



Spotting ethylene in forest soils—What influences the occurrence of the phytohormone?

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Received: 24 January 2023 / Revised: 14 August 2023 / Accepted: 15 August 2023 / Published online: 15 September 2023
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Abstract

Due to the rapid microbial degradation, ethylene (ethene; C₂H₄) detection in most soils is difficult. The knowledge about factors favoring the occurrence of C₂H₄ is mainly based on laboratory experiments which are not necessarily representative for real field conditions in forest soils. We report results from a total of 24 measuring plots in southwest Germany and more than 50,000 gas samples, including long-term forest monitoring sites and other study sites involving liming, artificial soil compaction, and temporary waterlogging. Many of the patterns and influencing factors identified in the laboratory were confirmed. In well-aerated forest soils, C₂H₄ was detected in 1.3% of the gas samples. C₂H₄ detection was higher at oxygen (O₂) concentrations below 10% in the soil. The effect was positively correlated with bulk density in compacted soils and CO₂, CH₄, and N₂O concentrations—factors that indicate reduced microbial activity and thus also facilitate the detection of C₂H₄. It could be detected 3.5 times more often in spruce than in beech stands, indicating that plant species plays a role and was not found to follow any distinct spatial or temporal pattern with the exception of seemingly random spatio-temporal clusters of root-born C₂H₄ near large roots of spruce trees. The long observation period and large dataset of this field study allowed valuable insights into C₂H₄ occurrence in forest soils under natural conditions supporting the theory that the plant hormone C₂H₄ is produced as a warning for anaerobic soil areas that are limiting root growth.

Keywords C₂H₄ · Ethylene · Ethene · Field study · Long-term measurement · Soil gases

Introduction

Most of the studies on soil gases in forest soils focus on soil respiration and other greenhouse gases. However, other trace gases can also provide indicators for important soil ecological processes and point to stress-related climate consequences (Conrad 1996). In plant physiology, the gaseous plant hormone C₂H₄ plays an important role throughout the whole life cycle in plants, from seedling to mature plants (Bakshi et al. 2015; Sisler and Yang 1984). Being associated with the ripening process (Reid 1995), C₂H₄ can induce abscission (enhanced dropping of leaves, flowers, and fruits) or senescence (accelerated aging of the plant). Plants produce C₂H₄ (Sisler and Yang 1984), whereas microorganisms and fungi can produce and degrade it (Fukuda et al. 1993; Primrose 1979). If C₂H₄ concentrations in the soil gas phase exceed certain thresholds, plants will be negatively influenced. Even though threshold values depend on plant species, C₂H₄ concentrations >0.01 μmol mol⁻¹ were identified to already have effects on plant growth, whereas C₂H₄

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concentrations $>10 \mu\text{mol mol}^{-1}$ cause severe plant damages (Primrose 1979; Smith and Russell 1969). C_2H_4 induces distinct changes in plant growth and morphology known as “triple response” (Binder 2020; Bleecker and Kende 2000; Zhong et al. 2014). These responses collectively enable plants to adapt to stressful conditions caused by mechanical obstacles or anaerobic soil atmosphere (Abeles et al. 1992).

In soils, the occurrence and concentration of C_2H_4 are affected by several physical and chemical soil properties. Smith and Dowdell (1974) list soil temperature, oxygen (O_2) availability, and soil water content (SWC) as most important factors, which alter the production and diffusion of C_2H_4 in and out of soil. These factors and additionally soil organic matter content (SOM) and soil pH (Otani and Ae 1993), change the rhizosphere microbial composition influencing C_2H_4 production dynamics. Roots can produce C_2H_4 under low-oxygen conditions, such as waterlogged or flooded soil since oxygen deprivation activates specific enzymes involved in C_2H_4 biosynthesis, leading to increased ethylene production (Drew 1997) and C_2H_4 degradation is inhibited (Smith and Restall 1971). This response helps plants cope with oxygen-deficient conditions. Physical damage or mechanical stress to roots, such as compaction, root displacement, and contact with stones can also stimulate C_2H_4 production (Mattoo et al. 1991). This also results in a positive correlation of soil bulk density (BD) to C_2H_4 detection (Danish et al. 2020; Smith and Restall 1971). In response to mechanical stress, C_2H_4 production helps coordinate root growth and morphology, allowing the plant to navigate and adapt to its environment. C_2H_4 production varies throughout the different developmental stages of roots (Negi et al. 2008). Further positive correlations with C_2H_4 occurrence were found to SWC (Dowdell et al. 1972), soil temperature (Xu and Inubushi 2009), and CO_2 concentration (Cornforth 1975). However, when related to SWC, increased C_2H_4 production was also observed during drought stress contributing to the regulation of plant growth (Sharp et al. 2000). On the contrary, other effects like tree type (Elsgaard 2001), OM content (Cornforth 1975; Goodlass and Smith 1978), and soil pH (Lindberg et al. 1979; Zechmeister-Boltenstern and Smith 1998) on C_2H_4 are not consistent between studies.

The C_2H_4 is a particularly reactive gas, normally consumed directly in the vicinity of its production and for this reason concentrations are generally low and accumulation of C_2H_4 occurs mostly in hot spots, making detection particularly difficult. Apart from incubation experiments, the detection of C_2H_4 in the field depends not only on the amount produced but also on the conditions that favor the accumulation of the trace gas in the soil and delay its degradation.

Dowdell et al. (1972) conducted a field study to investigate C_2H_4 occurrence in natural forest soils. Hunt et al. (1981), Meek et al. (1983), Otani and Ae (1993), and Smith and Dowdell (1974) conducted field studies with additional treatments of soil samples in the laboratory. Yet, a comprehensive field

investigation of C_2H_4 occurrence in soil has not been conducted. One reason for the paucity of (field) studies is the rare and accidental occurrence of C_2H_4 in non-compacted, well-aerated soils which mainly act as a net sink of C_2H_4 (Abeles et al. 1971; Arshad and Frankenberger 1990; Hendrickson 1989). The rare and accidental occurrence of C_2H_4 challenges the concept of short-term (<4 years) studies and requires long-term data series to get reliable results of C_2H_4 occurrence and contribute to a better understanding of C_2H_4 influencing factors in forest soils.

Our study will report on field observations of C_2H_4 occurrence and quantity in soil gas phase at forest sites. Our objectives were to quantify the occurrence of C_2H_4 in well-aerated forest soils with different tree species, artificially compacted soil, waterlogged forest sites, limed soils and to identify the influencing factors. The investigated soils provide properties which have so far been identified primarily in laboratory experiments as potential factors influencing C_2H_4 production, C_2H_4 degradation and transport in the soil ecosystem.

Material and methods

Study sites and plots

Data from 24 study plots set up at 14 sites in southwest Germany (Fig. 1) were used, originating from long-term soil gas monitoring ($n = 13$), and project studies ($n = 11$) on liming and soil compaction including in total 50,922 analyzed soil gas samples. The large number of plots allows us to investigate the effect of various soils, treatments, and stands on ethylene occurrence (Fig. 2).

The plots have a mean annual temperature between 7.4 and 9.6 °C and a mean annual precipitation total of 700 to 1385 mm. They are located at altitudes ranging from 172 to 816 m a.s.l. The acid topsoil (0–5 cm) had pH (KCl) values ranging from 2.9 to 4.1 and in humus from 2.6 to 5.0. Sites on carbonate rock or with clay texture are not included in the study. Each site has at least one plot area with one adjustment of multiple passive soil gas samplers.

Long-term environmental monitoring plots (LTEMPs)

Soil gas data of 13 plots at 6 different sites (Table 1) originate from long-term environmental monitoring plots (LTEMP) which are part of the International Cooperation Program Forests (ICP Forests). Five of the six sites have an adjacent beech plot (*Fagus sylvatica* L.) to the spruce plot (*Picea abies* L.), and two of the sites have additional liming plots. More detailed information on the long-term soil gas monitoring concept is presented by Maier et al. (2020). During establishment, permanent soil gas sampling positions were mapped with neighboring roots and trees, allowing for subsequent identification of root-influenced gas samplers. In

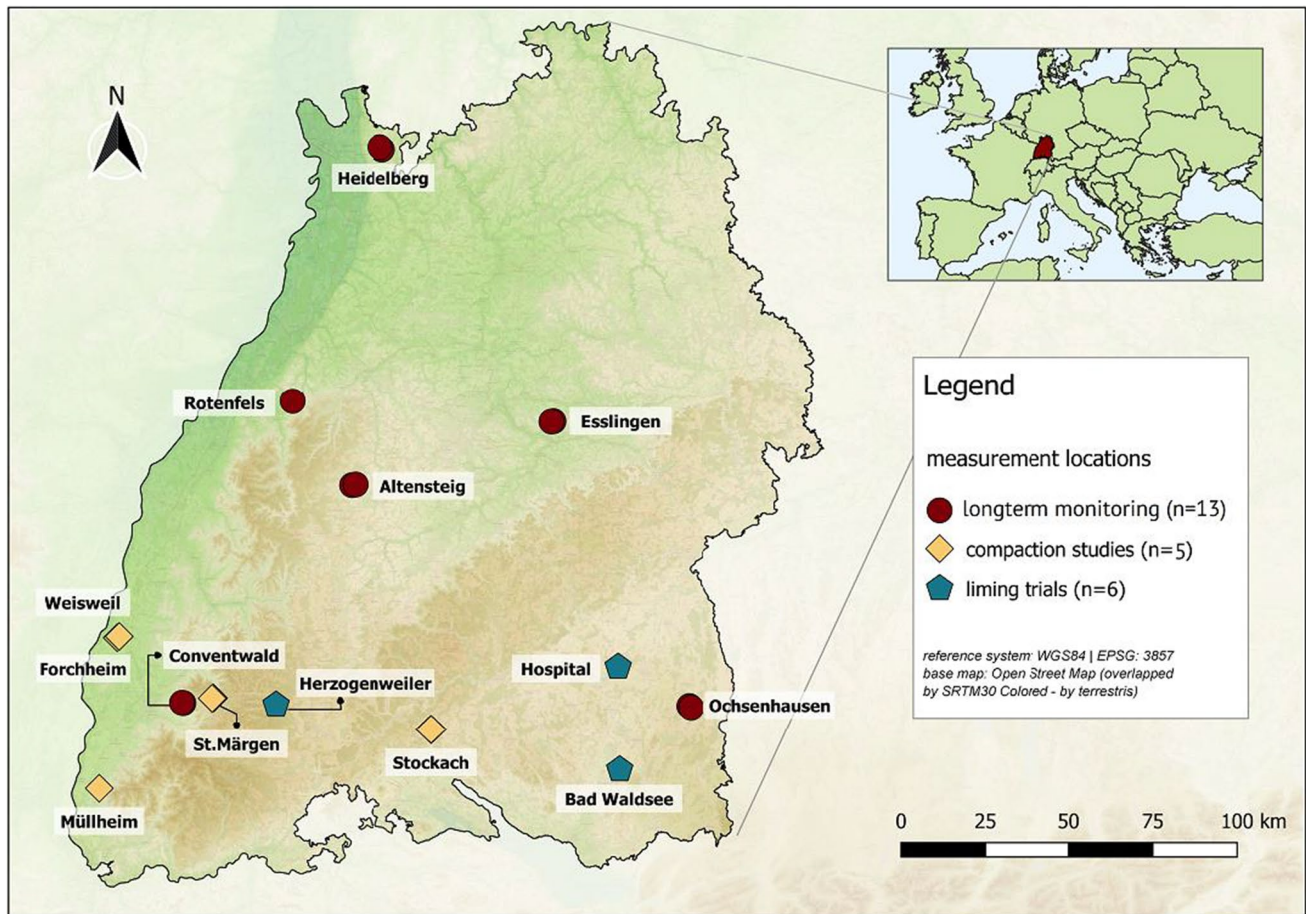


Fig. 1 Locations of the 24 study plots in Baden-Württemberg, southwest Germany. Symbols refer to their study category assignment

addition to the general site characteristics (Table 1), monitoring data on soil temperature, soil water content, as well as climate and soil gas diffusivity are available. The discretization of the SWC was modeled with LWF Brook 90 (Schmidt-Walter et al. 2020), and the soil temperature was modeled in Hydrus 1D (Maier et al. 2020; Simunek et al. 2005)

Project studies: soil compaction studies

Soil compaction studies were conducted at SM (Horn et al. 2007) and MU (Schäffer 2012) to investigate the effect of artificial soil compaction on soil functions. In these studies, the soil was compacted by typical forestry operations (e.g., operation of heavy forestry machinery). Soil gas was sampled within, and next to, wheel tracks as well as in nearby, non-compacted control areas as reference (Fig. 7). In WW and FO, the soil compacted by heavy machinery was afforested.

The soil at the ST site (Schack-Kirchner and Hildebrand 1998) was also compacted by heavy machinery. However, after 4 years, when soil gas was sampled, surficial signs of deformation were no longer detected. Additionally, temporary waterlogging and O_2 deficiency were evident in the appearance of distinct

hydromorphic features, typical for a Stagnosol, which is why the ST site was also assigned to the compaction study. General soil gas data (e.g., greenhouse gas fluxes) were already discussed in former publications (Schack-Kirchner and Hildebrand 1998; Schäffer 2012; Schäffer and Von Wilpert 2004), but C_2H_4 was largely omitted.

Project studies: liming trials

The study sites of the liming trials (BW, HW, HO) had previously been subject to intensive analysis after liming, which showed increased soil pH values and enhanced base saturation in limed soils (Jansone et al. 2020) compared to a corresponding unlimed reference plot nearby. Soil gas data should reveal a changing diffusivity of the soil due to liming.

Sampling and analyzing soil gas samples

The measurement results were obtained from all plots via the analysis of soil gas samples that were collected at regular intervals. To collect soil gas, passive soil gas samplers were used according to methods described by Schack-Kirchner et al. (1993)

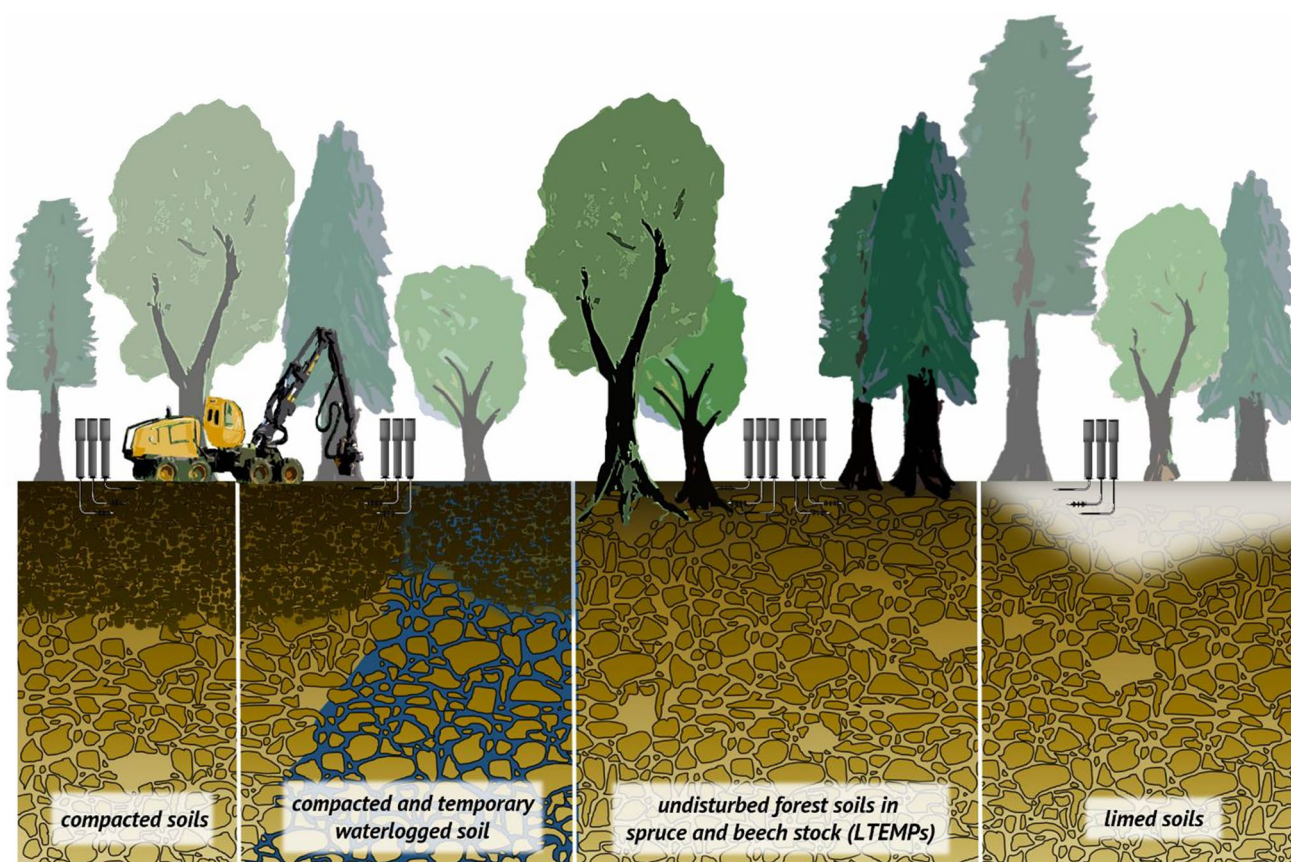


Fig. 2 The different soils, treatments, and site characteristics of the evaluated study categories, in which C_2H_4 in field experiments has been measured

(Fig. 8). An artificially perforated steel tube was placed in the soil, acting as a macropore and, thus, allowing diffusive gas transport via a cannula into a gas vial (4 ml) initially filled with helium. Although all gas samples were collected and analyzed in the same way, there is no uniform experimental design for the plots as our study is only an evaluation of existing data sets. As a consequence, the definition of the measurement depths was done according to the objectives of the study at that time. In well-aerated forest soils (LTEMP and liming trials), the focus was on microbial active topsoil, so gas samplers were only installed in humus (+3/+2 cm) and at depths of 0 cm (at the humus/mineral soil interface), –5 cm, and –10 cm. At each depth level, there are at least three (though typically five) replicates resulting in about 20 soil gas samplers on each of the plots. For the compaction study plots, the focus shifted to deeper soil layers. In order to capture the totality of soil changes in these plots, gas samplers were located at –15 cm, –20 cm, –25 cm, –30 cm, and –35 cm (Table 2). The exact position and number of gas samplers here can be seen in Fig. 7.

As gas exchange between soil pore space and the gas vial is passive, the gas composition in the vials represents the average soil gas atmosphere of the most recent hours; however, it is possible for the vials to still contain components of the soil

gas atmosphere of the previous day if high SWC slowed down the gas exchange. Similarly, if the cannula is clogged or there is water in the perforated steel tube of the samplers, the gas exchange with the soil gas phase cannot be completed. During the subsequent determination of the soil gas composition, a remaining helium content is then determined. These vials were then eliminated from further evaluation.

The gas vials were collected in a regular and at least 4-week cycle, and the soil gas composition (N_2 , O_2 , Ar, CO_2 , CH_4 , C_2H_4 , N_2O) was immediately analyzed in the laboratory with a gas chromatograph (GC) Clarus 680 GC (Perkin Elmer, Waltham, MA, US). In the GC, C_2H_4 was separated by a CP-SilicaPLOT column (Agilent Technologies) and determined by a flame ionization detector (FID). The respective GC system that was used did change over the years; however, the configuration of the GC system remained the same (more details in Maier et al. (2020)). The limit of quantification (LOQ) for C_2H_4 measurements was $0.12 \mu\text{mol mol}^{-1}$ ($10 \times$ standard deviation (SD) of C_2H_4 scattering of the calibration gas), and the limit of detection (LOD) was $0.036 \mu\text{molmol}^{-1}$ ($3 \times$ SD). LOD and LOQ values were validated by mixing and testing the signal to noise ratio of an artificial air mix, with C_2H_4 concentrations two times higher than the LOQ.

Table 1 General information on site data and soil of the investigated plots of the associated studies/treatments

Site	Tree type	Plot abbr.	Sampling period	Soil type (IUSS 2015)	Humus type	Texture (FAO)	BD [g cm ⁻³]	Treatment
Long-term environmental monitoring plots (LTEMPs)								
Altensteig	FA	AS _B	2010–2021	Stagnic Cambisol	Mull	Silt loam	1.02	
	PI	AS _S	2010–2021	Haplic Cambisol	Mull	Sandy loam	1.16	
Conventswald	FA	CO _B	2010–2021	Skeletal Cambisol	Moder	Silt loam	0.87	
	PI	CO _S	1998–2021	Haplic Cambisol	Moder	Sandy loam	0.63	
Esslingen	FA	ES _B	2010–2021	Haplic Stagnosol	Mull	Sandy loam	1.35	
	PI	ES _S	1998–2021	Vertic Stagnosol	Moder	Clay loam	1.28	
Heidelberg	FA	HD _B	2010–2021	Haplic Stagnosol	Mull	Loam	1.13	
	PI	HD _S	1998–2021	Haplic Cambisol	Moder	Sandy loam	1.05	
	PI	HD _L	1998–2021	Haplic Cambisol	Moder	Sandy loam	1.32	1984: 5 t ha ⁻¹ CaMg(CO ₃) ₂
Ochsenhausen	FA	OC _B	2010–2021	Epidystic Luvisol	Moder	Silt loam	1.14	
	PI	OC _S	1998–2021	Abruptic Luvisol	Moder	Silt loam	0.83	
	PI	OC _L	1998–2021	Abruptic Luvisol	Moder	Loam	0.76	1994: 10 t ha ⁻¹ CaMg(CO ₃) ₂
Rotenfels	PI	RO _S	1998–2021	Hyperalbic Podzol	Rawhumus	Loamy sand	1.02	
Compaction studies (different compaction sites compared to non-compacted control sites)								
St Märgen*	PI-AB	SM	06-2001 to 01-2005	Luvisol-Cambisol	Moder	Sandy silt loam	(0.76)-0.54°	2001: 4×5 tracks + 1 control plot
Müllheim ^Δ	QR-FA	MU	05-2009 to 04-2011	Luvisol	Mull	Clayey silt loam	(1.63)-1.23°	2009: 3 tracks + 4 control plots
Weisweil	D	WW	12-2000 to 11-2001	Gleyic Luvisol	-	Loam	(1.55)-1.10°	2000: 5 different compacted tracks
Forchheim	QR-FA	FO	11-2000 to 04-2002, 05-2005 to 11-2005	Gleyic Luvisol	Mull	Sandy loam	(1.22)-1.12°	2000: 1 track with different compactations
Stockach*	PI	ST	06-1994 to 10-1994	Stagnosol	Moder	Silty loam	(1.5)	1990: compaction
Liming study (limed and unlimed reference plot per site)								
Bad Waldsee	PI-FA	BW	06-2018 to 10-2019	Cambisol	Mull	Loamy sand	(0.96) 1.00	1983/84: 3 t ha ⁻¹ CaCO ₃ + 2003: 6 t ha ⁻¹ CaMg(CO ₃) ₂
Herzogenweiler	AB-PI	HW	06-2018 to 11-2019	Stagnosol	Moder	Loamy sand	(1.06) 1.04	
Hospital	PI-FA	HO	06-2018 to 10-2019	Stagnosol	Moder	Silty loam	(0.82) 0.90	

Tree types: FA beech, PI spruce, QR oak, AB fir, PD Douglas fir

BD values are mean values of all undisturbed soil samples in 0 to –10 cm depth, except MU (0 to –15 cm) and WW and ST (both 0 to –30 cm)

Values in brackets “()” reference to the treatment plots either compacted sites or limed plots

°Maximum (highest compaction) and minimum (non-compacted site) BD values

Sources for all data of the plot: *Schack-Kirchner and Hildebrand (1998), ^ΔSchäffer (2012), *Schäffer and Von Wilpert (2004); all other values FVA-BW

Statistical analysis

The C₂H₄ concentration dataset is left-censored and contains a high proportion of true-zero measurements (96%). Since a proper approach could not be found in related studies dealing with true-zero and left-censored data simultaneously (Brown 2008; Guideline 2005; Proctor 2008), an in-house procedure was developed based on Blackwood (1991), Helsel (2011), and Zuur et al. (2009), who developed their methodology mainly for the evaluation of the most prominently censored datasets from survival studies. Using the in-house methodology, 22% of values >0 μmol mol⁻¹ were below LOD and 58% were below LOQ. Concentrations below LOD or LOQ were not excluded from analysis or substituted by artificial values in order to avoid artificial assumptions or bias that could lead to

incorrect results or blur information contained in the measurements (Brown 2008; Helsel 2011). Statistical analyses were conducted using the open-access software R (version 4.0.3; R Development Core Team), with a significance level set to 5%.

For an initial assessment, the total data set was divided into multiple classes. Firstly, data was classified as “C₂H₄ detection” (C₂H₄ >0 μmol mol⁻¹) or “no C₂H₄ detection” (C₂H₄ = 0 μmol mol⁻¹), which allowed for the determination of promoting and inhibiting factors on C₂H₄ occurrence. To check for significant differences, the non-parametric Wilcoxon test (also known as Mann–Whitney-U-test) was conducted. For non-parametric Spearman correlation analysis, C₂H₄ values >0 μmol mol⁻¹ and <LOD were set to 0.02 μmol mol⁻¹ and values ≥LOD and <LOQ to 0.07 μmol mol⁻¹. As suggested by Helsel (2011) values between different measurement limits were set to equal

Table 2 Spatial distribution of the C₂H₄ occurrence in compacted soils

Plot	Depth (cm)	C ₂ H ₄ occurrence (%)	Median (μmol mol ⁻¹)	Mean (μmol mol ⁻¹)	SD (μmol mol ⁻¹)
SM	2.5	12.3	0.04	0.07	0.10
SM	0	13.1	0.04	0.06	0.07
SM	-10	20.8	0.11	0.76	2.04
SM	-30	26.0	0.13	0.49	1.29
MU	-15	0.4	0.35	0.35	0.21
MU	-25	1.0	0.57	1.19	1.64
MU	-35	1.2	0.28	0.28	0.10
FO	-10	4.1	0.05	0.09	0.09
FO	-20	5.6	0.16	0.18	0.17
FO	-30	13.7	0.21	0.34	0.46
WW	-30	18.7	0.14	0.23	0.23

Data from ST is not included since the water influence dominates over all other spatial influencing factors. Mean, median, and SD values refer to samples with C₂H₄ > 0 μmol mol⁻¹

numbers respectively enables to treat data as the same ranks with a degradation of values <LOD (lower) and <LOQ (higher).

The dataset was further divided into five classes: “0 μmol mol⁻¹,” “>0 μmol mol⁻¹ <LOD,” “≥ LOD < LOQ,” “≥ LOQ < 1 μmol mol⁻¹,” and “>1 μmol mol⁻¹”. To identify environmental influencing factors such as air temperature or precipitation amount, a Kruskal–Wallis test, as a non-parametric correspondent to an ANOVA, was conducted. If a significant difference was detected, Dunn’s test with Bonferroni correction was run to identify groups responsible for difference.

The maximum likelihood estimate (MLE) approach was used to conduct summary statistics, which performed well for our data when excluding zero values and with a censored data share between 50 and 80% (Helsel 2011). In order to apply the MLE approach, the data were tested for lognormal distribution. The implementation of MLE in *R* utilizes the NADA packages developed to handle censored data. As evaluation with NADA allows the use of only one reporting limit, LOD was selected, and concentrations ≥LOD were, thus, treated as absolute values, knowing that values between

LOD and LOQ cannot be determined correctly in concentrations. For checking differences of C₂H₄ concentrations between groups, a censored data adapted *t*-test for 2-factor variables and a censored data adjusted ANOVA for > 2-factor variables were conducted. The equivalent of both tests in *R* is censored regression. If there are no more censored data in partial data sets (e.g., ST), the MLE approach or censored regression was no longer necessary.

To identify correlations to other soil gases for the overall data set, a classification approach of logistic regression was used (Nwanganga and Chapple 2020). The graphical result is an s-curve, representing the range of an event’s occurrence probability between 0 and 1 (Nwanganga and Chapple 2020). For quantifying the effect of a predictor variable, an odds ratio is used. It represents the probability that an event occurs relative to the probability of the event’s non-occurrence (Peng et al. 2002). The higher the odds ratio, the higher the influence of a predictor variable. The model is validated by a chi-squared <0.05 and *R*². With test and training data sets, and accuracy of predicted probabilities, it can further be stated whether the fitted model leads to reasonable results (Nwanganga and Chapple 2020).

Results

Long-term environmental monitoring plots

LTEMPs data represent 80% of the samples. C₂H₄ was detected at least once on every LTMEP. In proportion to the total number of gas samples, C₂H₄ was detected most frequently at ES_S (2.55%) and least frequently at ES_B (0.07%) (Table 6). Analysis of all 13 LTEMPs combined shows an average C₂H₄ detection frequency of 1.3%. The range of measured C₂H₄ concentrations is from <LOD (0.01 μmol mol⁻¹) to 23.9 μmol mol⁻¹, with a mean value of 0.78 μmol mol⁻¹. Six out of 13 plots showed median C₂H₄ concentrations <LOQ.

Censored regression showed a significant depth gradient in mineral soil, with decreasing C₂H₄ concentration as depth increases (Table 3). However, when root-induced C₂H₄ release (mainly registered in the humus layer at ES_S)

Table 3 Depth distribution of C₂H₄ occurrence in soil at all LTEMPs combined

	Depth (cm)	Number of C ₂ H ₄ -detection	C ₂ H ₄ occurrence (%)	Median (μmol mol ⁻¹)	Mean (μmol mol ⁻¹)	SD (μmol mol ⁻¹)
	+3 / +2	108	1.76	0.26	5.14	102.17
(excl.)	+3 / +2	51	0.83	0.09	0.46	0.87
	0	134	1.26	0.08	0.60	1.37
	-5	127	1.18	0.06	0.47	2.15
	-10	128	1.19	0.04	0.26 ▼	0.48

Mean, median, and SD values refer to samples with C₂H₄ > 0 μmol mol⁻¹ and are calculated with the MLE approach.

(excl.) = gas samplers of the LTEMPs in the humus layer which were excluded due to clear root influence (*n* = 57)

is excluded, the differences between C_2H_4 concentrations in the mineral soil and humus layer were no longer significant (“(excl.)” line in Table 3).

During the establishment of the plots in 1998, field maps were made in which the position of samplers and also strong roots in the near environment (<1 m distance) were registered. At these three plots (ES_S , CO_S , AS_S), episodes of clustered ethylene detection were observed at the gas samplers located closest to the roots (Fig. 9). Therefore, root influence is clearly influencing C_2H_4 hot spots and is the most important factor influencing spatial patterns.

When analyzing the temporal evolution of C_2H_4 occurrence (Fig. 9), most years show no, or minimal C_2H_4 occurrence frequency but, overall, single intensive periods of C_2H_4 release. The dataset divided into classes was compared to different environmental parameter values (e.g., air temperature, SWC, precipitation) by conducting a Kruskal–Wallis test. The analysis was site specific. Overall, an influence of the climatic parameters on the ethylene occurrence showed no significance when considering the total time series. Trends are recognizable for some short-term periods, but when considering different locations at the same time, or the full time series, the trends are no longer present or contrary. Consequently, general conclusions could not be drawn regarding temperature or moisture being the main influencing factors for the temporal variability of many other soil gases.

To identify the tree-species effect, only the period of time from 2010 onward, when samples were taken on adjacent LTEMPs of different forest stands, was considered. At spruce sites, C_2H_4 was detected in 1.17% of the samples, with simultaneously elevated concentrations (Fig. 3), which represents a significant difference (Spearman’s rho: -0.110 ; $p < 0.05$) compared to the samples of beech sites, which had a C_2H_4 detection frequency of only 0.33% as well as lower C_2H_4 concentrations. This effect is also visible in a pairwise comparison of neighboring spruce and beech plots at the same site (Fig. 10). Low frequencies of occurrence on some plots, however, permitted statistical analysis of the pairwise comparison.

For a quantitative analysis of the effect of soil texture on C_2H_4 occurrence, the LTEMPs dataset was classified according to the sites’ main soil texture group (Table 1). The frequency of C_2H_4 occurrence was slightly higher in sandy soils (1.36% compared to 1.04% in silty soils). Median and mean C_2H_4 concentrations were higher in silty soils (median: $0.14 \mu\text{mol mol}^{-1}$) than in sandy soils (median: $0.05 \mu\text{mol mol}^{-1}$) and the difference was found to be significant ($p < 0.05$; censored regression). It must be noted that no clayey and less-sandy soils were included. Total pore space (TPS), air-filled pore space (AFPS), and bulk density (BD) showed no significant effect when examining LTEMPs’ soils.

Liming studies

The effect of liming was studied based on LTEMPs, including limed and non-limed reference plots in HD and OC. An influence of soil pH or carbonate content could not be identified for either the humus or the mineral soil. C_2H_4 occurred slightly less (not significant) on limed plots (1.30%) than on non-limed plots (1.41%) when the areas of both sites are evaluated together. The difference between C_2H_4 concentrations caused by liming was significant in censored regression analysis ($p < 0.05$), with C_2H_4 concentrations being slightly lower on limed plots (median: $0.04 \mu\text{mol mol}^{-1}$; mean: $0.13 \mu\text{mol mol}^{-1}$) compared to non-limed plots (median: $0.06 \mu\text{mol mol}^{-1}$; mean: $0.40 \mu\text{mol mol}^{-1}$). The three sites of the liming study (BW, HO, and HW), with a duration of 1.5 years, did not show sufficient C_2H_4 detection for statistical analysis, since C_2H_4 could only be measured in 5 of almost 2000 samples.

Compaction studies

Considering all five compaction study sites together (SM, MU, WW, FO, ST), C_2H_4 detection frequency was 11.24%—almost ten times higher than the detection frequency at the LTEMPs (Table 6). To investigate the compaction effect, the individual gas samplers were divided into “compacted” and “non-compacted” according to their position and the bulk density of soil samples collected there (Table 4).

C_2H_4 shows significantly higher ($p < 0.001$; censored regression) occurrence (Fig. 11) and concentrations in compacted soils (14.75%, median: $0.41 \mu\text{mol mol}^{-1}$) than in non-compacted soils nearby (6.95%, median: $0.12 \mu\text{mol mol}^{-1}$) (Fig. 4). There is also a positive correlation between C_2H_4 occurrence and bulk density ($p < 0.05$; Wilcoxon test), with samples showing C_2H_4 concentrations $> 0 \mu\text{mol mol}^{-1}$ having higher BD values (1.53 g cm^{-3}) than samples without C_2H_4 detection (1.44 g cm^{-3}).

SM and MU showed the highest C_2H_4 occurrence right after the artificial compaction of the forest soils in 2001 (20.37%)/2002 (27.53%) and in 2009 (0.91%), respectively. In the following years, the number of C_2H_4 measurements decreased to zero. At WW and FO, the analysis of temporal patterns was difficult due to short measurement time as well as large temporal gaps (Table 1). C_2H_4 occurred preferentially in the summer months from April to August.

To examine the depth gradient in compacted soils, ethylene results were pooled by study site and depth (Table 3), considering only gas samplers in compacted soils (Table 4). As the WW site was only sampled at the -30 cm depth level, these data are for comparison only. The heaviest machine in the soil compaction study at SM caused the most frequent C_2H_4 detection (Table 3) and the highest C_2H_4 concentrations underneath the tracks. This

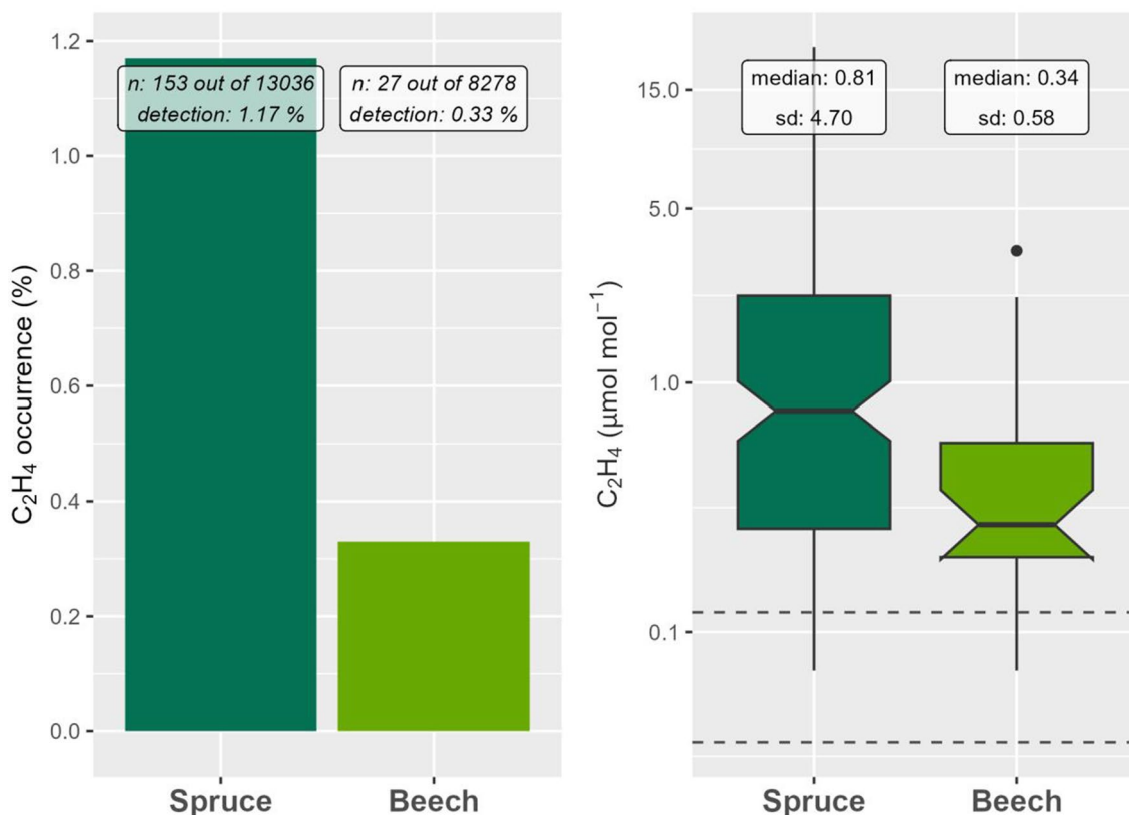


Fig. 3 C₂H₄ occurrence (%) and concentrations (µmol mol⁻¹ logarithmic transformation – log₁₀) in soil air under spruce and beech. Mean, median, and SD were calculated with the MLE approach (only C₂H₄

concentrations > 0 µmol mol⁻¹). LOD and LOQ are represented by the dashed lines

effect also emerged within the SM plots, where different driving operations were carried out, resulting in an effect of machine weight and track position on ethylene detection frequency (Table 5 and Fig. 12).

Contrary to the results of LTEMPs, all compacted plots where soil gas was sampled at different soil depths (SM, MU, and FO in Table 3) show rising C₂H₄ occurrence frequencies with increasing depth. C₂H₄ concentrations in mineral soil (median: 0.09 µmol mol⁻¹; mean: 0.39 µmol mol⁻¹) differ significantly from C₂H₄ concentrations in humus (median: 0.03 µmol mol⁻¹; mean: 0.06 µmol mol⁻¹; $p < 0.001$; censored regression). However, there are large variabilities in C₂H₄ occurrence frequencies and concentrations between the study sites (Table 3). When examining a depth gradient, it must be noted that the sampling depths are not uniform.

Temporary waterlogged site

Because of the predominant Stagnosol soil type, and the fact that the temporary water influence still overlaps the effects of compaction, the ST site was analyzed separately from

the other compaction studies. This fact is also reflected in the highest C₂H₄ detection frequency for ST, with a C₂H₄ detection frequency of 26.98% (Table 6), which was also the highest of all 24 monitoring plots. All C₂H₄ measurements exceeded the LOD (Fig. 4), and therefore, the MLE approach was not applied.

C₂H₄ correlated with O₂ (Spearman's rho: -0.345; $p < 0.05$) and CO₂ (Spearman's rho: 0.284; $p < 0.05$). Both gases differ significantly in samples with and without C₂H₄ detection ($p < 0.05$; Wilcoxon test). Anaerobic soils with low oxygen concentrations and correspondingly elevated CO₂ levels showed higher occurrence and concentrations of C₂H₄ (Fig. 4).

Combined analysis of all plots

Using the dataset of all 24 study plots, we could show that C₂H₄ was positively correlated ($p < 0.001$; Wilcoxon test) with CO₂, CH₄, and N₂O. Concentrations of the latter gas species are not only different in samples with and without C₂H₄ detection but also changes with rising C₂H₄ concentrations if only samples with > 0 µmol mol⁻¹ C₂H₄ are considered (Fig. 5) when tested with the Spearman correlation.

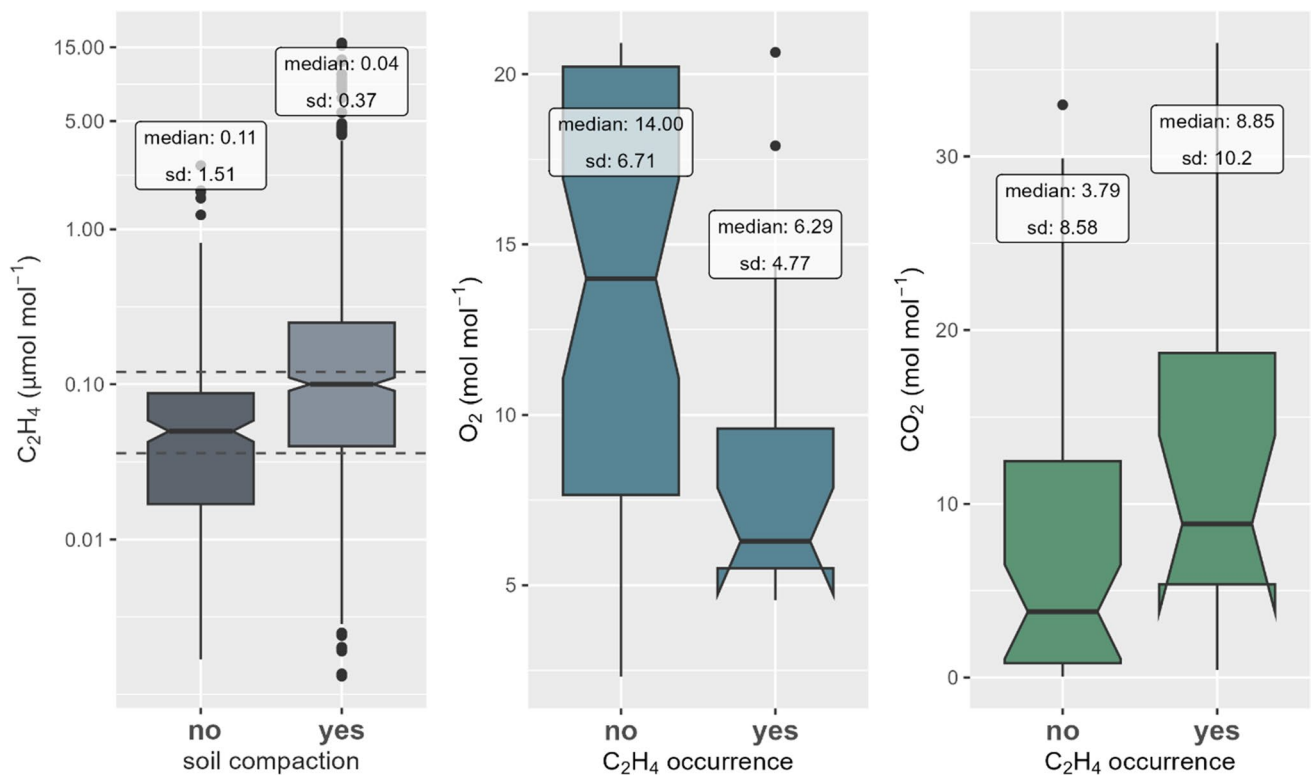


Fig. 4 C₂H₄ concentration (μmol mol⁻¹, logarithmic transformation–log10) in non-compacted and artificially compacted soils (left) of the compaction study sites. Data of FO were excluded since information of compaction status is missing. LOD and LOQ are represented by the dashed lines and mean, median, and SD were calculated with the MLE approach. O₂ (middle) and CO₂ (right) concentrations (mol

mol⁻¹) in samples with and without C₂H₄ detection. Differences in concentration are significant. The notches of the boxplots representing the 95% confidence interval in samples with C₂H₄ detection extend beyond the 25th percentile due to small sample size ($n = 17$). It shows the uncertainty of the true median

Quantitatively, a higher C₂H₄ concentration is detected in samples of higher CO₂, CH₄, and N₂O concentrations. Above a CO₂ concentration of 0.3 mol mol⁻¹, the C₂H₄ detection frequency seems to rise (Fig. 5). There is a significant positive correlation ($p < 0.001$) between CO₂ and C₂H₄ detection frequency if all data are included (Spearman's rho: 0.111) and if only C₂H₄ concentrations > 0 μmol mol⁻¹ are included (Spearman's rho: 0.391). Additionally, there is a 1.18 times higher chance of detecting C₂H₄ if CO₂ concentration rises by 1 mol mol⁻¹ (odds ratio). With logistic regression, it is shown that CO₂ concentration must be >21.05 mol mol⁻¹ to detect C₂H₄ by a probability >50%, which is hardly reached in our upland forest soils. The Chi² for the test model was <0.05 and R^2 was 0.2. Furthermore, the correlation of CH₄ and N₂O concentrations to C₂H₄ detection frequency was significantly positive ($p < 0.001$) for the whole dataset (Spearman's rho: 0.172 (CH₄) and 0.077 (N₂O)) and for C₂H₄ measurements > 0 μmol mol⁻¹ (Spearman's rho: 0.172 (CH₄) and 0.105 (N₂O)). The analysis of all monitoring plots combined was only conducted for the gas composition, as plot specific factors, such as compaction or soil type, overlay the singular influence of individual site parameters.

Discussion

Temporal and spatial occurrences

C₂H₄ field measurements showed that C₂H₄ could potentially be measured at all sites if the observation time is sufficiently long. This confirms the assumption that C₂H₄ is always produced in soil even under aerobic conditions (Jäckel et al. 2004). Furthermore, it suggests that the local C₂H₄ degradation rate is far higher than the C₂H₄ production rate in soils with high O₂ concentration, so much so that C₂H₄ emitted by any source will be directly consumed in the vicinity of the source (Hendrickson 1989). Well-aerated soils, therefore, serve primarily as a sink for C₂H₄ (Arshad and Frankenberger 1990). Our study confirms that C₂H₄ occurrence is characterized by a high spatial variability, affirming the results of the only pure field study on C₂H₄ conducted by Dowdell et al. (1972). The high C₂H₄ concentrations observed in the laboratory study by Smith and Russell (1969) are far from the mean C₂H₄ occurrence in 1.3% of the gas samples observed in well-aerated forest soils of our study. Our findings on factors influencing ethylene occurrence are summarized in the diagram

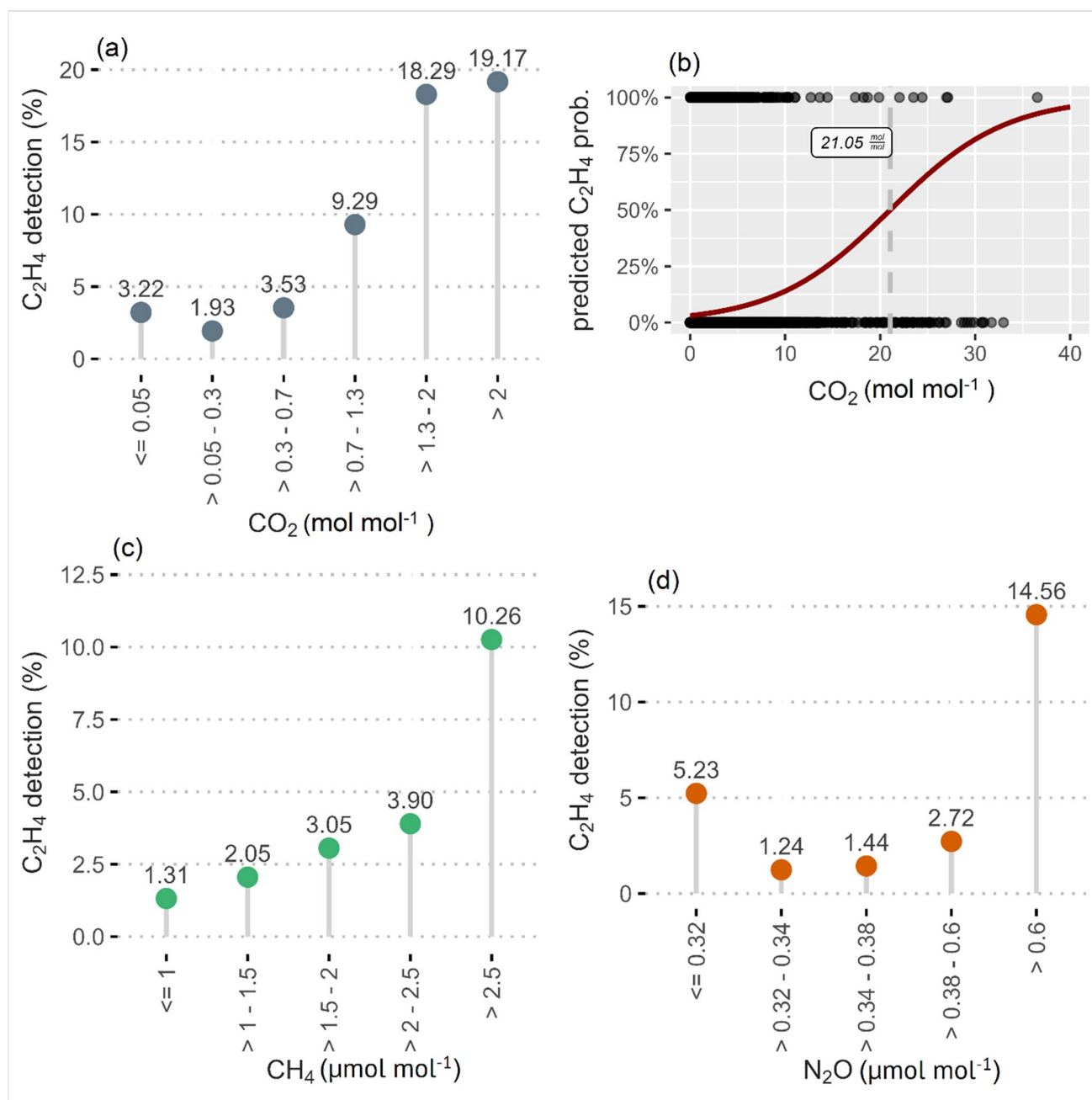


Fig. 5 C₂H₄ detection frequency depending on the CO₂ (a, mol mol⁻¹) and CH₄ (c, μmol mol⁻¹) and N₂O (d, μmol mol⁻¹) concentration in soil gas divided into classes and the graphical visualization of

the logistic regression of C₂H₄ occurrence with CO₂ concentration (b, mol mol⁻¹). Data of all 24 study plots were considered

Fig. 6. Significantly, more C₂H₄ can be observed in forest ecosystems with soil compaction, and this is further increased by the influence of waterlogging in soils. Concerning the depth distribution of C₂H₄, no clear pattern could be identified. While the C₂H₄ occurrence at the LTEMPs decreased with soil depth, the compaction study sites showed a higher ethylene occurrence frequency in deeper soil layers. The only clear spatial pattern of C₂H₄ was the enhanced C₂H₄ detection around roots, owing to C₂H₄ release by forest tree roots.

The episodes of increased ethylene detection in the near vicinity of woody roots, which often occurred many years after installation of the samplers, do not have to be caused by root-related C₂H₄ production. Increasing radial growth of the roots can compact the soil, too, resulting in increased C₂H₄ release due to local soil compaction. Fixed measurement installation positions prevent a clear understanding about the current root penetration of the surrounding forest soil.

Oxygen effect and the correlation with other gas compositions

Our analysis confirms that low oxygen concentration correlated negatively with C₂H₄ occurrence at the temporary waterlogged Stagnosol site (Fig. 6), with an average O₂ concentration in soils with C₂H₄ detection of about 6%. The oxygen effect, could not be observed in the total data set, as 80% of the gas samples originate from well-aerated forest soils with O₂ concentration >18%. Anaerobic conditions are considered to be the most important factor influencing the increased C₂H₄ production in soils (Elsgaard 2001; Primrose 1979; Xu and Inubushi 2009; Zechmeister-Boltenstern and Nikodim 1999). It is assumed that the accumulation of C₂H₄ results from the suppression of the aerobic process of microbial decomposition of C₂H₄ (Arshad and Frankenberger 1990; Cornforth 1975; Smith and Restall 1971). The O₂ concentration must be very low to have an influence on C₂H₄ (Hunt et al. 1981; Meek et al. 1983; Smith and Restall 1971).

Besides the oxygen effect, we found a significant positive correlation of C₂H₄ with CO₂, CH₄, and N₂O (Fig. 6). The positive correlations with these trace gases indirectly confirm the findings of low O₂ concentrations leading to C₂H₄

accumulation, as the increase in CO₂, CH₄, and N₂O indicates a reduced gas exchange (Pandey et al. 2021). Consequently, as the gas exchange is limited, this also leads to an accumulation of C₂H₄. High CO₂ concentrations of more than 1 to 2% indicate poor soil aeration, which are typically detected in compacted soils (Schack-Kirchner and Hildebrand 1998; Schäffer 2012), whereas, in our field study, the effect of a more frequent C₂H₄ detection could already be observed at much smaller CO₂ concentrations. C₂H₄ was preferentially detected in the subsoil of the compaction study plots, an outcome we interpret again as an effect due to low O₂ concentrations.

Our observation of methane being positively correlated with C₂H₄ is in line with results of Jäckel et al. (2004) and Xu et al. (2008), who explained this by the inhibition of methane-oxidizing bacteria in an environment of C₂H₄ accumulation. Furthermore, methanogenic microbes are more likely found in anaerobic soils (Conrad 1996), being favorable for C₂H₄ accumulation. Similarly, N₂O concentrations are positively correlated with C₂H₄ occurrence and concentration, as N₂O is formed under suboxic conditions during denitrification (Bremner and Blackmer 1978), which are favorable conditions for C₂H₄ evolution as well.

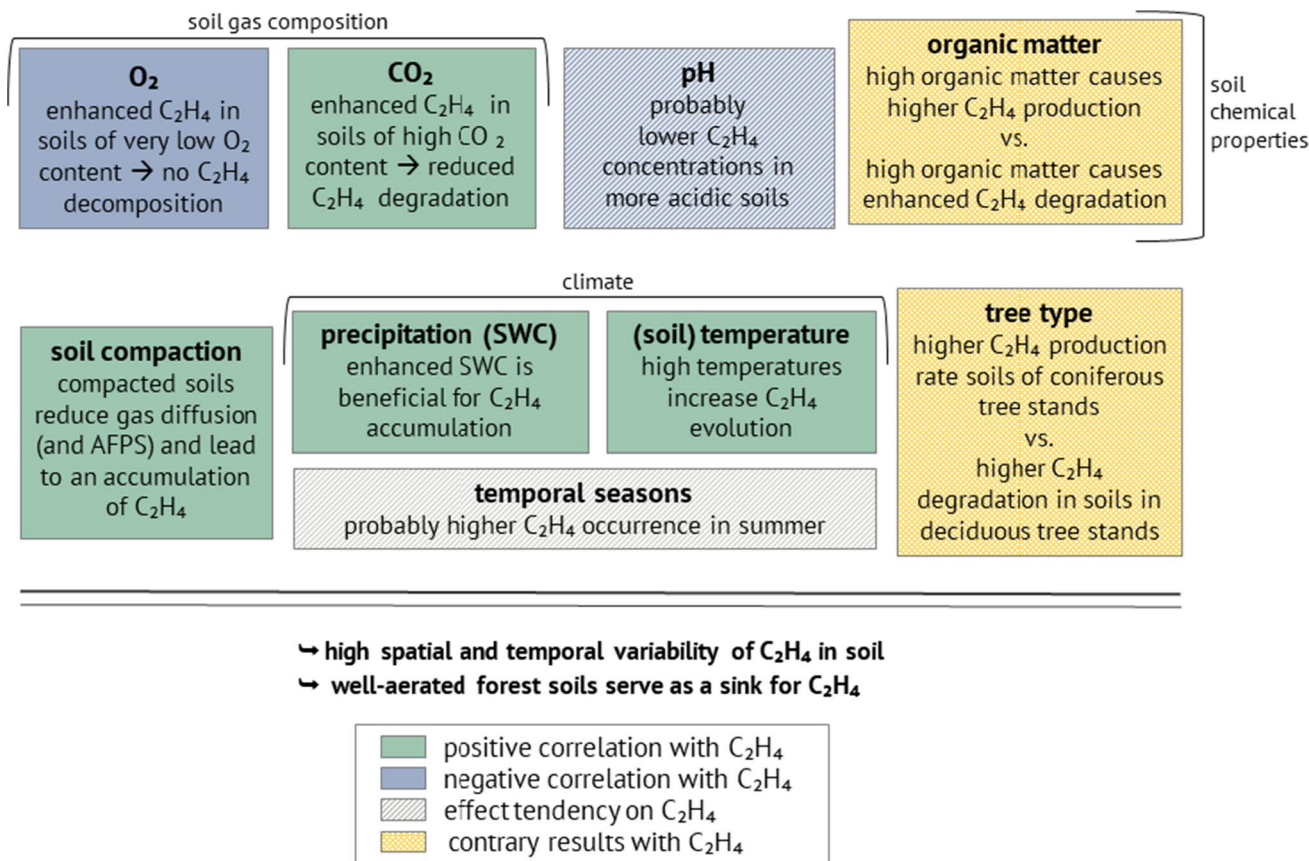


Fig. 6 Important site specific, physical, and chemical soil properties influencing C₂H₄ occurrence and concentration

Compaction effect

Although LTEMPs did not show any effect of BD on C_2H_4 occurrence, data of the compaction study sites clearly did (Fig. 6). The rather low BD in the topsoil of the LTEMPs prevents the accumulation of ethylene; thus, the effect of BD does not appear on these plots. Soil compaction leads to a twofold increase in the frequency of C_2H_4 occurrence (7% to 15%) and significantly higher C_2H_4 concentrations compared to reference plots (Fig. 11). This effect can be explained by a reduction of the gas diffusion in soils as TPS, and more importantly, AFPS are reduced (Pandey et al. 2021). Considering the study results of Pandey et al. (2021) on plant growth, this could confirm the theory that the release of the plant hormone C_2H_4 is a warning signal to prevent root growth into compacted soil areas.

Tree-type effect

Due to the common observation time of more than 10 years, a clear tree-type effect, with 3.5 times more frequent C_2H_4 detection under spruce than under beech, could be observed. Studies on C_2H_4 in coniferous and deciduous forest soils already indicated that C_2H_4 degradation is faster in deciduous forest soils (Zechmeister-Boltenstern and Smith 1998), whereas coniferous forest soils show a higher probability of C_2H_4 accumulation, especially under wet conditions (Rigler and Zechmeister-Boltenstern 1999; Sexstone and Mains 1990), which lead to contrary results on the tree type effect (Fig. 6).

Reasons for the observed tree species effect could be the combination of gas measurements being only down to 10 cm depth and differences in rooting. Whereas spruce consists of a shallow root system, beech is a deep-rooted tree (Schmid and Kazda 2005). Spruce stands therefore show an enhanced detected root release of C_2H_4 in the upper soil areas, as root density decreases exponentially from the upper to the lower soil layers (Schmid and Kazda 2001). This is validated by the fact that only spruce plots show patterns of C_2H_4 root release, which could be identified as the main source of C_2H_4 in soil. Roots are thus the most important factor influencing spatial heterogeneity of C_2H_4 in soil, followed by microbial C_2H_4 production (Hendrickson 1989).

The tree species effect was significant using the entire LTEMP dataset (Fig. 3) but also evident in a pairwise comparison of neighboring beech and spruce plots (Fig. 10). However, the observed root density at our plots was surprisingly the same and partly even lower on spruce sites compared to beech sites. An increased rooting of the spruce sites in the topsoil could therefore not be proven (Fig. 10). However, measuring root densities by counting root tips in soil profiles includes a high inherent uncertainty.

More obvious is a microbial component/contribution of the tree species effect. Arbuscular mycorrhizal fungi

(AMF) communities are different for tree species (Rožek et al. 2020). AMF on spruce roots could be specialized in C_2H_4 production, whereas AMF on beech roots adapted to C_2H_4 degradation. Yet this was not tested, nor is there clear evidence of this in the literature. Finally, it was shown that soils under beech and spruce differ in CO_2 respiration rate (Berger et al. 2010), resulting in the assumption that beech sites have higher C_2H_4 oxidation rates than spruce sites. In combination with the observed higher SOM-content, identified as influential on the C_2H_4 occurrence among others by Goodlass and Smith (1978), beech sites may provide a more microbial activity in soil (Achilles et al. 2021), leading to rapid degradation of C_2H_4 by microorganisms in the soil and complicating detection. The different characteristics of soils under beech and spruce were no object in our study.

Additional physical and chemical soil parameters

For pH, SOM-content, and liming, no effect on C_2H_4 could be detected (Fig. 6). This coincides with the result of the study conducted by Lindberg et al. (1979). Findings of laboratory studies in pH having a negative correlation with C_2H_4 concentrations (Arshad and Frankenberger Jr 1991; Zechmeister-Boltenstern and Smith 1998; Zechmeister-Boltenstern and Nikodim 1999) were not confirmed in our study. This is probably because all our sites are acidic, and soil pH values do not differ substantially between the monitoring plots. Furthermore, there are probably other relevant site characteristics having an impact on C_2H_4 that possibly mask the effect of soil pH. Unfortunately, the analysis of the data of our liming plots did not yield reliable results, since the overall occurrence of CH_4 was too low, or the monitoring period was too short.

Analysis of air and soil temperature effects on C_2H_4 at the LTEMPs led to ambiguous results. Reported heat activation by microorganisms producing C_2H_4 (Lynch 1975; Sexstone and Mains 1990; Smith and Cook 1974; Smith and Dowdell 1974; Smith and Restall 1971; Xu and Inubushi 2009) could only be partially detected due to a partial preferential occurrence in the summer months in the data of the project studies. Typical repeated temporal or even seasonal pattern could not be detected. The impact of precipitation and SWC on C_2H_4 , by contrast, seems to confirm the findings of other studies (Dowdell et al. 1972; Hunt et al. 1981; Lindberg et al. 1979; Otani and Ae 1993; Zechmeister-Boltenstern and Nikodim 1999). C_2H_4 measurements $>0 \mu\text{mol mol}^{-1}$ were predominately observed after rainfall, which can be explained by a reduced O_2 concentration in wet soils; thus, lower decomposing rates of C_2H_4 (Sawada et al. 1985; Zechmeister-Boltenstern and Smith 1998), as well as a reduced gas diffusion in the air-filled soil pore space (Lynch 1975).

Since sandy soils showed a higher C_2H_4 detection frequency than silty soils, but C_2H_4 concentrations were higher

in silty soils, there is a contrary effect of soil texture on C₂H₄. Results of the study of Van Cleemput et al. (1983), stating that C₂H₄ preferentially occurs in sandy soils, can thus only be partly validated. It must be noted that clayey soils were not present in our study.

Conclusion

The analysis of our extensive dataset (more than 50,000 from 1994 to 20201 on 24 plots) showed that the detection of C₂H₄ is extremely infrequent in forest soils, and, except for sampling gas next to main roots, it does not exhibit distinct temporal and spatial patterns. The investigation of the temporal and spatial distributions did not show any systematic or seasonal patterns. Therefore, a direct influence of environmental parameters, such as soil temperature and moisture, could not be observed. Nevertheless, C₂H₄ does not occur randomly in soils. A cluster structure with hot moments (C₂H₄-rich years) and hot spots (C₂H₄-rich plots) is evident, though thus far it cannot be explained. The most important soil-related and exogenous

factors influencing C₂H₄ occurrence are soil compaction and high water contents, leading to low O₂ and elevated CO₂ concentrations in the soil. Both factors inhibit microbial activity, allowing accumulation of produced C₂H₄ in anaerobic soils. Furthermore, the tree species had a clear effect on C₂H₄. Soils under spruce show an increased C₂H₄ occurrence than soils under beech. A reason for this might be the different root system or higher microbial activity in beech stands, which leads to faster degradation of C₂H₄ and reduces the C₂H₄ detection frequency. In well-aerated upland forest soils, in turn, high oxygen levels usually prevail, and an unhindered gas exchange can take place. This leads to the rapid diffusion and degradation of C₂H₄ with low probability of C₂H₄ accumulation in soil. Furthermore, the study presents a statistical approach for the challenging evaluation of left-censored data sets with a high number of zero measurements, which could provide reliable results about the factors influencing C₂H₄ occurrence even in well-aerated forest soils. Although the scope of our study on ethylene occurrence is unique, the importance of long term monitoring programs must be emphasized. Each additional measurement facilitates the statistical analysis and identification of natural influencing factors.

Appendix

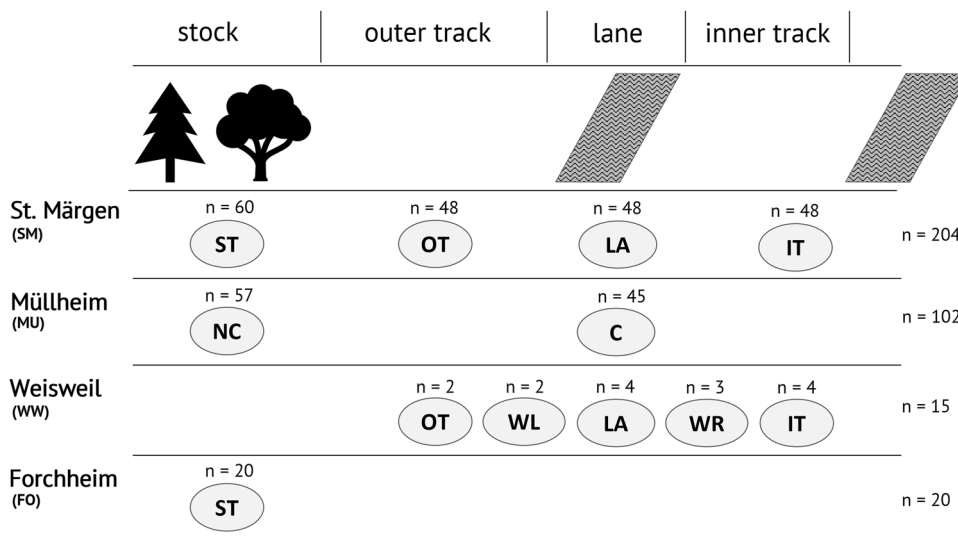


Fig. 7 Track positions at the different soil compaction study sites with “n” indicating the numbers of soil gas samplers installed at the respective positions. Note that lane does not automatically indicate a compacted soil. At Weisweil, the compaction status is reversed because soil loosening was done on compacted soil within the lane. Soil gas was sampled at: directly on the lane (LA); at the inner track

(IT), between both lanes; Wall left/right (WL/WR), 30 cm left of the lane; at the outer track (OT), 50 to 80 cm from the lane; and in forest stock (ST) where no influence of forest machinery on soil was assumed. At Müllheim (MU) a distinction could only be done between compacted (C) and non-compacted (NC) soil

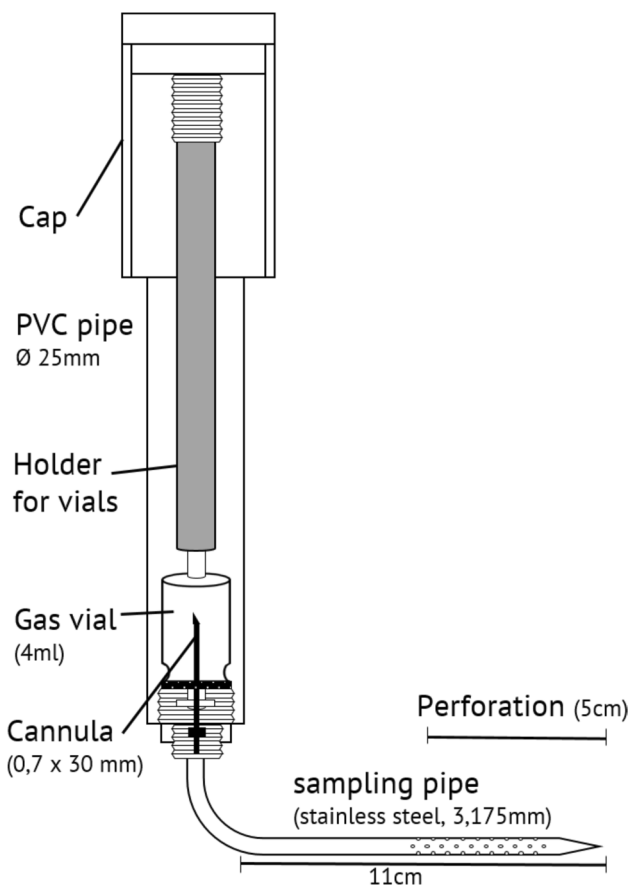


Fig. 8 Cross-section through the passive soil gas samplers installed on all plots according to Schack-Kirchner et al. (1993)

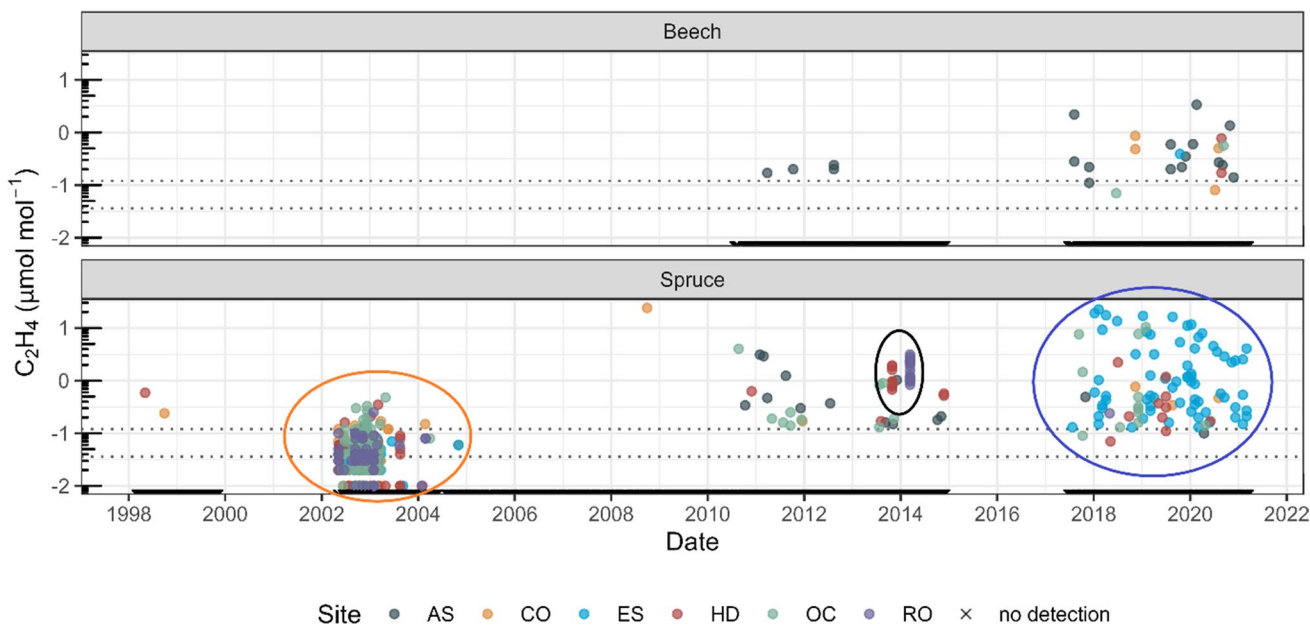


Fig. 9 Time series of C_2H_4 measurements at all LTEMPs combined representing upland forest soils. Y-axes are logarithm-transformed (\log_{10}); dashed lines represent the LOD and LOQ. Orange circle:

enhanced C_2H_4 detection frequencies in 2002 and 2003. Black circle: several C_2H_4 measurements at HD_S and RO_S on the same day. Blue circle: root-borne C_2H_4 measurements in humus at ES_S

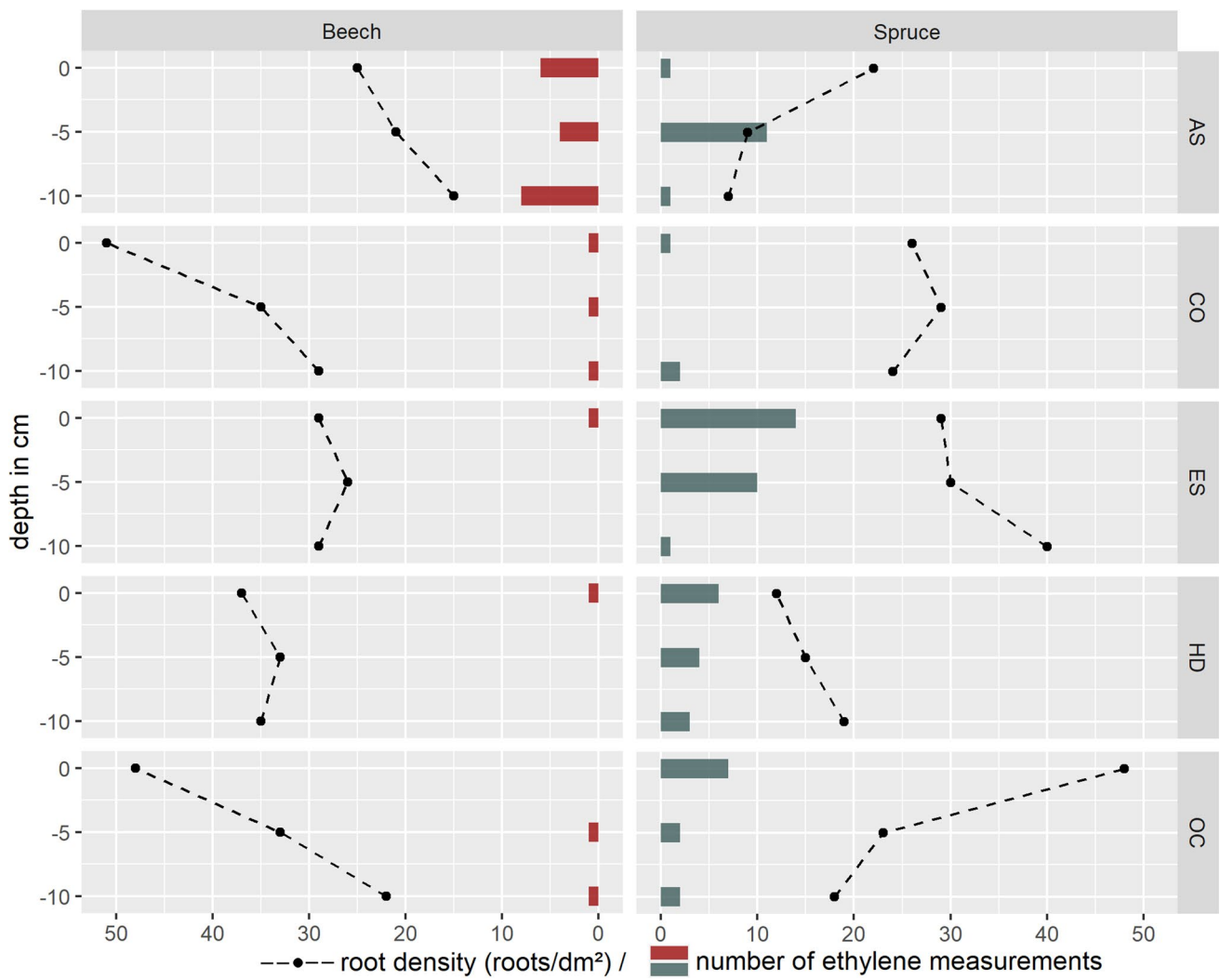


Fig. 10 Pairwise comparison of number of ethylene measurements since 2010 of adjacent beech and spruce plots of the same site. The dashed line shows the depth profile of root density determined by root counts at the same depth as the gas collection. It is true that

spruce plots generally showed a higher ethylene occurrence in the same observation period. However, a correlation to a simultaneously increased root density in the topsoil under spruce could not be determined

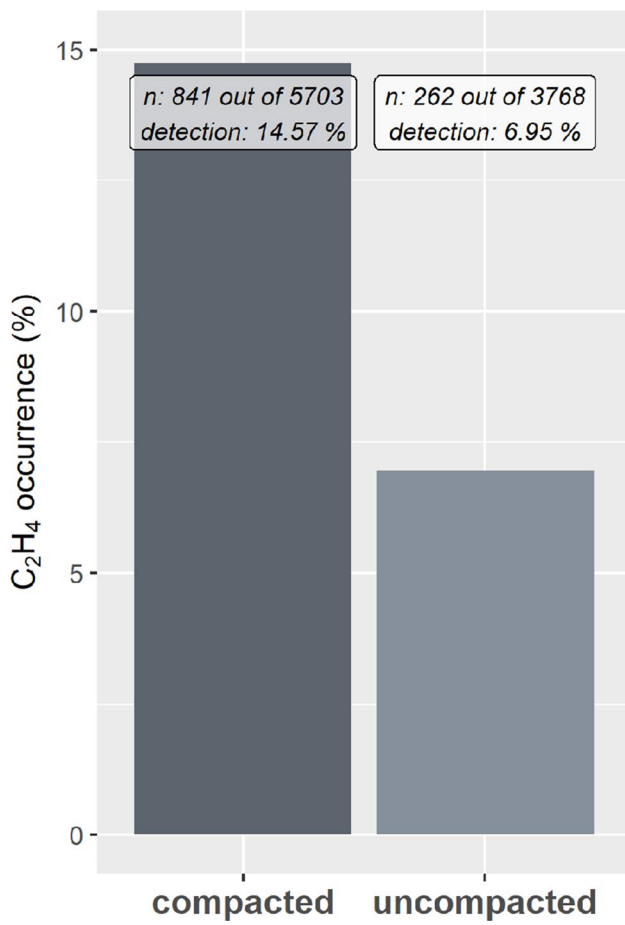


Fig. 11 C₂H₄ occurrence (%) in non-compacted and artificially compacted soils of the compaction study sites (data of FO were excluded since information of compaction status is missing)

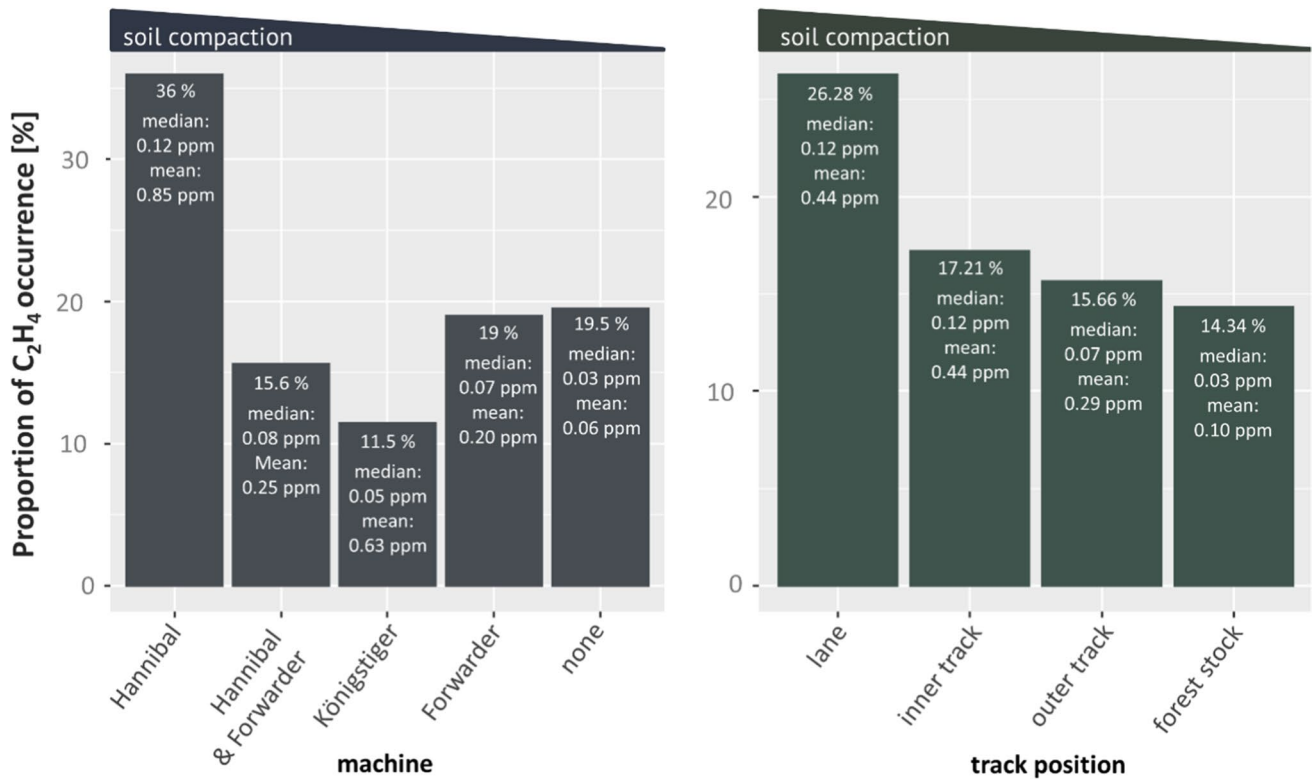


Fig. 12 The influence of machines (left) and track positions (right) on the C₂H₄ occurrence frequency at SM plots. Soil compaction decreases from left to right, respectively

Table 4 Separation of the compaction plot positions into compacted and non-compacted soils. Data of FO was excluded from analysis as information on soil compaction was not available. Position abbreviations are explained in Fig. 7

Study site	Position	Compacted	Non-compacted
SM	LA, IT, OT	X	
	ST		X
MU	C	X	
	NC		X
WW	IT, OT, WL, WR	X	
	LA		X
FO	Data not included as soil was not treated		

Table 5 Forestry machines and their characteristics used at the two plots of SM

MS	Eastern plot of SM			Western plot of SM	
	October 2000			May 2001	
Machine	Forwarder “Timberjack 810 B” (FO)	Harvester “Königstiger” (KT)	Control plot (NU)	Harvester “Hannibal” (HA)	Harvester and forwarder (HF)
Weight [t]	20	28	-	45	32.5 (estimated)
Mean track depth [cm]	7.7	8.9	-	13.4	13.2
Maximal track depth [cm]	25	25	-	13	11

Table 6 Information on C₂H₄ measurements on all plots and summarized by studies and total data set

Plot	Total <i>n</i> of samples	Number of C ₂ H ₄ detection	C ₂ H ₄ occurrence (%)	Range (μmol mol ⁻¹)*		Median (μmol mol ⁻¹)*	Mean (μmol mol ⁻¹)*	SD (μmol mol ⁻¹)*
				Min	Max			
LTEMPs								
AS _B	1762	18	1.02	0.11	3.38	0.24	0.61	0.87
AS _S	1730	14	0.81	0.1	3.13	0.36	0.79	1.00
CO _B	2072	4	0.19	0.08	0.86	0.49	0.48	0.32
CO _S	3721	57	1.53	0.01	23.9	0.04	0.50	3.16
ES _B	1406	1	0.07	0.39	0.39	0.39	0.39	-
ES _S	4268	109	2.55	0.01	22.3	0.27	2.13	4.45
HD _B	1818	2	0.11	0.17	0.77	0.47	0.47	0.42
HD _S	3717	57	1.53	0.01	1.95	0.05	0.25	0.46
HD _L	3242	52	1.60	0.01	2.23	0.04	0.15	0.35
OC _B	1220	2	0.16	0.07	0.56	0.32	0.32	0.35
OC _S	5384	71	1.32	0.01	10.33	0.06	0.55	1.79
OC _L	3732	39	1.05	0.01	0.3	0.05	0.07	0.06
RO _S	4249	71	1.67	0.01	3.15	0.05	0.55	0.89
	38321	497	1.30	0.01	23.9	0.07	0.78	2.57
Compaction								
SM	5594	1009	18.04	0.01	15.99	0.07	0.40	1.32
MU	3427	20	0.58	0.15	4.1	0.39	0.70	0.97
WW	450	74	16.44	0.01	1.16	0.13	0.20	0.23
FO	1121	88	7.85	0.01	2.8	0.16	0.26	0.38
ST	63	17	26.98	0.27	5.31	1.55	2.02	1.47
	10655	1208	11.34	0.01	15.99	0.09	0.40	1.25
Liming								
BW	614	0	-	-	-	-	-	-
HO	665	2	0.30	0.23	0.66	0.45	0.45	0.30
HW	667	3	0.45	0.06	0.51	0.51	0.36	0.26
	1946	5	0.26	0.06	0.66	0.51	0.39	0.24
All data								
	50922	1710	3.36	0.01	23.9	0.08	0.51	1.75

Median, mean, and SD values were calculated by the MLE approach for all study sites except ST

*Only of measured C₂H₄ concentrations >0 μmol mol⁻¹

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00374-023-01763-z>.

Funding Open Access funding enabled and organized by Projekt DEAL. This work was funded by the WKF (Waldklimafond/Forest Climate Fund) and the FNR (Fachagentur Nachwachsende Rohstoffe e.V.), jointly managed by the Federal Ministry for the Environment (BMU) and the Federal Ministry of Food and Agriculture (BMEL)—grant number 2218WK58X4.

Data Availability The authors confirm that the data supporting the findings of this study are available within the article or its supplementary materials.

Declarations

Conflict of interest The authors declare no competing interests.

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