SOIL ECOLOGY LETTERS

SEL RESEARCH ARTICLE
Volume 6 / Issue 4 / 240250 / 2024
https://doi.org/10.1007/s42832-024-0250-6

Soil type and temperature determine soil respiration seasonal dynamics in dairy grassland

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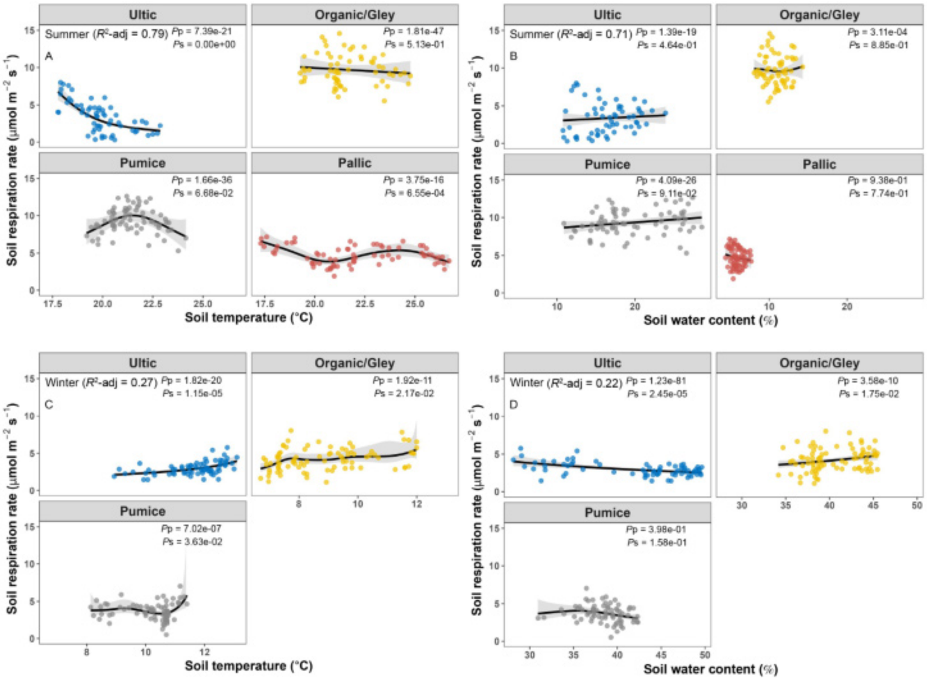
Received November 22, 2023; Revised April 2, 2024; Accepted April 4, 2024

ABSTRACT

- Soil respiration rates (R_s) were measured in New Zealand dairy grassland.
- Both season and soil type significantly affected R_s.
- Soil temperature and soil type dominated overall R_s.



Soil respiration (R_s), the CO_2 release from root respiration and microbial metabolism, affects global soil carbon storage and cycling. Only few studies have looked at R_s in the southern hemisphere, especially regarding the interaction between soil type and environmental factors on R_s in dairy grassland. We investigated the relationship between R_s and soil temperature (T_s), soil water content (SWC), soil type, and other environmental factors based on summer and winter measurements at four sites in New Zealand. Across sites, soil respiration rates ranged from 0.29 to 14.58 with a mean of 5.38 ± 0.13 (mean ± standard error) μmol CO_2 m^{-2} s^{-1}. Mean summer R_s was 86.5% higher than mean winter R_s, largely driven by organic/gley and pumice soils while ultic soils showed very little seasonal temperature sensitivity. Overall mean R_s in organic/gley soils was 108.0% higher than that in ultic soils. The high R_s rate observed in organic/gley was likely due to high soil organic matter content, while low R_s in ultic and pallic soils resulted from high clay content and low hydraulic conductance. Soil temperature drove overall R_s. Our findings indicate that soil type and soil temperature together best explain R_s. This implies that a mere classification of land use type may be insufficient for global C models and should be supplemented with soil type information, at least locally.

Keywords agriculture, agricultural soils, land use, livestock farming, soil carbon emission, soil temperature

1 Introduction

Soil respiration (R_s), the CO_2 flux from soil to atmosphere, is the second-largest carbon flux on earth (Friedlingstein et al., 2022). It plays an important role in regulating terrestrial carbon cycling, both at a regional and global scale (Green and Byrne, 2004). Plant roots together with their mycorrhizal partners (autotrophic respiration, R_a) and soil microbes (heterotrophic respiration, R_h) are the major components

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Cite this: Soil Ecol. Lett., 2024, 6(4): 240250

that make up R_s (Bond-Lamberty et al., 2004; Subke et al., 2006). The amount of R_s per unit surface area is usually calculated by CO_2 increases inside a dark measuring chamber placed over a known surface area with the aboveground biomass removed (Pumpanen et al., 2004). Over long time periods and integrated over large areas, soil respiration is ultimately driven by plant productivity (Raich and Tufekciogul, 2000; Caprez et al., 2012), as 'you can only eat as much food as you have produced' (Raich and Nadelhoffer, 1989). In the short term however, R_s is influenced by soil characteristics (e.g., soil type; Cable et al., 2008), environmental factors (e.g., soil temperature and moisture; Lloyd and Taylor, 1994; Moyano et al., 2013), and the present microbial communities (Bardgett et al., 2008). Changes in these short-term drivers can lead to R_s variation, thus potentially causing large increases in atmospheric CO_2.

Soil respiration increases exponentially with temperature and displays a seasonal pattern with higher summer rates if moisture does not become limiting (Lloyd and Taylor, 1994; Suseela et al., 2012). Warming often stimulates decomposition, contributing to increases in soil heterotrophic respiration (Sierra et al., 2015; Moonis et al., 2021). Temperature can also influence R_s indirectly through the availability of soil substrate according to seasonally varying litter input (Zhang et al., 2020). This temperature induced substrate change possibly affects the rhizosphere microbes and interacts with microbial biomass, as newly generated carbohydrates largely consist of labile C readily used by soil microbes, which contributes to R_s change (Wan and Luo, 2003).

Both soil moisture and soil organic matter are correlated with temperature as well as with each other, as soils often become drier with rising temperature, and soil water status influences the availability and decomposition of soil organic matter (Borken and Matzner, 2009; Manzoni et al., 2012). Soil moisture levels that are often optimal for soil respiration rates around field capacity, when the macropores are air-filled and the micropores are water-filled (Davidson et al., 2000). Soil moisture alters R_s through 1) physiological process of soil microbes, and 2) soil substrate transport and soil O_2/CO_2 diffusivity. Soil water deficiency restricts both soil microbes and plant root metabolism. Drained soil pores limit the movement of soil microbes (Yang and van Elsas, 2018) and the availability of water-soluble substrates for microbial consumption. Additionally, dry conditions can reduce the efficiency of microbes using soil resources (Schimel, 2018), or even induce dormancy in non-sporulating bacteria (Jones and Lennon, 2010). Water scarcity in soils may thus reduce microbial biomass and/or activity, and hence soil respiration. When soil water content exceeds optimal conditions, the overabundance of water-filled soil pores suppresses soil gas diffusion, thus limiting soil O_2 availability (Iiyama et al., 2012), while the effect on microbial respiration depends on the composition of the microbial community, i.e., the proportion of obligatory aerobes, facultative anaerobes, and obligatory anaerobes (Keiluweit et al., 2017). Because of its close link to water holding capacity, soil texture is also an important driver of soil respiration. Increasing soil moisture restricts R_s rates more strongly in fine-textured soils than in the sandy soils due to reduced porosity (Bouma and Bryla, 2000). In clayish soils, reduced R_s at a certain soil moisture level results from limited free water for substrate diffusion, as clay binds soil water strongly (Moyano et al., 2013).

High grassland coverage combined with high CO_2 emission rates means that grasslands can contribute greatly to the atmospheric CO_2 pool. Grassland covers ca. 25% of global soil carbon stocks (FAO, 2023; Jordon et al., 2024). Globally, soil CO_2 efflux rates are consistently higher in grassland than in forests and croplands under similar climatic conditions (Raich and Tufekciogul, 2000). Mean R_s rates of global temperate grassland were estimated at 1.03−1.61 μmol CO_2 m^{-2} s^{-1} (Raich and Potter, 1995; Wang and Fang, 2009). In New Zealand, grassland is the most common type of land cover, accounting for about 40% of the total land area (Ministry for the Environment and Stats NZ, 2021). In 2021, the net carbon emissions from grassland (excluding livestock emissions) amounted to over 4 million t CO_2-equivalent, of which around 98% originated from CO_2 emissions, and only 2% were due to N_2O and CH_4 from biomass burning and nitrogen mineralisation. The estimated net CO_2-equivalent emission rate was around 4 times higher in 2021 (0.01 μmol CO_2 m^{-2} s^{-1}) than in 1990 (0.003 μmol CO_2 m^{-2} s^{-1}) (Ministry for the Environment, 2023). New Zealand dairy accounted for about 42% of export revenue in primary industries in 2023 (Ministry for Primary Industries, 2023). The profitable dairy industry has encouraged the intensification of dairy farming for decades, e.g., dairy cattle numbers have doubled from 1990s to 2019 (Ministry for the Environment and Stats NZ, 2021). Quantifying soil CO_2 emissions and investigating the driving factors of R_s in dairy grassland are essential for understanding the impacts of dairy farm intensification to soil C stock and are prerequisite to soil C sequestration in such land use. Many studies in New Zealand dairy farm grassland have been focusing on carbon balance using Eddy Covariance, and the soil respiration rates were only estimated or interpolated (Hunt et al., 2002, 2016; Brown et al., 2009; Kirschbaum et al., 2015; Giltrap et al., 2020). Here, we present the first field-based study to systematically measure R_s and investigate the relationships between R_s and its driving factors in New Zealand intensified dairy grasslands. Two research questions to be addressed include: 1) What is R_s in New Zealand dairy grassland? 2) What are the major factors affecting the magnitude and dynamic of dairy grassland and how? Correspondingly, we propose the following hypotheses.

1) Mean R_s are higher than those in global temperate

grassland due to the intensified dairy farming.

2) Both seasonal and diurnal changes have significant effects on R_s. Summer R_s is higher than winter R_s, while R_s at noon is higher than during the morning and late afternoon.

3) Soil temperature explains summer R_s best, while soil water affects winter R_s the most.

4) Soil type affects soil respiration. We estimate that R_s is highest in organic/gley (OG) soils and lowest in pumice (Pu) soils.

2 Materials and methods

2.1 Study site

The study sites included four dairy farms in New Zealand. Three in the North Island (Mangakura, Tauhei, Rotorua) and one in Teviotdale, Southland with soil types ultic (U), organic/gley (OG), pumice (Pu) and pallic (Pa) respectively (Table 1). Soil taxonomy was based on Hewitt (2010). The corresponding soil classifications were Acrosols, Gleysols, Arenosols, and Cambisols in FAO world reference database (Schad, 2023). The study took place in early January to mid-February (summer), and early to mid-July (winter) in 2020. The sites were no more than 400 metres above sea level, and all were dominated by the temperate oceanic climate. Ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) were the two most abundant plant species. Fertilisers were not applied. No tillage happened in the paddocks measured in this study. The herd size of each dairy farm was around 300 cows. Multi-paddock rotational grazing was scheduled to 1 to 3 days per paddock. Soil type, drainage, texture, carbon stock, phosphorus retention rate, and pH were retrieved from S-Map Online website, Landcare (Lilburne et al., 2012), while climate information (i.e., windspeed, air pressure, hourly sunlight duration, weekly rainfall, monthly rainfall, three-monthly rainfall) was retrieved from the National Climate Database, NIWA (National Institute of Water and Atmospheric Research, n.d.) (Table 1).

2.2 Experimental design

Twelve plots (10 m × 10 m) were randomly selected across four study sites (three plots per site). Each plot contained four sub-plots (polyethylene collars) and was measured one day in summer and another in winter (except missing winter measurements at the Pa site). During any given measurement day, soil respiration at each sub-plot was measured six times i.e., at two-hourly intervals from 8:00 until 18:00. Every soil respiration measurement was coupled with three soil temperature and three soil water content measurements. We carried out 496 individual R_s measurements.

2.3 Field measurement of soil respiration, temperature, and moisture

Soil CO_2 efflux was measured by the closed static chamber method. Chamber design and construction followed Bader and Körner (2010). The chamber housing (diameter × height: 19.0 cm × 29.4 cm) had an internal volume of 8.34 L and featured a sealable vent to minimize pressure fluctuations involved with chamber placement on soil collars (Gschwend Kunststoff AG, Basel, Switzerland). 24 hours prior to the initial measurement for each season, the above-ground grasses were trimmed to ca. one centimetre and the polyethylene collars (height: 7.0 cm) were inserted 2 to 3 cm into the soil. This protocol was used to minimise both above-ground autotrophic respiration and extra CO_2 release from potentially damaged plant roots (wound respiration) following the insertion of the collars into the soil. For the duration of the R_s measurement, the customised chamber was placed on the collar. A 5V electric fan was attached inside the chamber to gently rotate the air, avoiding CO_2 accumulation at the soil surface. The chamber was equipped with a CO_2 probe (GMP343, Vaisala, Finland) coupled with a tempera-

Table 1 Soil characteristics and climate data of the study sites.

Site	Coordinates	Mean air temperature (°C)	Mean precipitation (mm/month)	Soil type	Soil texture	Soil pH	Soil carbon storage (t ha^{-1})	Soil drainage	Dominant species
Mangakura	36°24′11.6″S 174°26′60.0″E	18.4 (S) 12.9 (W)	6.0 (S) 110.8 (W)	Ultic (U)	Clay	5.5–5.6	92.7–105.6	Imperfectly	Ryegrass Kikuyu
Tauhei	37°37′15.6″S 175°24′26.4″E	18.3 (S) 9.9 (W)	14 (S) 77.7 (W)	Organic/Gley (OG)	Peat/Loamy Peat over clay	4.4–5.3	90.3–167.7	Very poorly	Ryegrass White clover Annual blue grass
Rotorua	38°20′52.7″S 176°14′39.8″E	18.4 (S) 8.4 (W)	11.6 (S) 135.6 (W)	Pumice (Pu)	Sand/Loam over sand	5.4–5.6	83.1–84.8	Well	Ryegrass White clover
Teviodale	43°05′23.9″S 172°52′54.6″E	18.8 (S) N/A (W)	35.2 (S) N/A (W)	Pallic (Pa)	Silt over clay	5.8–6.0	124.5–139.1	Imperfectly	Ryegrass White clover

Mean air temperature and precipitation data were retrieved from the National Climate Database, NIWA (National Institute of Water and Atmospheric Research, n.d.), based on the records of the month when the R_s measurement took place. Soil type, texture, carbon stock and pH were obtained from S-Map Online website, Landcare (Lilburne et al., 2012). (S) represents summer, while (W) for winter.

ture/humidity (T/RH) probe (HMP75B, Vaisala, Finland) to correct for the effect of water vapour on CO_2 measurements. Both probes were connected to a hand-held data logger (MI70, Vaisala, Finland), which stored temporal changes in air temperature, air humidity and CO_2 concentration inside the chamber. For each R_s measurement, both probe readings were recorded at an interval of 5 seconds with a 5-minute duration. First-minute recordings were excluded for R_s calculation to account for flux disturbances involved with chamber placement.

Soil temperature was measured using a Pocket Digital Thermometer (FOOD FM10, DigiMate, Digitron, UK) at a depth of 10 cm. Soil water content was measured by a handheld time domain reflectometry (TDR) soil moisture sensor (HydroSense II, HS2, Campbell Scientific, USA) integrated over a depth of 0−12 cm. Soil temperature and soil water content were measured within 30 cm radius outside the collar.

2.4 Statistical analysis

Multi-panel scatterplots with spearman correlation coefficients were used for exploratory data analysis to visualise the relationship between R_s and covariates. Two-way ANOVA followed by a post-hoc test based on Tukey contrasts was used to check for significant differences in R_s between each site and each season. Variance Inflation Factors (VIF) were used to detect multicollinearity among the explanatory variables, which included season, soil characteristics (i.e., temperature, water content, type, drainage, phosphorus retention rate, pH, carbon stock), climatic information (i.e., windspeed, air pressure, hourly sunlight duration, weekly rainfall, monthly rainfall, three-monthly rainfall), time of the day, air temperature in the chamber. Variables with high VIF values ($\geqslant 10$) were excluded. Then multiple regression with ANOVA was used to calculate the significance of the remaining variables. The non-significant predictors were excluded. Principal component analysis (PCA) was used to validate the selection of variables. Soil temperature, soil water content, and soil type were selected as independent variables for further analysis. Soil carbon storage and soil pH were highly correlated with PC2, and further analysed by one-way ANOVA with post-hoc test against soil type, respectively.

Because soil respiration likely follows a non-linear relationship with its predictor variables (e.g., soil temperature) and the rates are distinct between seasons, we used a generalised additive modelling (GAM; 'mgcv' package; Wood, 2021) approach to model R_s with those selected independent variables and the goal was to determine the most influential variables and then investigate the R_s trends in summer and winter separately. We checked for concurvity to detect multicollinearity among smoothed non-linear predictors (i.e., soil temperature and soil water content) and used a backwards model selection procedure and the Akaike Information Criterion (AIC) to find the most parsimonious model.

We also applied R_s nonlinear least-squares models to investigate the relationship between R_s and temperature. The equation is as follows,

$$R_s = A * e^{BT}$$

where R_s is soil respiration rate (μmol CO_2 m^{-2} s^{-1}), T is soil temperature (°C), and the parameters are A and B (van’t Hoff, 1898; Lloyd and Taylor, 1994).

The entire dataset, season-grouped, and soil-type-grouped data were fitted to the above equation, respectively. F tests were performed to compare the full model and grouped models, with null hypothesis ‘the more grouped model does not explain significantly more variation’. We used a generalised nonlinear least-squares framework (GNLS) with variance modelling to address the residual heterogeneity ('nlme' package; Pinheiro et al., 2023). AIC comparisons identified the optimal variance structure, i.e., varExp.

We checked for ANOVA and GAM model assumptions using standard diagnostic plots. Residual vs. fitted values were plotted to assess the variance homogeneity assumption. Residuals were also plotted against each predictor variable to detect model misfits. No gross violations of model assumptions were detected.

All statistical analyses were performed using the statistical software R (version 4.0.5; R Core Team, 2021).

3 Results

3.1 Soil respiration rates

Overall, soil respiration rates (R_s) ranged from 0.29 to 14.58 μmol CO_2 m^{-2} s^{-1} with a mean of 5.38 ± 0.13 μmol CO_2 m^{-2} s^{-1}. Both maximum and minimum R_s occurred during summer, while winter R_s ranged from 0.51 to 8.03 μmol CO_2 m^{-2} s^{-1}. The seasonal R_s mean was significantly different with 6.84 ± 0.20 and 3.67 ± 0.09 μmol CO_2 m^{-2} s^{-1} in summer and winter, respectively ($F_{1,\ 494}$ = 190.96, P < 0.001; GNLS, P < 0.001) (Fig. 1A). Mean R_s differed significantly between all four measured sites, except between the organic/gley (OG) and the pumice (Pu) sites (Fig. 1B), with means of 3.17, 6.59, 6.51 and 4.71 μmol CO_2 m^{-2} s^{-1} for the ultic (U), organic/gley, pumice, and pallic (Pa) soils, respectively ($F_{3,\ 492}$ = 52.47, P < 0.001; GNLS, P < 0.001). The interaction between seasons and sites was significant ($F_{2,\ 489}$ = 129.95, P < 0.001). In summer, the mean R_s at the OG and Pu sites were significantly higher than those at the U and Pa sites (post-hoc test, P < 0.001), while in winter, the mean R_s at the OG and Pu sites were significantly higher than that at the U site (post-hoc test, P <

0.001 and P = 0.03 respectively). Slight diurnal patterns in R_s were found based on soil types and seasons (Fig. 2). In general, the mean soil respiration rate was lowest in the morning and increased by 43.5% to reach a maximum around noon, followed by a decrease in the afternoon. Soil pH had a significantly negative effect on R_s ($F_{1,\,494}$ = 52.24,

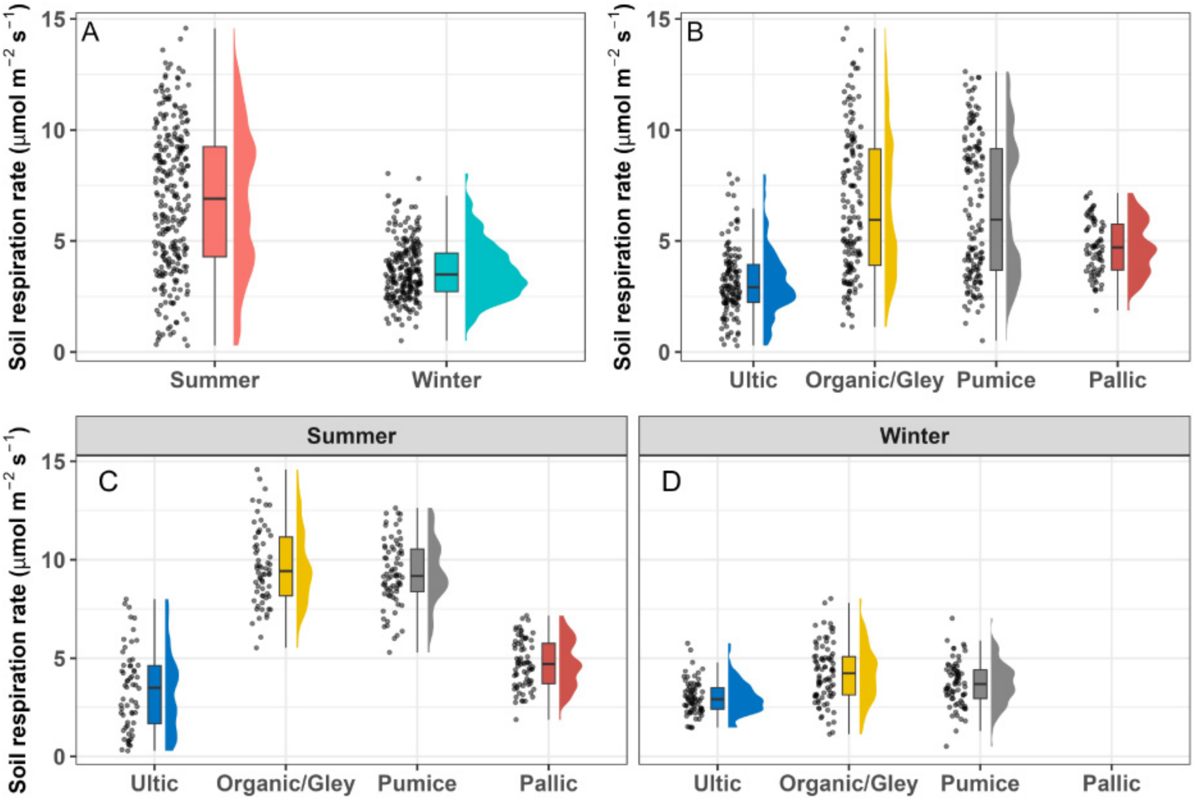


Fig. 1 Soil respiration rates categorised by seasons (A), sites (B) and both (C, D). The density plots indicate the sample sizes.

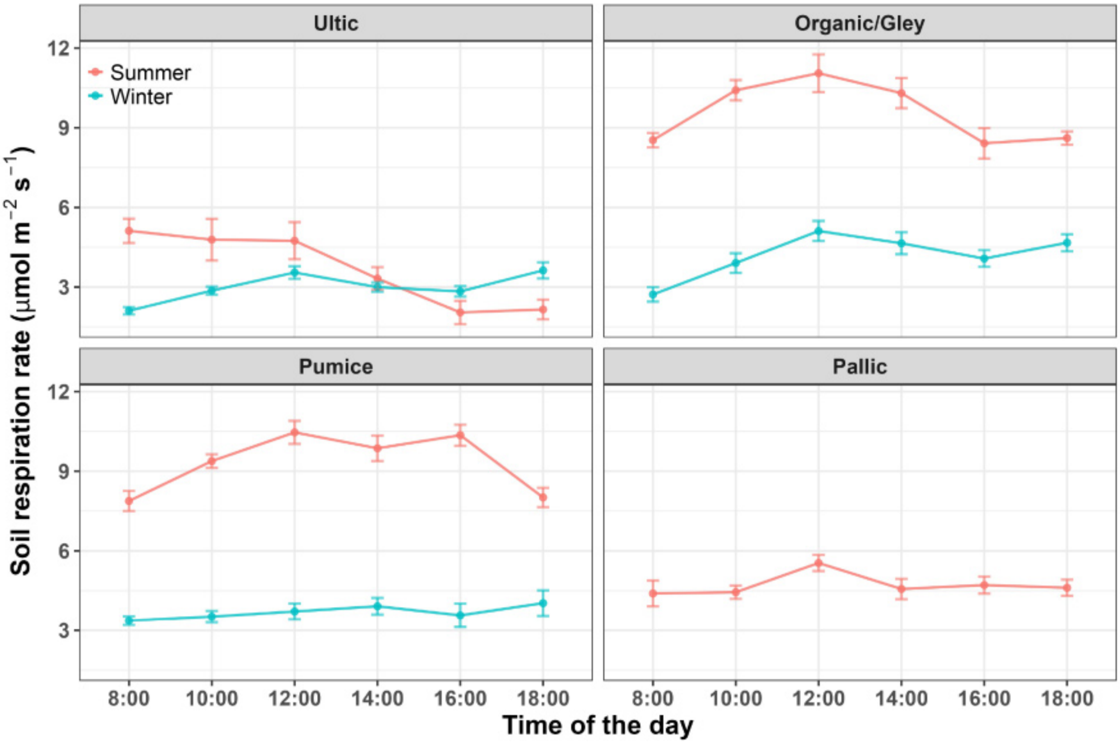


Fig. 2 Diurnal pattern of soil respiration (R_s) in summer and winter across the study sites from 8:00 to 18:00. Data shown are means with standard error bars based on a sample size of 12 per time period, site and season.

$P < 0.001$), while soil carbon had no direct effect on R_s ($F_{1,\,494} = 1.17$, $P > 0.1$).

3.2 Microclimate and soil data

Soil temperature and soil water content were fluctuating strongly according to season and site. Soil temperature (T_s) ranged from 17.3 to 26.7 °C in summer and from 6.7 to 13.1 °C in winter. This significant seasonal T_s difference was consistent among sites. During summer, the mean soil temperature at the U site (19.9 ± 0.2 °C) was significantly lower than those at the OG (21.7 ± 0.2 °C), Pu (21.4 ± 0.1 °C) and Pa sites (22.1 ± 0.3 °C). In winter, the mean soil temperatures at the U, OG and Pu sites differed significantly from each other, with the highest in the U (11.6 ± 0.1 °C) and the lowest in the OG soils (8.9 ± 0.2 °C).

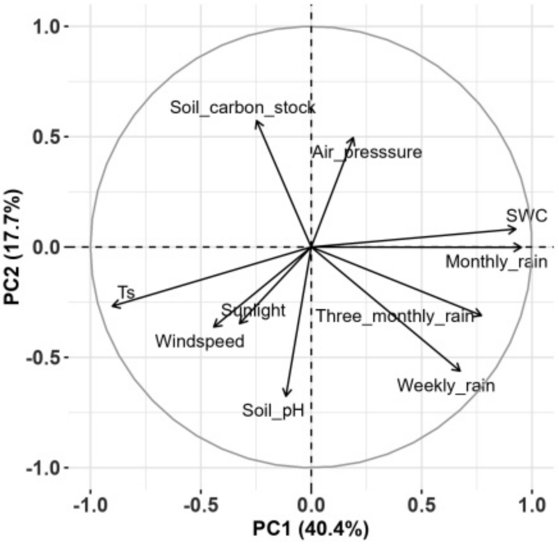
Soil water content (SWC) was high in winter (28.1% to 49.6%) and low in summer (4.4% to 28.6%) across all sites. In summer, mean soil water content (in descending order) was 19.6% 16.5%, 10.9%, and 5.9% at the Pu, U, OG and Pa sites respectively, while during winter, values increased to 42.0%, 40.6%, and 38.4% for the U, OG, and Pu sites respectively. The Pa site was not measured during winter due to COVID-19 lockdown.

Soil carbon storage and soil pH were significantly different among sites (ANOVA, $P < 0.001$ respectively). Mean soil carbon storage (in descending order) was 142.4, 129.4, 96.3 and 84.2 tonnes per hectare (t/ha) at the OG, Pa, U, and Pu sites respectively (Post-hoc, all $P < 0.001$). Mean soil pH (in ascending order) was 4.7, 5.5, 5.6, and 5.9 at OG, Pu, U, and Pa sites respectively (Post-hoc, all $P < 0.001$).

3.3 The R_s dependence on soil temperature, moisture, type, and others

PCA results showed that the first and second axes (PC1 and PC2) explained 40.4% and 17.7% of variance, respectively. Soil temperature and soil water content were highly weighed on PC1, while soil carbon stock and pH on PC2 (Fig. 3). Soil respiration was sensitive to soil temperature changes, but the relationship varied strongly with soil type (Fig. 4A). The relationship between soil respiration and soil temperature was mostly following a pattern of increasing R_s with T_s until around 21 °C, and beyond which R_s decreased. Soil respiration rates were less temperature sensitive in the low-temperature range (6−13 °C) and responded differently at low vs. high SWC (Fig. 4B). At low to medium SWC ($\leqslant$ 30%), soil respiration rate generally increased with SWC. Soil respiration peaked around 10% and 25% SWC, then decreased. At high SWC (> 30%), soil respiration rates remained low and steady until they decreased at 45% SWC and beyond. Soil pH had a negative correlation with R_s (linear regression, adjusted R^2: 0.096; $P < 0.001$), while soil carbon storage had no significant effect on R_s (linear regression, $P > 0.1$). Soil pH had a significantly negative effect on R_s ($F_{1,\,494} = 52.24$, $P < 0.001$), while soil carbon had no direct effect on R_s ($F_{1,\,494} = 1.17$, $P > 0.1$).

At a seasonal scale, soil type had a significant effect on R_s according to GAM model comparison and GNLS model (likelihood ratio comparison between models with soil type interaction vs. without, $P < 0.001$; GNLS, $P < 0.001$). Soil temperature and soil type best explained the variation in both summer (79%) and winter R_s (27%) (Fig. 5). The typical hump-shaped R_s–T_s relationship was only seen during summer in pumice soil (Pu site) with peak R_s values around



	PC1	PC2
Soil_pH	-0.057	-0.508
Soil_carbon_stock	-0.123	0.430
SWC	0.461	0.061
T_s	-0.448	-0.201
Sunlight	-0.162	-0.260
Air_presssure	0.095	0.373
Windspeed	-0.220	-0.272
Weekly_rain	0.336	-0.422
Monthly_rain	0.474	-0.001
Three_monthly_rain	0.384	-0.233

Fig. 3 Principal Component Analysis (PCA) of overall soil respiration as explained by soil temperature (T_s), soil water content (SWC), soil carbon stock, soil pH, hourly sunlight duration (Sunlight), air pressure, as well as one-week, one-month and three-month rainfall volume prior to measurement (Weekly_rain, Monthly_rain, and Three_monthly_rain, respectively).

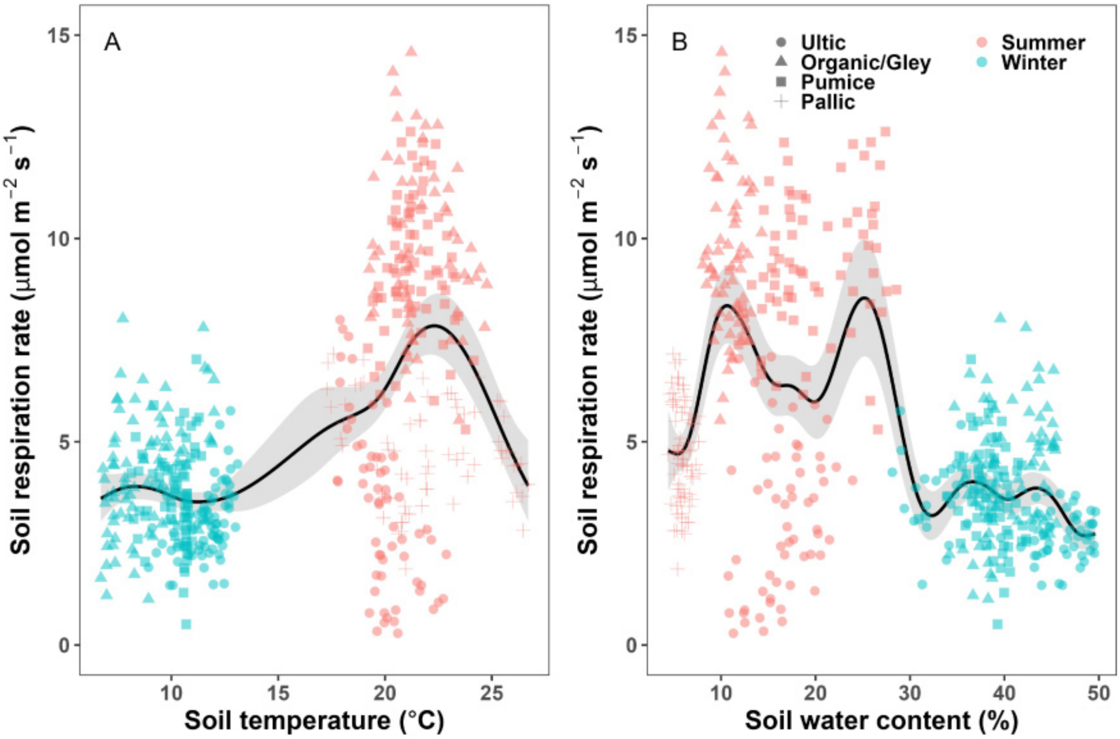


Fig. 4 Response of soil respiration to soil temperature (A) and to soil water content (B) during summer and winter. Solid lines represent generalised additive model fits, and the grey surrounding areas indicate the 95% confidence intervals.

21 °C (Fig. 5A). Summer respiratory CO_2 release from the ultic grassland soil (U site) showed an exponential decline with increasing T_s, while the two remaining soil types displayed no distinctive pattern (Fig. 5A). During winter, R_s increased slightly with soil temperature in the U and OG soils, while R_s in the Pu soil remained unchanged until 11°C, then increased (Fig. 5C). The relationship between R_s and SWC was generally steady but with some site-specific changes. During summer, R_s increased slightly with SWC in the U and Pu soils, while there were no distinctive patterns in the OG and Pa soils (Fig. 5B). During winter, at the U soils, R_s decreased slightly with SWC, opposite to the increasing R_s-SWC trend in the OG soils. At the Pu site, R_s remained unchanged until SWC reached around 36%, then slightly decreased (Fig. 5D).

4 Discussion

4.1 Comparison of soil respiration to global data and studies under similar climate

Mean summer and winter R_s rate at our study sites were 178% and 564% higher than these of global temperate grassland, respectively (Jian et al., 2020). Under similar climates, the mean R_s rate at our sites was also 111% and 53% higher than those measured by Francioni et al. (2019) and Mukumbuta et al. (2019), respectively. In New Zealand, mean summer R_s at our study sites was 19% higher than that measured at an extensive sheep farming grassland in Canterbury, Southland, by Moinet et al. (2016), while mean winter R_s was about three times higher than that measured at the same place by Moinet et al. (2017). This overall higher R_s values might result from high soil organic carbon due to parental materials in OG soils and the more intensely farmed sites of the present study. High soil organic carbon levels support a large microbial biomass and consequently higher microbial respiration and thus greater R_s (Zarafshar et al., 2023). Soil type may affect soil respiration directly through soil pH, soil compaction, and soil organic matter (Lohila et al., 2003), and indirectly through temperature and moisture (Howard and Howard, 1993).

4.2 The effect of soil type on soil respiration

In our study, soil type had a strong influence on R_s. OG and Pu soils yielded higher R_s, compared to U and Pa soils. At the OG site, this might be caused by high levels of organic matter (max: 167.7 t ha^{-1}, Table 1). OG soils are formed on the remains of wetlands and are thus high in organic matter and shrinkage potential (Hewitt et al., 2021a). This also suggests that OG soils are prone to sharply increased soil respiration rates when exposed to aerobic conditions (i.e., oxidation and biodegradation). Particularly in farm grassland, grazing and tillage can also be responsible for aerobic soil conditions (McCourty et al., 2018; Zhou et al., 2019). At the

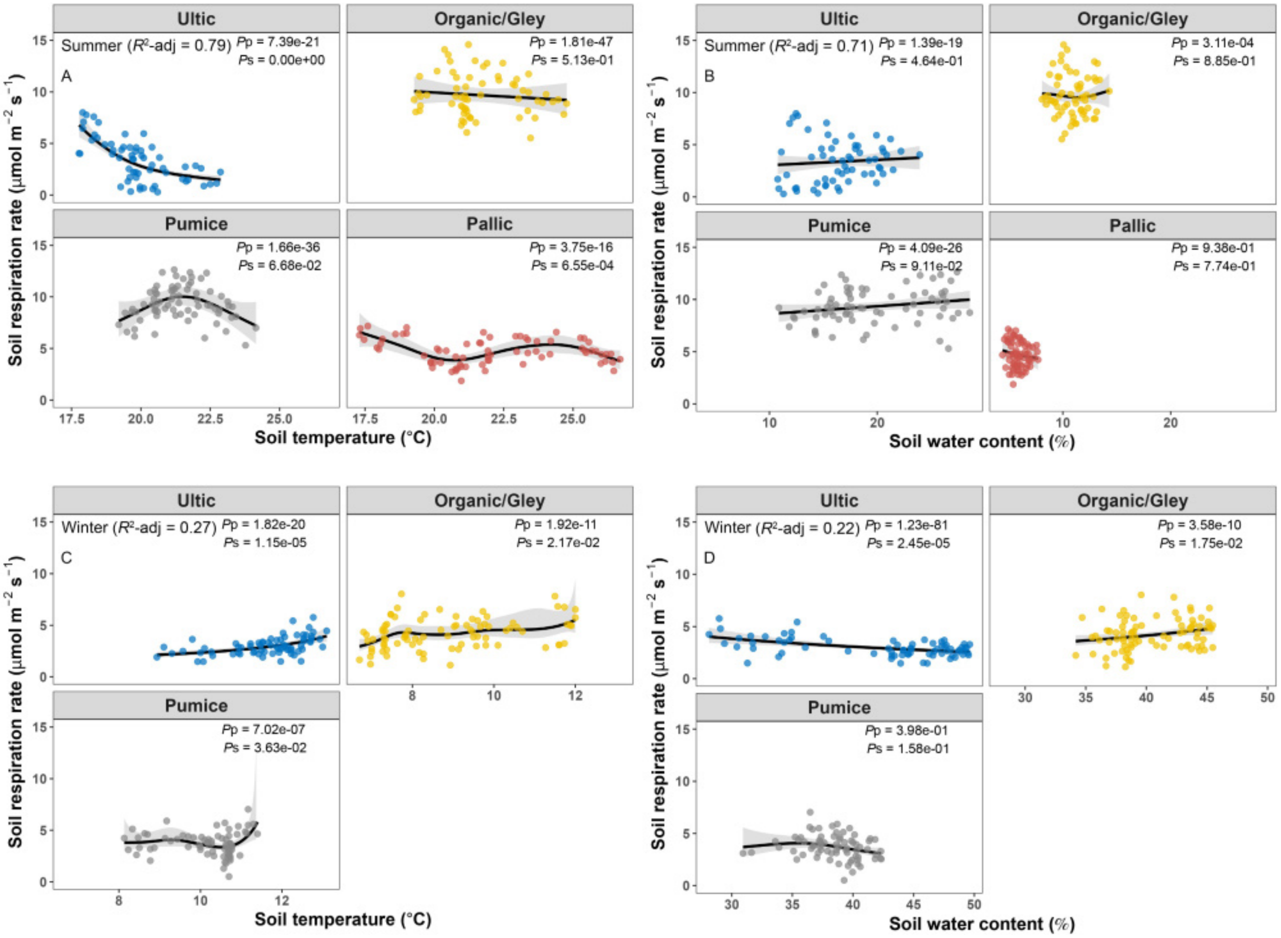


Fig. 5 The relationship of soil respiration with summer soil temperature (A), summer soil water content (B), winter soil temperature (C) and winter soil water content (D). Solid lines represent generalised additive model fits, and the grey surrounding areas indicate the 95% confidence intervals. *P*p is the abbreviation of *p* value for parametric term and *P*s is the abbreviation of *p* value for smoother.

Pu site, high R_s rates are caused by favourable soil moisture (Hewitt et al., 2021c). Soil water content at the Pu site was highest in summer and lowest in winter, compared to other sites, which led to overall high R_s. Generally, R_s was positively correlated with SWC (during dry spells) or showed no correlation with SWC (wet conditions), then decreased once field capacity was reached (Smith et al., 2003; Xu and Shang, 2016). Thus, at our Pu site, high SWC promoted R_s in summer when soil moisture levels are usually low. In contrast, low SWC facilitated soil diffusivity thus R_s in winter when soil moisture was often high at the other sites (> 30% vol.). Low R_s rates at the U and Pa sites are possibly due to clay content and low SWC, respectively. At the U site, high clay content might confine soil organic matter and microbes in small pores, inducing a protective effect on C mineralisation (Rutherford and Juma, 1992; Wang et al., 2003). At the Pa site, the lowest SWC occurred in summer as Pa soils are prone to desiccation during summer (Hewitt, 2010; Hewitt et al., 2021b).

4.3 The effect of soil type and temperature on soil respiration

Soil temperature was the primary driver of soil respiration, which explained 83%, 79% and 27% of the variance in R_s during the entire study, summer, and winter period respectively. The trend we observed is not aligned with general R_s−T_s relationships in grasslands where R_s commonly reaches peak rates or decreases only when T_s is around 25° C (Carey et al., 2016). The early increase likely resulted from the temperature-induced stimulation of both autotrophic and heterotrophic R_s (Wang et al., 2009; Graham et al., 2012), as temperature sensitivity is usually high at low temperatures. The early declining trend was mainly driven by low rates of R_s at the Pa site, which might be due to the low metabolic activity of plant roots and microbes, caused by the low SWC levels. In summer, the rapid R_s decrease at the U site was likely due to drought-induced soil desiccation as a result of low midsummer rainfall during the measurement period (Table 1). The restrictive effect of drought on R_s was probably largely confined to the topsoil, while in the typically clay-rich and well-moistened ultic subsoil, oxygen-poor conditions due to low gas diffusivity are likely to suppress R_s (Hewitt et al., 2021d). At the OG site, the nonsignificant R_s−T_s trend showed that R_s remained at high but slightly decreasing rate. This could have been due to sufficient soil carbon and thermal acclimation, where microbial growth was limited by temperature, reflected in declining R_s (Crowther and Bradford, 2013). At the Pu site, the hump-shaped relationship between R_s and T_s was probably due to high soil porosity and a low level of organic matter in the topsoil (Hewitt et al., 2021c). The high level of macropores facilitated the O_2/CO_2 pathways, allowing the plant roots and soil microbes to produce more respiratory CO_2 in an aerobic environment. The decreasing part might be due to the limitation of soil organic matter. Under rising soil temperatures and high soil microporosity, low organic matter content in the topsoil was likely to decrease to the extent that adversely affected R_s. The weak R_s−T_s relationship at the Pa site was possibly due to limiting soil water availability, which may also explain the lack of a temperature effect. During winter, an R_s increase with soil temperature was expected. Low magnitudes of this increase might be due to high soil moisture and a narrow range of soil temperature change.

4.4 The effect of soil type and moisture on soil respiration

Soil water content only explained 22.3% of the variance in winter R_s, with higher rates at the OG and Pu sites. This might be due to high organic matter content and high SWC in winter. High water holding capacity also likely contributed to the high R_s rates because of high microporosity and generally deep rooting plant cover in the Pu soils (Hewitt et al., 2021c). The decreasing trend beyond 45% SWC was largely influenced by the low R_s rates at the U site. The clayey soils at the U site increased the water storage and reduced the permeability, which may have led to diminished soil O_2/CO_2 diffusivity, reducing respiration rates of grass roots and soil microbes. Ultic soils have high water holding capacity due to high clay content (Hewitt et al., 2021d), which supports the high SWC we observed in winter (between ca. 30% and 50%). A high level of moisture led to restricted O_2/CO_2 diffusion in the soils, likely reducing R_s rates. At the OG site, R_s showed an unexpected increasing trend with SWC, which may be explained by increased soil C decomposition and cation exchange capacity (CEC) of these soils (Ramos et al., 2018; Hewitt et al., 2021a). Improved SWC below field capacity can benefit the microbial activities through the availability of extracellular enzymes, thus enhances soil microbial respiration (Liu et al., 2009). High CEC might result from increased soil pH in winter (Goulding, 2016), as increasing SWC promotes the concentration of anions (OH^-). An accelerated exchange may occur between elevated OH^- concentration in soil water and trace elements in soils. As a result, more nutrients bound to organic matter probably became available for plant growth and maintenance, leading to a slight increase in R_s. At the Pu site, the nonsignificant R_s-SWC trend showed that SWC had little effect on R_s, probably due to the high porosity (Hewitt et al., 2021c). During summer, the insensitivity of R_s to soil water content in U and Pu soils suggests that soil moisture was not limiting R_s. The summer R_s−SWC relationship was unclear in OG and Pa soils due to the narrow SWC range.

5 Conclusion

Soil respiration in New Zealand dairy grassland is higher, compared to global temperate grassland. Soil temperature and soil type can best explain the magnitude and trend of seasonal R_s. In ultic soils, low R_s was due to clay-rich texture impeding decomposition, while the observed exponentially decreasing T_s−R_s trend in summer was caused by desiccation in the topsoil and clay-related poor gas diffusivity in subsoil. In organic soils, high R_s was observed due to high soil organic matter from degraded peat-forming wetlands. In pumice soils, high R_s was observed due to the high water holding capacity, retaining moisture for plant and microbial growth in both seasons. Our findings showed that soil type can play an important role in R_s estimation at local scale.

Conflict of interest

The authors declare that they have no conflicts of interest.

Funding note

Open Access funding enabled and organized by CAUL and its Member Institutions.

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