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Plant-soil interactions drive GHG dynamics in organic soils under variable water tables: a case study with poplar

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Abstract. Organic soils provide a substantial capacity for carbon storage both in below- and above-ground biomass, but they are also a significant contributor to natural terrestrial Greenhouse gas (GHG) emissions. Organic soil melioration, carried out to increase the primary productivity, often leads to increased CO_2 emissions. By monitoring a controlled environment, it is possible to determine how organic soil management practices influence the carbon cycle, including plant vitality and productivity, and consequently shape future carbon sequestration potential.

The aim of this study was to develop a system under semi-controlled conditions to assess the impact of different groundwater levels on GHG emissions, accumulated biomass, and tree vitality. We conducted experiments in semi-controlled conditions to determine the effects of different groundwater levels (-2 cm; -15 cm; -25 cm; -35 cm) on CH_4 and CO_2 emission, soil chemical analyses, and plant morphological (biomass, root and leaf area, shoot length) and physiological (leaf chlorophyll a and b content) parameters. Temporal and diurnal variation strongly impacted GHG fluxes due to the changes in temperature, moisture, and plant growth activity. During soil temperature extremes, extremely high CH_4 emissions occurred at a -2 cm groundwater level. Higher plant productivity had a greater influence on GHG fluxes: it decreased both CH_4 and CO_2 emissions during the day compared to bare soil. Therefore, the autotrophic respiration rate increased with increased productivity, but the primary determinant was heterotrophic respiration.

1 Introduction

Organic soils in the hemi-boreal zone have a notable capacity for carbon and nitrogen storage, holding the largest amount of carbon in terrestrial ecosystems (Gorham, 1991; Byrne et al., 2004). However, they are also among the main natural sources of greenhouse gas (GHG) emissions (Gorham, 1991; Fischlin et al., 2007; Jauhiainen et al., 2019). Historically, anaerobic conditions from high water tables and low temperatures in Northern Hemisphere peatlands have allowed thermodynamically unstable peat to persist for thousands of years, primarily regulated by environmental and biological factors rather than its chemical composition or structure (Schmidt et al., 2011; Straková et al., 2012; Buschmann et al., 2020). The course of the development of land management and new drainage techniques in the early 20th century led to an increase in land use change from peatland to agricultural land, peat extraction, and active peatland forest management, thereby also altering the role of organic soil in climate regulation and socio-economical aspects (Bragg et al., 2003; König & Varma, 2006; Joosten, 2010;

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Kløve et al., 2017). In general, the drainage of peat soils alters peat microbiology promoting soil mineralization, increasing CO_2 and N_2O emissions, decreased CH_4 emissions, reducing carbon content, and potentially causing leaching of minerals (N, P, Dissolved Organic Carbon (DOC)), all of which can lead to soil compaction and a decrease in productivity in the long term (Kasimir et al., 2007; Kløve et al., 2017). Although these are the main threats after peat drainage, recent studies show that whether the ecosystem on organic soil acts as a carbon source or sink is significantly determined by local environmental conditions, vegetation, land use, chemical and physical properties of peat, and thickness of different peat layers, density and humification level, bedrock composition, and the history of peat accumulation (Mustamo et al., 2016).

Global warming potential (GWP) on drained peat soils can be reduced through reclamation or recultivation, with the choice depending on various factors such as geology, chemical composition, as well as local socio-economic aspects (Hytönen et al., 2020). Poplars are fast-growing, early-successional alluvial species whose growth is highly dependent on water availability and precipitation, and they have previously shown good performance on peat soil if the pH level is optimal (Rytter et al., 2016; Adler et al., 2021). Populus maximowiczii Henry × P. trichocarpa Torr. & Gray hybrid “OP42” is one of the most widely used poplar clones in Europe, and it has good biomass accumulation performance as well as being easy to reproduce with stem cuttings (Rytter et al., 2016; Adler et al., 2021; Ranjan et al., 2022). Poplar has been a significant source of renewable raw materials, and its importance and interest as an alternative energy source to fossil fuels have grown along with the resolution of the energy crisis in many European countries (Kozuch et al., 2023). Due to clonal rank stability, individual response variation to environmental factors in OP42 grown from stem cuttings is limited, while still being phenotypically plastic to biotic and abiotic factors, which makes it a valuable object of study to investigate the external effects on plant growth and physiology (Adler et al., 2021; Nelson et al., 2018; Vanden Broeck et al., 2018).

To understand the carbon cycle and determine an ecosystem's carbon sink, it is essential to evaluate the accuracy of methods used to estimate GHG emissions. CO_2 soil emissions, or total soil respiration (TR), consist of two components: heterotrophic respiration (HR), from microorganisms and soil organic matter mineralization, and autotrophic respiration (AR), from roots, mycorrhizae, and rhizosphere-associated microorganisms (Hanson et al., 2000). Although the accuracy of detecting CO_2 emissions is high nowadays, the division of emissions into AR and HR faces several challenges. A key issue is the difficulty in accurately determining HR under field conditions, as the widely used methodology may introduce errors. For instance, the contribution of roots from adjacent vegetation, such as vascular and woody plants extending into the plot, may lead to an overestimation of HR emissions (Jauhiainen et al., 2019). Trimming the root system at the perimeter of the plot can improve this methodology but does not fully resolve the issue and may also have an indirect effect on soil emissions (Jauhiainen et al., 2019). The determination of AR also faces challenges, as microorganisms involved in AR processes can also participate in HR processes. Due to the close relationship between the two types of soil respiration, and the fact that AR is primarily regulated by plant physiological activity, carbon partitioning, and root–soil nutrient exchange, vegetation structure and vitality play a significant, yet often underestimated, role in soil respiration (Haydon et al., 2013; Oertel et al., 2016; Tang et al., 2020). In addition, plants also indirectly affect CH_4 emissions through their participation in production and transport (Bastviken et al.,

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2023), while the diurnal and monthly regulation of each system component—such as plant, microbial, and fungal activity—should also be considered (Harmer et al., 2000; Sander and Wassmann, 2014; Zhao et al., 2021).

The effect of both the above- and belowground plant parts on carbon cycling is critical for evaluating the overall carbon cycle in an ecosystem (Ojanen et al., 2014). Determining HR and AR separately under natural conditions may encounter various parallel influencing factors, so controlled conditions would help avoid errors, such as the presence of living roots in HR measurement plots. We conducted research under semi-controlled conditions to investigate the differences between undrained shallow-drained and deep-drained conditions in organic soil, focusing on their effects on vegetation physiological performance and GHG exchange. This study addresses the following research questions: (1) Do plant-productivity parameters, such as chlorophyll concentration and plant morphological and biomass parameters, explain changes in soil respiration rate trends under different groundwater levels; (2) How do autotrophic and heterotrophic respiration vary temporally and diurnally?

2 Methods

2.1 Study site and experimental design

The experiment was conducted under semi-controlled condition in greenhouse in the Latvian State Forestry Research Institute ″Silava″ (N 56°87008100 E 24°34746500) from mid-April to early July 2023 (table 1). Shading and daylight length were not controlled and were consistent with natural conditions in the region. The average air temperature in the greenhouse was 7.6°C higher during the day and 5.7°C higher at night than outside. An automatic greenhouse ventilation system was used to limit the risk of plant overheating during hot weather conditions. No irrigation system or fertilization of any kind was applied during the study period.

Table 1.

Monthly and diurnal environmental conditions in study site

Parameter	April		May		June	
	D	N	D	N	D	N
Air moisture in greenhouse (%)	40.7 SE 0.007	62.6 SE 0.007	34.7 SE 0.006	59.9 SE 0.007	38.6 SE 0.006	60.3 SE 0.009
CO_2 concentration in greenhouse (ppm)	805.4 SE 0.003	807.6 SE 0.013	751.1 SE 0.010	763.1 SE 0.022	710.5 SE 0.008	739.1 SE 0.026
Air temperature in greenhouse (°C)	18.8 SE 0.003	9.1 SE 0.002	23.3 SE 0.003	13.8 SE 0.003	27.0 SE 0.002	18.6 SE 0.003
Air temperature outside (°C)	10.1 SE 0.157	5.4 SE 0.124	15.5 SE 0.148	6.4 SE 0.131	20.6 SE 0.136	12.6 0.135
Soil temperature (°C)	NA	NA	17.5 SE 0.011	17.5 SE 0.023	21.8 SE 0.013	21.2 SE 0.035
Vapor Pressure Deficit	12.7 SE 0.022	4.7 SE 0.016	17.9 SE 0.047	5.8 SE 0.030	16.0 SE 0.051	6.4 SE 0.030

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D – day N – night (Daylength: in April form 6.15 AM till 20.30 PM total 14 h 15 min; in May form 5.00 AM till 21.30 total 16 h 30 min; in June form 4.30 AM till 22.20 total 17 hours 50 min)

Water regulation system was installed inside each of the five hydroisolated boxes at four different levels depending on the depth from the soil surface: -2 cm, -15 cm, -25 cm, and -35 cm. Soil boxes was designed to fit in water boxes (100x50x50 cm) (Fig. 1). In the middle of the box there was separation wall to create two sections – with and without vegetation under the same groundwater level (one section size: 50x50x50 cm) creating 10 sections in total. In the lower part of the box nine round circles per outer walls for water circulation was made (R = 2.5 cm). To prevent soil entering in the water box geotextile fabric was placed in front of the circle holes inside the soil box.

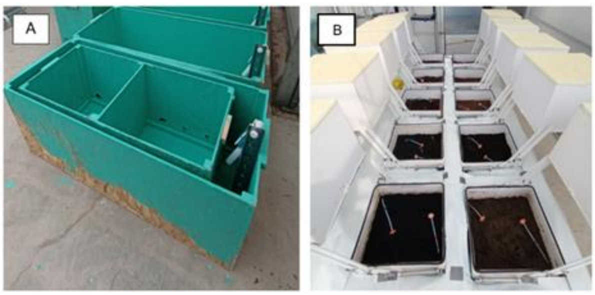

Figure 1. Experimental design of the experiment. A – soil boxes; B – gas measurement chambers on soil installed in soil boxes.

Organic soil substrate was placed inside each box. Soil was collected from the study site in Skrīveri Municipality, on a plantation forest located on former agricultural land with mineral soil (Luvic Stagnic Phaeozem Hypoalbic and Mollic Stagnosol). The soil was collected separately from two depths: 0–30 cm and 30–50 cm, in March 2023. Mineral soil was supplemented with organic substrate (neutralized fine peat fraction, 0–7 mm, pH/KCl 5.1–6.1) to achieve the organic matter content required for organic soils, which must be at least 20% (Nikodemus, 2008). The substrate was mixed in a 1:1 volume ratio and 1.3:6.5 kg mass ratio for peat and mineral soil. Soil from the two depths was combined separately and installed in the boxes at the same depths as in natural conditions (table 2).

Table 2

Soil chemical analyses for substrate used in experiment

Sample	Absolute soil moisture	C_{total}, g kg^{-1}	pH_{CaCL2}	N_{total}, g kg^{-1}	C/N	K, g kg^{-1}	Ca, g kg^{-1}	Mg, g kg^{-1}	P, g kg^{-1}
Mineral soil 0-30 cm	2.0 SD 0.058	26.8 SD 3.177	6.6 SD < 0.001	2.4 SD 0.289	11.3 SD 0.060	2.0 SD 0.892	6.4 SD 1.364	3.6 SD 0.820	0.5 SD 0.228

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Mineral soil 30-50 cm	1.7 SD 0.153	23.0 SD 1.450	6.7 SD 0.060	1.9 SD 0.115	12.3 SD 0.427	2.4 SD 0.110	6.8 SD 0.769	3.6 SD 0.091	0.6 SD 0.058
Peat	12.4	480.7	6.2	10.3	47	0.35	33.63	2.22	0.22
Peat and mineral soil 0-30 cm mix	3.4	153.9	6.4	4.8	32	2.33	13.49	3.72	3.72
Peat and mineral soil 30-50 cm mix	4.1	77.4	6.5	3.2	24	2.58	9.82	3.71	3.71

K, C, Mg values are HNO_3 extractable

For planting material, perennial grassland species *Festuca ovina* and vegetative stem cuttings of the poplar clone OP42 (Hybrid 275 NE 42, *P. maximowiczii* x *trichocarpa*) were chosen to create plant composition similar to a poplar plantation. For *F. ovina*, optimal seedling rate is 200–400 kg ha-1, we selected the minimum optimal rate of 200 kg ha-1 and calculated the required mass (Sm) for one soil box section (50x50x50 cm) which was 5 g Eq. (1):

$$S_m = (50 \times 50) \times 20 \div 10000 \quad (1)$$

OP42 Stem cuttings were prepared from approximately 1 cm thin stem sections with leaf buds. Stems were cut into 20 cm long sections and placed in water for at least 24 hours. Before planting, all other buds were removed, leaving only the upper one. Cuttings were planted in the soil up to the upper leaf bud line, with five cuttings per soil box. Both *F. ovina* was seeded, and poplar cuttings were planted in one section of each soil box, creating one section with bare soil and one with developing vegetation cover. Seeding and planting were carried out on April 14th, two weeks before the first gas measurement.

For gas measurement, ten hermetic gas sample chambers were constructed, one for each soil box section. The chamber closing system was automated, with pneumatic hinges connected to an air compressor (Oil-free Air Atlas Copco Nacka Municipality Sweden) and regulated by custom made Syntpot application (v9.2.1001.19 (March 24 2021 - 09:52:05). A sealing ribbon was applied to the closure edges to prevent airflow during measurements. The spectrometer was connected to each chamber through inlet and outlet gas sample pipes located 10 cm above the soil surface, with the pipe ends secured by air filters (Minisart, 0.45 µm, Sartorius AG, Göttingen, Germany) to prevent soil particles from entering the system.

2.2 Measurements and data collection

A near-infrared spectrometer (NIRS) OMEGA 5 (Bruker, Billerica, Massachusetts, United States) was used to measure GHG emissions, including methane (CH_4), carbon dioxide (CO_2), and water vapor (H_2O). Measurements were operated via the OPUS GA software program (v5.2.11.8, Nov 29, 2021 – 16:32:04). The spectrometer analyzed one chamber at a time, completing a full measurement cycle across all ten chambers. To enable continuous measurements, a programmed mode (total duration: 5 h 3 min) was created in 'OPUS GA': (1) Pause (90 s), (2) Background measurement (48 s), (3) Pause (42 s), (4) Time series (19,620 s), with the repeat measurement function enabled. During 'Time series,' measurements were carried out in all ten chambers, controlled by the 'Syntpot' software application, following a repeated program: (1) Analyzer ventilation (180 s),

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(2) Chamber analysis (1,800 s). Each chamber measurement (1,800 s) included gas sampling every 6 s, totaling 300 measurements. GHG samples were collected in six measurement periods from April 28 to July 1: 28.04.–01.05., 08.05.–13.05., 15.05.–17.05., 26.05.–02.06., 08.06.–14.06., and 28.06.–01.07. GHG flux was calculated from CO_2 (t C ha^{-2} $year^{-1}$) and CH_4 (kg C ha^{-2} $year^{-1}$) emissions and room temperature data (Kahmark et al., 2020). GHG emission data were categorized into day and night measurements based on diurnal time (Sunrise and Sunset Times API, n.d.). Soil temperature was monitored for each soil box section with temperature sensor plugs at 10 cm depth (Plug&Truck by Progres Plus Willems France). The temperature was monitored each 5 minutes for multiple periods during the study time: (1.) 28.04.–30.04.; (2.) 08.05.–18.05; (3.) 22.05.–29.05.; (4.) 08.06.–15.06.; (5.) 21.06.-26.06.; (6.) 28.06-01.07. The chlorophyll a (Chl A) and chlorophyll b (Chl B) content of the leaves was measured by a non-invasive method using a near-infrared 'The SpectraVue' leaf spectrometer (CID Bio-Science Camas WA USA). Measurement of CCI started when first fully developed leaves was observed and was carried out in total 9 weekly measurements (28.04.; 11.05.; 23.05.; 31.05.; 08.06.; 16.06.; 22.06.; 26.06.; 28.06.) taking 10 measurements form new leaves (first 5-10 leaves form visual observation) for each group chlorophyll total 40 measurements each week.

At the end of the experiment (3rd of July) plant morphologic data were collected. Fresh and dry biomass (dried at 70°C for four days, 96 hours) was measured for different poplar plant parts (roots, stem, leaves) and F. ovina aboveground parts. Additionally, the number of leaves per poplar and shoot stem length were recorded. Total leaf area for each OP42 individual was determined by scanning all leaves using the 'WinFolia2019' software (Regent Instruments Inc., Québec City, QC, Canada). Specific Leaf Area (SLA) was calculated as the ratio of leaf area to dry mass. Root area (mm^2) and volume (mm^3) were measured in three root diameter classes (0.5–1.5 mm, 1.5–3 mm, >3 mm) using the 'WinRhizo2019' software (Regent Instruments Inc., Québec City, QC, Canada).

After the experiment, soil analyses were conducted for each soil box section at three depths (0, 20, and 40 cm) using the 'Soil Sampling Ring Kit-Model C53' (Royal Eijkelkamp, Giesbeek, Netherlands). Sample preparation followed the standard LVS ISO 11464:2006 requirements. Moisture, pH, N, P, K, Ca, Mg, and total C content were determined. Soil moisture analysis was performed using analytical scales ('Sartorius AX224') and a laboratory dryer ('BMT Ecocell 55') (LVS ISO 11465:2002). Total C and N content in the substrate and leaves were determined using the elemental analyzer 'Elementar El Cube' (Elementar, Langenselbold, Germany), while total P content was measured with the spectrometer 'Shimadzu UV-1900' (Shimadzu, Kyoto, Japan) (LVS ISO 10694:2006 L; LVS ISO 13878:1998; LVS 398:2002 L). Substrate pH was determined using the pH meter 'Adrona AM 1605' (Adrona, Riga, Latvia) (ISO 10390:2021). K, Ca, and Mg concentrations were analyzed using an Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) spectrometer ('Thermo Fisher Scientific iCAP 7200 Duo', Thermo Fisher Scientific, Waltham, US) (LVS EN ISO 11885:2009).

2.2 Data analyses

We used the R-Studio software package for data analysis and visualization (R Core Team 2019). Before all analyses, we examined potential outliers and performed the Shapiro-Wilk test for normality and the Breusch-Pagan test for homoscedasticity. For plots with error bars, we used the standard error (SE), as most visualizations depict mean value

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differences within groups. To determine the effect of groundwater level on plant parameters, we applied one-way ANOVA for parametric data (total biomass, above-ground biomass, stem length, and SLA) and the Kruskal-Wallis test for non-parametric data (below-ground biomass), followed by Tukey's HSD and Dunn's post-hoc tests to assess differences between groundwater level groups. For root volume as a function of groundwater level and root diameter class, we used two-way ANOVA with Tukey's HSD post-hoc test. Although both Chl A and Chl B data were homoscedastic, they were not normally distributed; therefore, we used the Kruskal-Wallis test to assess concentration differences between groundwater levels and to compare linear regression models incorporating groundwater level and week of the year as factors. We further performed linear regression with the week of the year as an indicator variable for each groundwater level to evaluate the significance of weekly measurements, as no clear non-linear pattern was observed.

For GHG emission analyses, we built a linear mixed-effect model to determine which factors had the most significant impact on emissions. The model included the date as a random factor, and the soil and vegetation boxes, groundwater level, month, daytime and night time soil temperature, room temperature, moisture, and CO2 concentration as fixed factors Eq. (2):

$$GHG\ emissions \sim Vegetation + Groundwater + Month + DayNight + Soil_t + Room_t + Room_{Moist} + Room_{CO_2} + \frac{1}{Date} \quad (2)$$

After the results of the model, we created additional models to examine the interaction of significantly influencing factors with groundwater level Eq. (3), Eq. (4):

$$CH_4\ emissions \sim Groundwater * Soil_t + Vegetation + Month + DayNight + Soil_t + Room_t + Room_{Moist} + Room_{CO_2} + \frac{1}{Date} \quad (3)$$

$$CO_2\ emissions \sim Groundwater * Vegetation + Groundwater * DayNight + Month + DayNight + Soil_t + Room_t + Room_{Moist} + Room_{CO_2} + \frac{1}{Date}$$

We performed further analysis on categorical factors that significantly impacted vegetation parameters (vegetation groups, and day and night time). Two-way ANOVA and post hoc Tukey's HSD tests were used to assess the interaction significance between variables across different soil types, site preparation methods, and microtopography within each soil type. We also performed regression analysis with continuous factors (soil temperature) that had a significant effect on emissions. For data analysis, calculation, and visualization, we used several RStudio packages: 'dplyr', 'ggplot2', 'gridExtra', 'dunn.test', 'tidyverse', 'ggpmisc', 'lme4', 'MuMIn', 'car', and 'ggpubr' (Aphalo, 2023; Auguie, 2017; Bartoń, 2023; Bates et al., 2015; Dinno, 2017; Fox & Weisberg, 2019; Kassambara., 2023; Wickham, 2016; Wickham et al., 2019, 2023).

3 Results

3.1 Poplar trait responses to water table depth

Total above-ground dry biomass and stem length were higher starting from -15 cm and lower groundwater levels but did not show significant differences between shallower groundwater depths (Tukey's HSD results: Total – -2 cm and -15 cm p < 0.001

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-2 cm and -25 cm p < 0.001 -2 cm and -35 cm p < 0.001; Above-ground – -2 cm and -15 cm p = 0.001 -2 cm and -25 cm p < 0.001 -2 cm and -35 cm p < 0.001; Stem length – -2 cm and -15 cm p < 0.001 -2 cm and -25 cm p < 0.001 -2 cm and -35 cm p < 0.001) (Fig. 2). The exception was root biomass, which was higher at a groundwater level of -25 cm but decreased at -35 cm. However, as this was the very early stage of plant development, root mass differences did not influence total biomass trends. On average, root wet and dry biomass accounted for only one-seventh of the total accumulated biomass in new poplar plant parts (stem and leaves vs. root ratio—fresh biomass 6.1, dry biomass 6.2) (Dunn's test results: -2 cm and -15 cm p < 0.001 -2 cm and -25 cm p < 0.001 -2 cm and -35 cm p = 0.002; -25 cm and -35 cm p = 0.025). Groundwater levels from -15 cm to -35 cm did not show significant differences. However, with an increased sample size, shallow groundwater could demonstrate better performance in biomass accumulation, as the plots exhibited a trend of biomass gradually increasing with decreasing groundwater level.

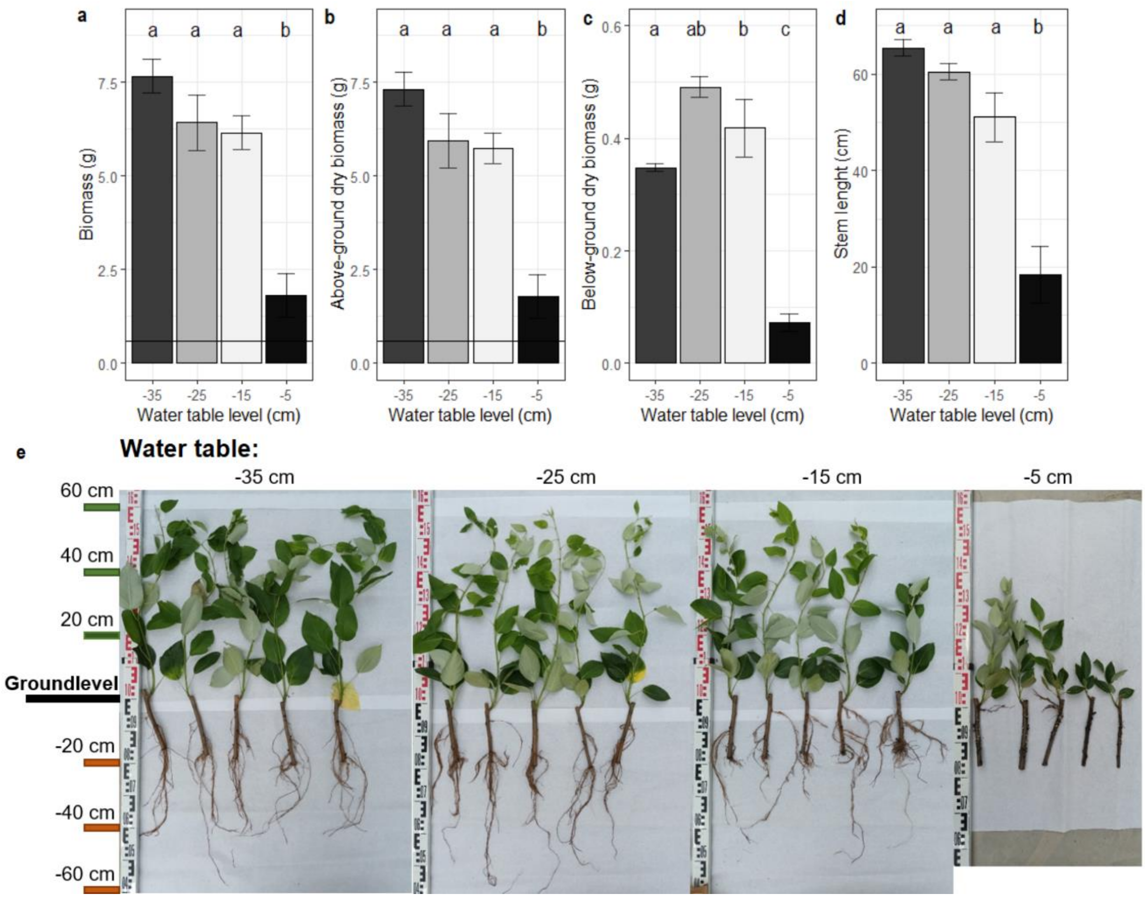

Figure 2 Plant dry biomass and length parameters: (a) total accumulated biomass, (b) above-ground biomass, (c) below-ground biomass, (d) stem length, and (e) plant at the end of the experiment (12 weeks after planting). The y-axis scale is not uniform across all biomass plots; the continuous line in subplots 'a' and 'b' indicates the y-axis limits for subplot 'c'. Letters represent significant differences (p < 0.05, Tukey HSD for a, b, c, d). Error bars indicate SE.

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Lateral roots with a diameter above 3 mm occupied the largest root volume starting from -25 cm groundwater level and higher in groups with -25 cm and -15 cm occupying a significantly larger volume than smaller roots (Fig. 3). The volume of lateral roots was significantly lower in the -35 cm variant although the volume of fine roots was not significantly different from the -25 cm and was higher than in the -15 cm and -2 cm levels. The largest total leaves area was the in lowest groundwater level although the difference was significantly higher only comparing with the highest groundwater level (Tukey's HSD results – -2 cm and -15 cm $p = 0.002$ -2 cm and -25 cm $p = 0.001$ -2 cm and -35 cm $p < 0.001$). SLA was higher at the lowest water level but not different at the other levels (Tukey's HSD results – -2 cm and -15 cm $p = 0.013$ -2 cm and -25 cm $p = 0.023$ -2 cm and -35 cm $p = 0.02$).

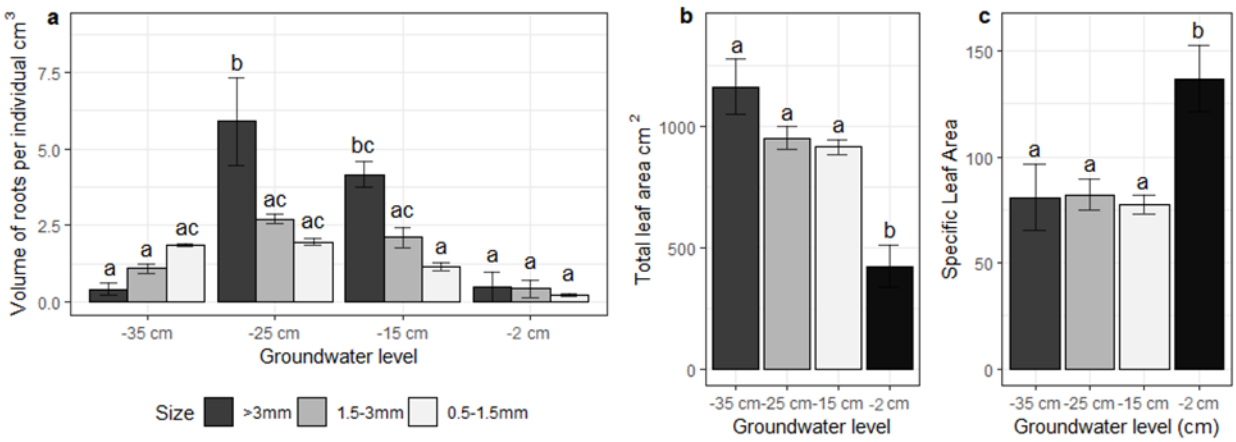

Figure 3 (a) Root volume depending on root diameter size, (b) total leaf area, (c) specific leaf area (SLA). Letters represent significant differences (p < 0.05, Tukey HSD). Error bars indicate SE.

Chl A and Chl B concentrations exhibited high weekly variability, and although significantly different from a normal distribution, the data were homogenous (Fig. 4). The issue with normality could be related to relatively long intervals between measurement times and a small number of measurements (average 7-day intervals, 10 measurements for each group). The average results for Chl A and Chl B concentrations did not differ significantly depending on the groundwater level, but when the time factor was included in the analysis, the relationship became significant. (Chl A by Groundwater Kruskal-Wallis chi-squared = 1.24 df = 3 $p = 0.744$ Chl A by interaction (Groundwater, Week) Kruskal-Wallis chi-squared = 105.94 df = 31 $p < 0.00$; Chl B by Groundwater Kruskal-Wallis chi-squared = 1.1 df = 3 $p = 0.778$ Chl B by interaction (Groundwater Week of year) Kruskal-Wallis chi-squared = 101.8 df = 31 $p < 0.001$). The linear regression model for each groundwater level showed that weeks 18, 25, and 26 were the most important for Chl A, while weeks 18, 23, and 25 were the most significant for Chl B concentration in leaves across all groundwater level groups. This highlights the importance of seasonal variation and plant development phases on chlorophyll concentration in the leaves. At the lowest groundwater level, the most pronounced decreases in Chl A ($R^2 = 69$) and Chl B ($R^2 = 64$) concentrations in the leaves were observed.

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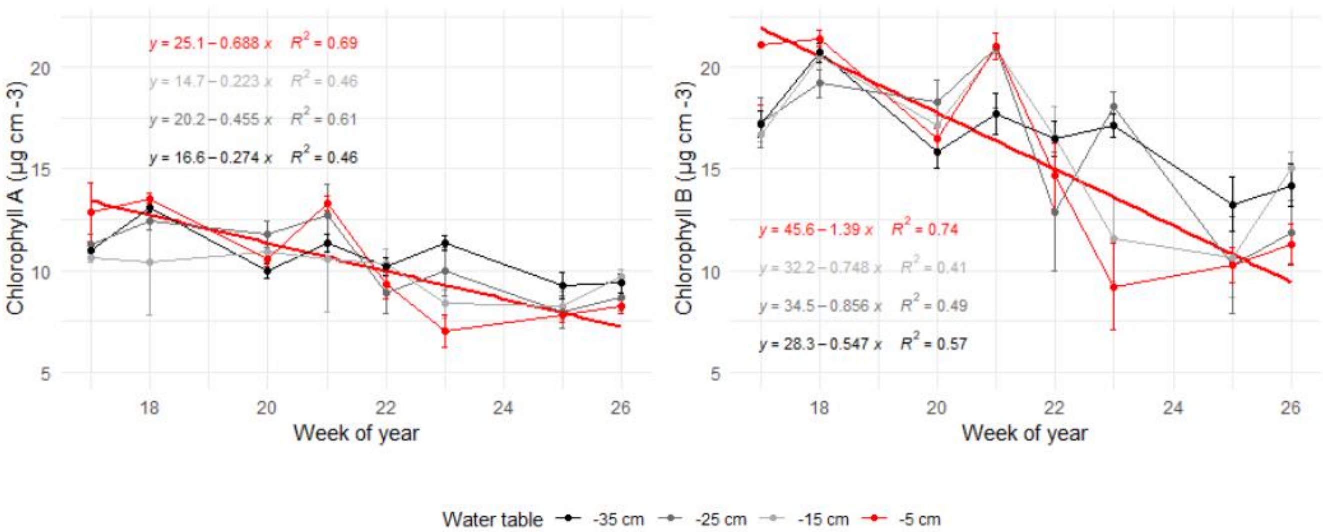

Figure 4 Chlorophyll A (a) and Chlorophyll B (b) content depending on weekly measurements. Error bars indicate SE.

3.2 Water table depth influence on soil respiration depth

Linear mixed effect model showed that CO_2 emissions were impacted by groundwater level: significantly lower at the -2 cm groundwater level and higher at the -35 cm groundwater level **(**Fig. 5). At the lowest groundwater level, CO_2 emissions also differed between Day and night time ($p = 0.003$) and between the poplar and bare soil groups ($p = 0.029$) being higher during the day and lower during the night. The difference was more notable in the plots with vegetation. Although the lowest groundwater level had significantly higher emissions during the daytime, there were no significant differences compared to the other levels during the night time ($p = 0.04$). CH_4 emissions were not impacted by vegetation or time but were significantly higher at higher groundwater levels (-2 cm and -15 cm $p < 0.001$ -2 cm and -25 cm $p < 0.001$ -2 cm and -35 cm $p < 0.001$). Low room air moisture and high soil temperature increased CH_4 emission (Moisture: -15 cm $p < 0.001$, -25 cm p = 0.001, -35 cm $p < 0.001$; Soil temperature: -15 cm $p < 0.001$ -25 cm $p < 0.001$, -35 cm $p < 0.001$). Nevertheless, the regression analyses showed that the highest groundwater level was the most sensitive to changed soil temperature the extremely high CH_4 emissions (<10000 kg c ha^{-1} $year^{-1}$) occurred together with extremely high soil temperatures (<23°C**)** **(**Fig. 6**).**

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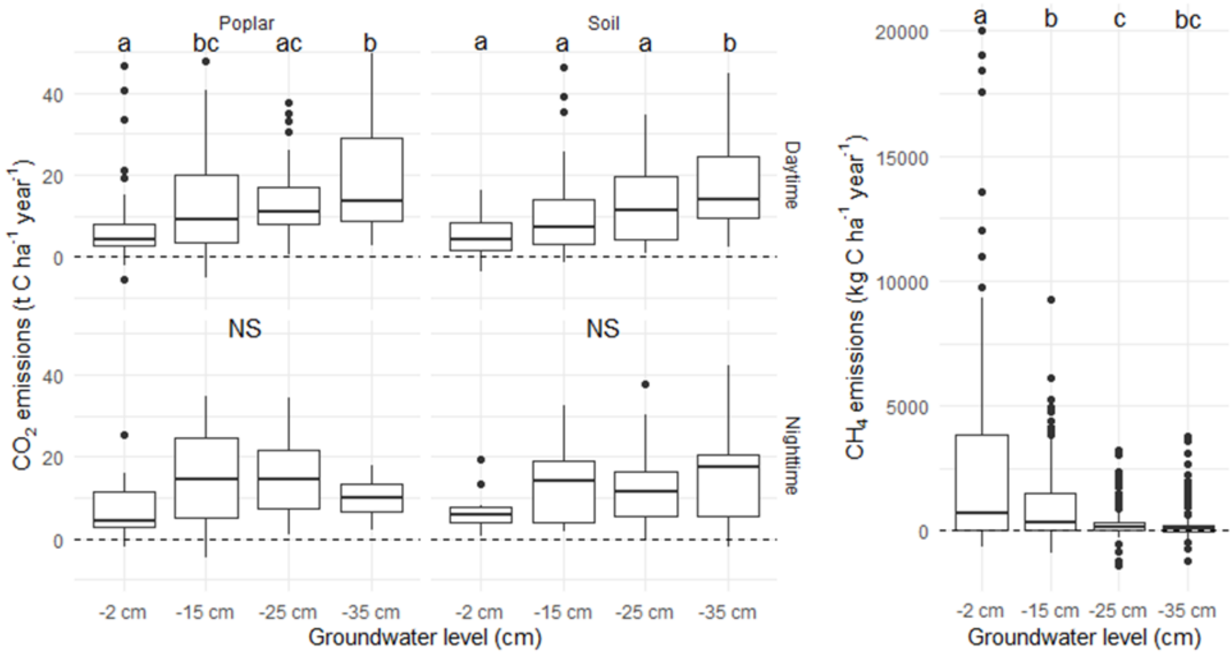

Figure 5 CO_2 emissions depending on daytime in groups with bare soil or with vegetation cover (poplar and Festuca) and CH_4 emissions depending on water table depth.

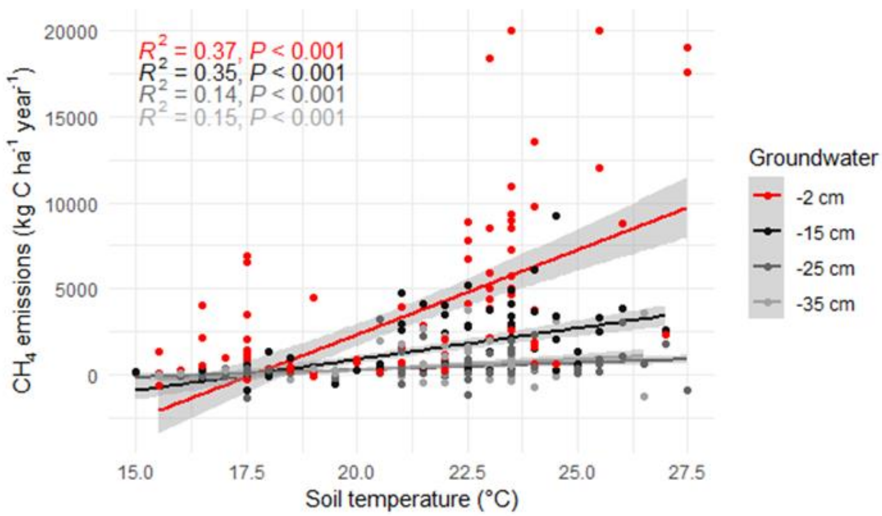

Figure 6 Regression analyses of CH_4 emissions in relation soil temperature at different groundwater levels.

Temporal variation in CH_4 emissions, as indicated by the linear model, showed a near-significant effect (p = 0.054). A rapid increase in mean emission values was observed between April 28th–May 16th and June 3rd–July 1st, with notably higher

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emissions in the latter period due to increased temperatures during the peak of the growing season (April 28th–16th of May $Avg_{CH_4 emission}$ = 71.9, SE 0.549 (C kg ha^{-1} year^{-1}); June 3rd–July 1st $Avg_{CH_4 emission}$ = 3489.7, SE 15.649 (C kg ha^{-1} year^{-1})). In the last period, differences between bare soil and vegetation were most pronounced in the -35 cm and -25 cm groups, where higher plant productivity coincided with lower CH_4 emissions (Table A4**).** CO_2 emissions increased between April 28th–May 16th and June 3rd–July 1st across all bare soil treatments. However, in vegetation-covered treatments, this increase was observed only at -15 cm and -2 cm groundwater levels or in groups with lower productivity (Table A5).

The heterotrophic and total respiration ratio increased with decreasing groundwater level, indicating that the rise in respiration at lower groundwater levels was primarily driven by heterotrophic respiration, as supported by the data showing no significant differences in accumulated biomass and chlorophyll concentration between -15 cm and -35 cm groundwater depths (Table 5).

Table 5

Ratio of average heterotrophic and total soil respiration under different groundwater level

Water table level	Heterotrophic and Total respiration ratio
-35 cm	1.14
-25 cm	0.91
-15 cm	0.66
-2 cm	0.74

Factors positively correlated with CH_4 emissions showed a negative correlation with CO_2 emissions (Fig. 7). CO_2 emissions were positively correlated with most plant parameters, particularly total accumulated biomass in both above- and below-ground plant parts. CH_4 emissions were positively correlated with SLA and Chl A and Chl B content in leaves, both of which can indicate denser leaves, as SLA reflects biomass accumulation per unit leaf area. This may be due to limited nutrient availability in plots with high CH_4 emissions (-2 cm groundwater level), leading to the formation of smaller, denser plant cells.

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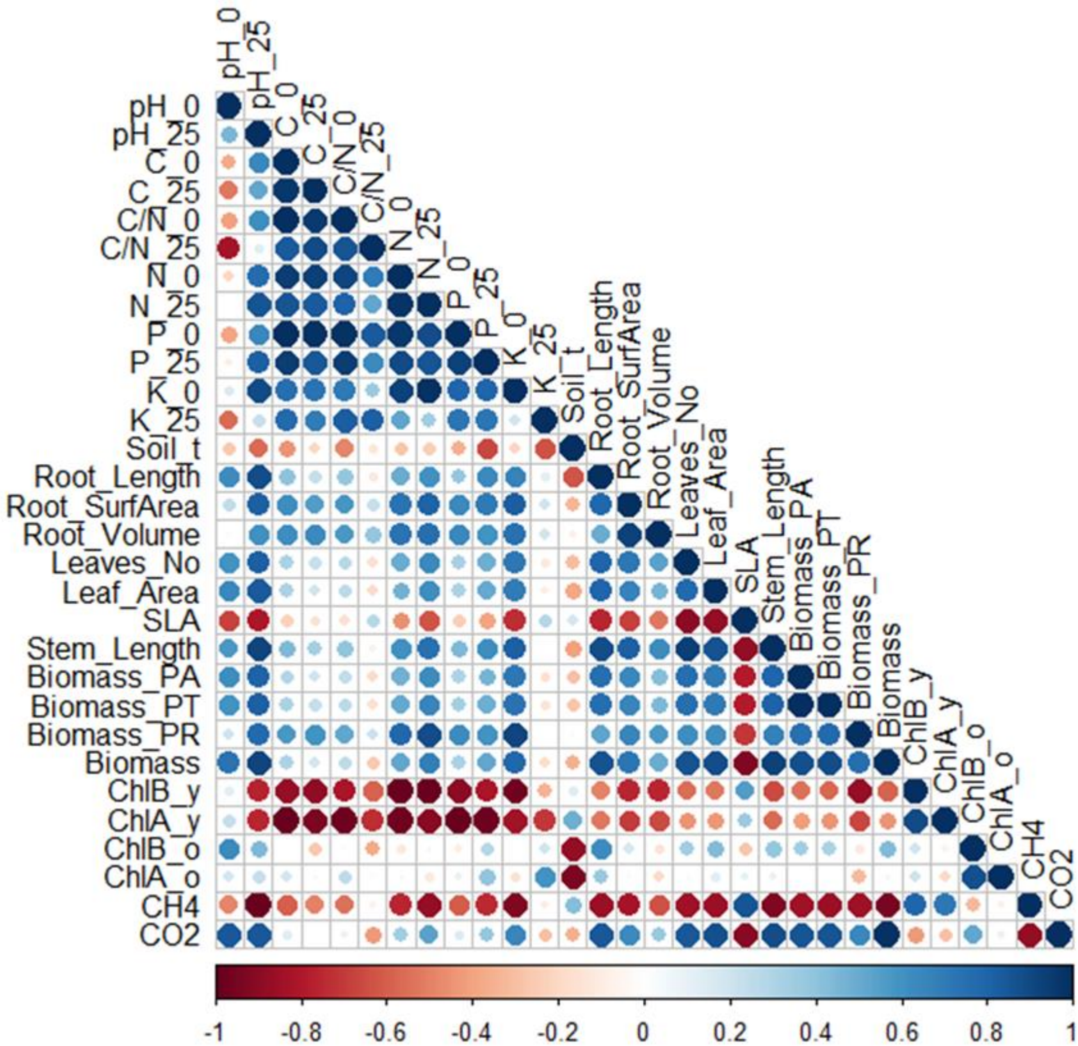

Figure 7 Correlation heatmap of soil chemical environment, plant, and emission parameters. x_0 – analyses at 0–5 cm soil depth; x_25 – analyses at 25–30 cm soil depth; x_PA – Poplar Aboveground; x_PT – Poplar Total; x_PR – Poplar Roots; x_y – young leaves; x_o – old leaves.

4 Discussion

Results showed that using this study design with deep drained conditions (-35 cm), accumulated dry biomass in both above- and below-ground parts, total leaf area, and shoot length were higher. Although poplars are a species highly dependent on water availability in the soil and drought conditions can limit growth, the results of this study suggest that overly moist soil, as observed in shallow-drained conditions (-15 cm), can decrease productivity (Semerci et al., 2017). The most active water and dissolved nutrient uptake by the roots takes place in the region of maturation after the meristematic and elongation zone

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where both root hair and vascular tissue have formed, but no accumulation of suberin and lignin has occurred in the cell walls of the vascular tissue (Calvo-Polanco et al., 2021). However, under conditions of intense transpiration water uptake can also occur in the root zone with for fully differentiating cells (Frensch et al., 1996). Although root water uptake is a passive process it is negatively affected by low O_2 and high CO_2 and transpiration inhibitors while transpiration is negatively correlated with high humidity (Else et al., 2001). It is important to emphasize that although with increasing transpiration rate from poplar leave, increases stomatal conductivity and photosynthetic rate, the first growth limiting factor is root absorption capacity therefore the volume and area of the active root region (Zhang et al., 2005). But nutrient absorption through roots is also partly regulated by light and diurnal rhythms (Zhao et al., 2021). Lateral root biomass in the deep-drained group was smaller than in shallow drained but the highest accumulated biomass, as well as total leaf area advocates the previously discussed research that roots smaller than 3 mm account for most water and nutrient accumulation and total plant below parts volume may not have strong correlation with tree transpiration rate or productivity.

Another productivity indicator is plant greenness or photosynthetic pigment content: the higher chlorophyll content per unit area the higher the light absorption and the rate of photosynthesis can increase if the other limiting factors are optimal – water and nutrient availability temperature. Poplars with higher chlorophyll content in leaves have later senescence higher productivity and longer growth period (Adler et al., 2021). On the other side the total plant photosynthetic capacity is dependent on both: chlorophyll content and photosynthetic (mostly leaves) area therefore the higher pigment content does not always indicate higher plant vitality and needs to be analyzed in the context of other plant traits. As the groundwater level decreases the amount of photopigment content increases in poplar leaves but after reaching the optimum water level the content decreases, therefore chlorophyll content does not correlate with soil moisture, but with plant capacity to absorb the nutrients (Zhang et al., 2022). This suggests that the optimal water level of OP42 could be even lower as the amount of photosynthetic pigments continues to increase as the considered groundwater levels decrease. The highest ChlA and ChlB content at the beginning of the measurement was in the -2 cm group, but this group also had the most rapid decrease. Chlorophyll content for healthy vegetative cutting propagated poplars increases after leaf initiation until maturation and decreases towards the end of the growing season starting from the middle or end of August (Castro and Sanchez-Azofeifa, 2008; Marron et al., 2008). A faster decrease of leaf photosynthetic pigment content can indicate stress factors for plant growth in this case – poplar grown at a high groundwater level did not form a functional root system which could initial small cell size and leaf formation at the beginning of plant growth therefore higher photosynthetic pigment density per area but the rapid decrease in photosynthetic pigment content later can indicate that saved nutrient in cutting had been used and due to the lack of root system no new uptake occurs. In field conditions, the differences between chlorophyll content depending on groundwater level could be higher because chlorophyll content in plant leaves grown in a greenhouse tends to be smaller compared to the field conditions as greenhouse transmit only 30-80% of light depending on cloudiness which has negative effect on photosynthetic pigment synthesis (Farré and Weise, 2012; Cabrera-Bosquet et al., 2016; Poorter et al., 2016; von Elsner et al., 2000).

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Both CH_4 and CO_2 were primarily influenced by groundwater level, CO_2 had increased emissions with decreasing groundwater level, but significant CH_4 emissions occurred only in shallow drained or undrained conditions (above -15 cm water level), but not in deep drained (below -25 cm), with similar results are described in field studies for CH_4, where its seasonal variation is 78% explained by groundwater level (Klemisch & Pfadenhauer, 2002). It is well known that high groundwater level has a positive correlation with CH_4 emission due to the need for an anaerobic environment for methanogen microorganisms, but flooded organic soils can be significant for both CO_2 (967 kg C ha^{-1} year^{-1}) and CH_4 (435 kg C ha^{-1} year^{-1}) emission sources (Butlers & Lazdiņš, 2022). In this study in group with -2 cm groundwater level the carbon emission during the beginning of May was approximately 350 kg C ha-1 year^{-1}, but in June increased by about 970 kg C ha^{-1} year^{-1}, but for CH_4 during the beginning of May emissions were only 16 kg C ha^{-1} year^{-1}, but in June increased up to 5838 kg C ha^{-1} year^{-1}, showing the very high variation only in two month period due to the high-temperature variation. The high CO_2 and CH_4 temporal variation during the year also can be seen in other studies, where CH_4 emissions are reported to be unimportant during the winter frost period, but during the first part of the growing season peaks of emission can occur (Chapman & Thurlow, 1996; Maljanen et al., 2004; Viru et al., 2020). Vegetation influence was negligible with high groundwater level and low productivity, but with lower groundwater level and higher productivity CH_4 emissions were lower (up to 460 kg ha^{-1} year^{-1}) compared to the bare soil (up to 1366 kg ha^{-1} year^{-1}), which can indicate the vegetation negative influence solar radiance and temperature impact on soil due to the higher albedo than bare peat soil (Tuittila, 2000). Similar results with higher CH_4 uptake in soils with vegetation are also documented in field studies (Maljanen et al., 2004). On a temporal scale plant cover also helped to decrease CO_2 emissions, as emission from bare organic soil increased both in day and night comparing May and June emissions, but decreased with vegetation in June during daytime, when, due to the higher temperature, photosynthetic rate and carbon assimilation was higher than in May (Domingo & Gordon, 1974). Although we could observe photosynthesis and plant productivity influence on total ecosystem respiration, especially with lower groundwater levels, the proportion of heterotrophic respiration increased with decreasing groundwater levels, indicating, that ecosystem respiration is primarily controlled by microorganism activity regulated by groundwater level and temperature. The temperature influence on heterotrophic respiration can also be seen in the results, that for lower groundwater level, the CO_2 emission rate was significantly higher with lower groundwater levels during daytime, but no statistical differences were observed during nighttime, indicating that measuring emission only at certain times during the day can lead to overestimation of the total emissions (Brændholt et al., 2017). The temperature had a positive, but air moisture negative effect on CH_4 emissions, in advance, extreme CH_4 emissions only occurred with extremely high soil temperatures. This should be considered for future management practices, that increasing summer temperature extreme events every year in the hemiboreal zone generates the threat of increased emission extremes and that plant cover can limit these events.

Although the greenhouse environment creates limitations for the experiment since it is not possible to directly explain the natural processes with the obtained results, it can be used as a useful tool to accurately understand the trends and interactions of the factors under consideration to improve the fundamental knowledge base about the carbon cycle in nature. Either in

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greenhouse or in field conditions, light quantity, CO_2 concentration, air humidity, and air and soil temperatures have medium to high diurnal variability, although air temperature and humidity have higher variability in field conditions than soil temperature in greenhouse conditions (Poorter et al., 2016). The high diurnal variability of soil temperature in greenhouse experiments usually occurs due to the small container size as well as the material used, typically dark-colored plastic. In this experiment with a relatively large vegetation vessel volume constructed from wood products, we succeeded in not overcoming the average diurnal variation of the soil temperature at a 10 cm depth higher than 1 °C (**table 1**) which is close to the average variation in field conditions – 1.2 °C (Bell et al., 2013; Poorter et al., 2016). Greenhouse conditions also provide higher air temperature and moisture which significantly affect plant-soil interactions. In the context of tree growth in temperate climate zone higher air temperature can increase the photothermal ratio and extend the growth period for tree species in which dormancy is regulated by both photoperiod and temperature including poplar (Domingo & Gordon, 1974; Kalcsits et al., 2009). Nevertheless, temperature and moisture are also some of the main influencing abiotic factors of soil emissions and will influence both levels individually as well as their interaction but the future forecast in this region predicts higher air and soil temperature as well as higher air humidity therefore it could be beneficial to carry trails in this direction modified environmental conditions. With this experiment design we partly decreased the limitations of greenhouse experiments: variation of soil temperature (with large volume vegetation vessels and material choice) and no inter-species competition (with OP42 an *F. ovina* combination (Thomas and Lang, 2020)) but did not limit the higher air temperature and humidity comparing to the field conditions in this way creating likeable conditions for future climate scenarios.

Conclusions

Poplar is an alluvial species, but soggy soil conditions inhibit root system formation, which leads to inefficient nutrient absorption and decreases photopigment synthesis and overall plant productivity. Plant vitality indicators need to be analyzed in groups because specific environmental conditions can have different effects on these parameters. The relationships are not always linear, which can lead to false conclusions when looking at a parameter outside the overall context. For example, physiological parameters, such as leaf chlorophyll content alone, do not indicate the overall vitality of the tree. The root absorption capacity is critically limiting factor for plant growth, which is determined not by root mass but by root active region volume and area, as well as soil conditions. Temporal and diurnal variation strongly impacts GHG fluxes due to the changes in temperature, moisture, and plant growth activity. Higher temperatures increase both CO_2 and CH_4 emissions; the most notable impact was for extremely high soil temperatures on CH_4 emissions at a -2 cm groundwater level, but air moisture had a negative relationship with CH_4 emissions. Higher plant productivity had a higher influence on GHG fluxes: it decreased CH_4 emissions as well as CO_2 emissions during the day compared to the bare soil. Therefore, the autotrophic respiration rate increased with increased productivity, but the primary determinant was heterotrophic respiration, as its proportion of total respiration increased with decreasing groundwater level. Although the greenhouse environment creates limitations for the experiment, it can be used as a useful tool if the limitation effect is decreased.

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Appendices

Table A1

Soil chemical composition after experiment

Water table depth, cm	Group	Soil depth, cm	Moisture, %	$C_{tot.}$, g kg^{-1}	pH_{CaCL2}	$N_{tot.}$, g kg^{-1}	C/N	K, g kg^{-1}	Ca, g kg^{-1}	Mg, g kg^{-1}	P, g kg^{-1}
-35	Organic soil	0-5	3.80	88.20	7.00	3.40	25.94	2.68	9.69	3.67	0.65
		20-25	3.70	67.80	7.00	3.30	20.55	2.64	8.23	3.61	0.68
		40-45	2.60	51.10	6.80	2.10	24.33	2.46	7.42	3.40	0.65
	Poplar-*festuca*	20-25	3.00	69.10	7.00	3.20	21.59	2.31	8.30	3.59	0.66
		40-45	3.10	51.80	7.00	2.70	19.19	2.28	8.78	3.83	0.65
-25	Organic soil	0-5	3.90	86.50	7.10	3.20	27.03	2.04	8.06	3.26	0.60
		20-25	3.30	55.30	6.90	2.60	21.27	2.06	8.51	3.41	0.64
		40-45	3.40	68.20	6.90	2.70	25.26	1.82	7.34	3.04	0.55
	Poplar-*festuca*	0-5	3.70	90.90	6.80	3.40	26.74	2.47	9.97	3.96	0.76
		20-25	3.90	73.90	7.00	3.00	24.63	2.39	9.90	3.82	0.66
		40-45	2.50	51.70	6.90	2.50	20.68	1.98	7.95	3.39	0.63
-15	Organic soil	0-5	3.50	72.60	7.10	3.20	22.69	2.21	8.23	3.45	0.63
		20-25	3.50	54.30	6.90	2.50	21.72	2.07	8.46	3.39	0.60
		40-45	2.90	51.60	6.80	2.30	22.43	2.01	7.36	3.21	0.55
	Poplar-*festuca*	0-5	3.20	63.90	6.90	3.20	19.97	2.31	10.10	3.80	0.65
		20-25	3.00	54.10	6.90	2.70	20.04	2.19	8.00	3.43	0.64
		40-45	2.90	60.90	6.90	2.30	26.48	2.09	7.35	3.38	0.56
-2	Organic soil	0-5	3.10	67.50	6.90	2.80	24.11	2.18	8.45	3.43	0.63
		20-25	2.90	61.80	6.80	3.00	20.60	2.28	7.78	3.41	0.65
		40-45	2.80	68.40	6.90	2.80	24.43	1.95	7.54	3.20	0.58
	Poplar-*festuca*	0-5	2.60	64.10	6.80	3.10	20.68	2.05	7.43	3.38	0.64
		20-25	2.80	51.90	6.80	2.40	21.63	2.32	9.81	3.65	0.64
		40-45	2.90	53.50	6.90	2.30	23.26	2.09	8.00	3.26	0.56
	Mineral soil	0-5	2.00	29.20	7.00	2.50	11.68	2.10	6.59	3.62	0.69
		20-25	2.00	28.30	6.60	2.40	11.79	2.35	6.60	3.65	0.74
		40-45	2.10	29.70	6.90	2.50	11.88	2.12	7.18	3.77	0.70
	Peat	0-5	18.50	435.10	6.80	8.90	48.89	NA	NA	NA	NA
		20-25	19.40	480.80	6.40	8.70	55.26	NA	NA	NA	NA
		40-45	18.40	494.70	6.30	9.10	54.36	NA	NA	NA	NA

Table A2

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Fresh and dry biomass of *Festica ovina* and its impact on total accumulated plant biomass

Groundwater level, cm	Fresh biomass: *F. ovina* biomass, g	Fresh biomass: Total plant biomass, g	Fresh biomass: *F. ovina* from total biomass, %	Dry biomass: *F. ovina* below biomass, g	Dry biomass: Total plant biomass, g	Dry biomass: *F. ovina* from total biomass, %
-35	61	188	32	13	49	26
-25	36	122	29	9	39	24
-15	42	121	34	10	38	26
-5	22	46	47	6	15	41

Table A3

Water content depending on plant part (g of water per g of dry mass)

Groundwater level	*Festuca ovina* above-ground, g	OP42 Leaves, g	OP42 Stem, g	OP42 Roots, g
-35 cm	4.59	3.69	3.20	2.06
		SD 0.27	SD 0.12	SD 0.27
-25 cm	3.73	2.99	2.75	2.65
		SD 0.20	SD 0.12	SD 0.74
-15 cm	4.16	2.86	2.63	2.68
		SD 0.11	SD 0.08	SD 0.32
-2 cm	3.48	2.83	2.79	2.33
		SD 0.18	SD 0.18	0

Table A4

CH_4 emissions (C kg ha^{-1} year^{-1}) from organic soil with vegetation (OP42 and *Festuca ovina*) and without depending on the temporal and diurnal scale

Ground water	April 28th–16th of May				May 17th –June 2nd				June 3rd–July 1st			
	Poplar-*festuca*		Organic soil		Poplar-*festuca*		Organic soil		Poplar-*festuca*		Organic soil	
	D	N	D	N	D	N	D	N	D	N	D	N
-35	-20.2	-64.3	17.4	18.4	62.4	12.9	14.6	42.9	305.4	337.4	1366.6	1230.7
	*3.6	*0	*7.7	*8.1	*6.2	*12.6	*8.3	*26.8	*29.9	*109.9	*81.9	*214.9
-25	-32.6	46.0	0.5	-32.2	-78.0	128.7	126.1	228.6	294.5	459.2	841.7	1004.1
	*6.5	*8.1	*4.8	*5.4	*24.1	*19.9	*10.8	*9.4	*20.1	*67.8	*33.4	*97.8
-15	0.5	NA	15.8	NA	57.4	-98.4	171.0	440.1	2293.1	2543.1	1879.0	2297.1
	*7.7		*3.7		*16.4	*81.4	*19.9	*39.6	*92.2	*283.0	*70.9	*265.6
-2	16.1	NA	10.8	16.1	1559.1	1402.7	1720.0	230.1	5838.5	2658.5	5817.6	3362.4
	*2.8		*15.2	*7.0	*101.2	*413.7	*271.5	*86.0	*236.0	*322.4	*307.7	*673.0

D – day N – night (Daylength; in May form 5.00 AM till 21.30 total 16 h 30 min; in June form 4.30 AM till 22.20 total 17 hours 50 min)
* – Standard Error

Table A5

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CO_2 emissions (C t ha^{-1} $year^{-1}$) for organic soil with vegetation (OP42 and *Festuca ovina*) and without depending on the temporal and diurnal scale

Groundwater	April 28th–16th of May				May 17th –June 2nd				June 3rd–July 1st			
	Poplar-*festuca*		Organic soil		Poplar-*festuca*		Organic soil		Poplar-*festuca*		Organic soil	
	D	N	D	N	D	N	D	N	D	N	D	N
-35	30.2 *1.1	10.4 *1.1	25.4 *1.7	14.4 *1.1	13.9 *0.6	11.8 *0.4	13.7 *0.7	20.8 *5.1	15.6 *0.9	17.5 *3.7	26.6 *1.2	18.8 *3.7
-25	15.1 *0.6	22.1 *0.9	7.7 *0.7	6.3 *0.6	13.5 *0.4	13.4 *1.1	11.9 *0.3	17.4 *1.3	11.0 *0.4	8.7 *1.4	12.9 *0.5	15.7 *1.2
-15	13.6 *1.7	8.5 *2.3	3.3 *0.1	4.2 *0.6	7.1 *0.6	5.6 *5.1	4.6 *1.2	15.6 *0.6	18.6 *0.7	21.5 *1.9	13.2 *0.7	17.6 *1.9
-2	3.5 *0.1	2.8 *0.8	1.8 *0.5	4.8 *0.5	6.6 *0.5	10.9 *1.3	4.2 *0.2	6.6 *0.3	9.7 *0.4	6.3 *1.0	6.7 *0.3	9.5 *1.9

D – day N – night (Daylength; in May form 5.00 AM till 21.30 total 16 h 30 min; in June form 4.30 AM till 22.20 total 17 hours 50 min)
* – Standard Error

Code availability

The data underlying this study are available from the corresponding author upon reasonable request.

Data availability

The data underlying this study are available from the corresponding author upon reasonable request.

Author contribution:

All the authors contributed to the study conception and design. Data collection was performed by V.V. and A.Z. Material preparation was performed by A.Z., and V.V. Data visualization and analyses were performed by A.Z. and V.V. The first draft of the manuscript was written by A.Z., and A.L., V.V., and D.L. commented on, reviewed, and edited previous versions of the manuscript. Supervision, project coordination, and funding acquisition were performed by A.L. and D.L. All the authors read and approved the final manuscript.

Competing interests

The authors declare no conflict of interest.

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