favor the formation of stable aggregates (Bossuyt et al., 2001; Steffens et al., 2009). This matches our finding that aggregate stability and OC were positively correlated (Fig. 6). In addition, an increased macroaggregate (250–2000 μm) turnover in croplands and the concurrent decrease of the formation of stable microaggregates (53–250 μm) within macroaggregates was shown to reduce the potential of arable soils to store OC (Six et al., 2000). The correlation between aggregate stability and OC was therefore also shown in previous studies (Al-Kaisi et al., 2014; Follett et al., 2015).

The formation of stable macroaggregates is supported by the presence of soil fungi wherefore they play a major role in the sequestration of OM in agricultural systems (Frey et al., 1999; Guggenberger et al., 1999). Unlike expected, we did neither find aggregate stability to be correlated to the amount of fungal PLFA (as a proxy for the fungal biomass; Table S6) nor was the amount of PLFA biomass related to aggregate stability (data not shown). This could be due to the large clay contents in soils of the Kulunda steppe, with average clay contents of 26–34%. Kiem and Kandelier (1997) reported that microbial-induced aggregate stabilization is of less importance in clayey soils, as minerals already act as strong binding agents. Thus, soil fungi seemingly do not mediate aggregate stability in the soils under study. In soils of FS, grassland to cropland conversion reduced the fungi : bacteria ratio significantly (Table 3). This can be explained by the destruction of fungal hyphae due to soil tillage (Bromnick and Lal, 2005; Six et al., 2006) or by different residue placement under grassland as
compared to cropland (Six et al., 2006). Frey et al. (2000) showed that the presence of surface residues under grassland favors fungal communities, as fungi are able to bridge the interspace between residues and bulk soil and translocate N-rich compounds to the C-rich, but N-depleted surface litter. However, the fungi : bacteria ratio did not decrease after grassland to cropland conversion in DS. This is assigned to initially lower fungi abundance under grasslands in DS, therefore diminishing the negative effect of LUC on fungi (Calderón et al., 2000).

Summing up, mineral-associated OM was the dominant OM fraction in the soils under study and the main source of declining OC stocks upon LUC. The decline of soil OC was associated to a concurrent decrease in aggregate stability, which in turn was not related to the amount of fungal PLFA.

4.3. Microbial abundance and community composition as affected by land-use change along the climatic gradient

Microbial biomass and OM contents of soils are intimately connected (e.g. Ingram et al., 2008), as OM serves as carbon and energy source for most soil microorganisms (Drenovsky et al., 2004). The larger microbial PLFA biomass in topsoils of the Kulunda steppe under grassland than under cropland can therefore, largely be explained by the larger OC stocks in grasslands. However, irrespective of steppe type and initial microbial biomass in grasslands, the PLFA biomass decreased to a similar level in cropland soils (Table 3). Thus, higher OC contents in arable soils of FS do not result in a larger abundance of microbes. Moll et al. (2015) showed that the abundance of fungi is largely dependent on the amount of residue inputs in arable topsoils, while Xiao et al. (2015) found this for the whole microbial community in steppe soils of Inner Mongolia. The similar amount of PLFA biomass in croplands along the climatic gradient could therefore be attributed to similar plant residue inputs across croplands throughout the Kulunda steppe.

The composition of the microbial community is sensitive to changes in environmental conditions, such as climate or the quantity and quality of litter inputs (Fanin et al., 2014; Frey et al., 2008). Also LUC-related soil disturbance was found to change microbial communities significantly (Li et al., 2014; Zhang et al., 2014). PLFA is a rapid and sensitive method to detect changes in the microbial community composition, however, it cannot compete with rRNA methods in the phylogenetic resolution by which a microbial community can be characterized (Frostegård et al., 2011). Nevertheless, PLFA analysis of soils of the Kulunda steppe revealed that the microbial community composition was more controlled by steppe type than by land-use type and the climatic effect on microbial communities was different in each land-use type (Fig. 5). Changes in the microbial community composition due to climatic shifts were more pronounced under grassland than under cropland, as indicated by a sharp increase in the Gram+ : Gram− ratio from wet to dry climate under grassland, while no trend was apparent under cropland (Table 3). The relative amount of fungal PLFA was lower under dry than wet climate (Fig. 5). Hence, drier conditions are expected to cause a relative decrease of fungi, while gram-positive bacteria would relatively increase. This is in contrast to some studies that concluded fungal biomass being superior to bacteria at conditions of water stress (Schimel et al., 2007; Drenovsky et al., 2004; Zhang et al., 2005). But our finding is supported by Zogg et al. (1997) and Frey et al. (2008), who found a smaller contribution of fungi and a larger contribution of Gram+ with increasing temperature in warming experiments, i.e. drier soil conditions. Billings and Ballantyne (2013) hypothesized that the thicker cell walls of Gram+ makes them more resistant to dry conditions than Gram−. In addition, De Vries and Shade (2013) noted, that the ability of Gram+ to sporulate allows them to withstand disturbances, including drought. In summary, our data emphasize a small but significant climatic effect on PLFA-based microbial groups, which is more pronounced in grassland than in cropland soils. Drier climate in the future is expected to change the microbial community more than the conversion of the soils from grasslands to croplands.

5. Conclusions

The main goal of the current study was to determine the climate-dependent effect of land-use change from grassland to cropland on soil OM in a semi-arid steppe ecosystem of Siberia. Cultivation of grassland soils decreased OC stocks by about 31% in the upper 25 cm, which was independent from climate. The loss of OC went along with a reduction of aggregate stability but this was not related to the amount of fungal PLFA. Unlike expected, POM accounted generally for only <10% of the total OC pool, and the majority of OC across all steppe types was bound to minerals (>90%). Despite the low 14C age of POM (<400 yrs B.P.) and large relative losses due to soil cultivation (up to 70%), most management-induced OC losses (80–90%) could be assigned to a decrease of mineral-bound OC. Stocks of mineral-associated OC decreased in A horizons by 20–50% due to cultivation of grasslands. This demonstrates that a considerable portion of mineral-bound OM is vulnerable to LUC, while other mineral-associated OC components are stable and largely unaffected by LUC, as can be inferred from the high 14C ages (500–2900 yrs B.P.) of mineral-bound OM in croplands. PLFA-based soil microbial communities varied along the climatic gradient with larger relative abundance of fungal PLFA and Gram− bacterial PLFA in moist climate and a larger relative abundance of PLFA assigned to gram-positive bacteria under dry conditions. The climate had a larger impact on microbial communities than LUC, and communities under grassland were more affected by climatic shifts than those under cropland.

We conclude that at the predicted drier climate in the semi-arid steppes of southern Siberia there will be a pronounced OC loss under both, grassland and cropland, due to generally reduced biomass inputs under dry conditions. Converting grassland to cropland under drier conditions will keep the LUC-induced OC losses at the same critical level as is observed in soils at present. Soil microbial communities are expected to change more as a result of drier climate than due to the conversion from grassland to cropland.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.10.022.
References


