

Sensitivity of organic matter mineralisation to water availability: role of solute diffusivity and the ‘Birch effect’

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ABSTRACT

Context. Several functions are used to describe the effects of soil water content on organic matter mineralisation. A meta-analysis of published studies identified relative water content (RWC; available water relative to the soil’s available water holding capacity) as the best water descriptor for N mineralisation. **Aims.** To evaluate RWC as a predictor of C and N mineralisation in New Zealand soils; and to investigate how solute diffusivity and the ‘Birch effect’ may help to explain this relationship. **Methods.** Three agricultural soils (0–15 cm), differing in water holding capacity were incubated (8-week; 20°C) under a range of RWCs to measure carbon (respiration) and net N mineralisation. After 4 weeks, a subset of samples from each treatment were re-wetted to field capacity for a further 4-weeks to quantify the respiration response to re-wetting. **Key results.** For all three soils, there was a linear relationship between respiration and RWC where the C respired at the wilting point (RWC = 0) was ~25–30% of that at field capacity (RWC = 1.0). Results from a solute diffusivity model suggested that a decrease in microbial substrate supply, owing to restricted diffusion of dissolved organic compounds, contributed to moisture-induced decline in respiration. A respiration flush was not observed when RWC was >0 at re-wetting. Nitrogen mineralisation was non-linearly related to RWC, with small decreases in RWC below 1.0 (optimum) having a greater effect on N, than C, mineralisation. **Conclusions.** RWC may be a reliable ‘water modifier’ to describe the influence of soil moisture on respiration. Further work is recommended to verify the RWC vs net N mineralisation relationship observed in this study.

Keywords: Birch effect, first-order model, incubation, net N mineralisation, relative water content, soil respiration, SOM mineralisation-moisture relationship, substrate diffusion.

Introduction

Turnover of soil organic matter (SOM) is strongly influenced by environmental parameters, particularly soil temperature and water availability (Raich and Schlesinger 1992; Lützow *et al.* 2006). While the effects of rising temperatures on soil C stocks and soil heterotrophic respiration (HR) have attracted considerable attention, much less work has been carried out to understand soil water–respiration responses (Falloon *et al.* 2011; Moyano *et al.* 2013). Mechanisms determining the response of respiration to soil moisture remain poorly quantified (Moyano *et al.* 2013).

Knowledge of the moisture–SOM mineralisation response is needed to predict how soil C stocks may change in response to moisture changes associated with climate change and irrigation (Falloon *et al.* 2011; Mudge *et al.* 2017), and to predict the release of plant-available mineral N (mineralisation) under field conditions where soil moisture is temporally dynamic (Paul *et al.* 2003). It is well accepted that SOM mineralisation is greatest at about field capacity and decreases as the soil dries (Orchard and Cook 1983). However, the reported sensitivity of mineralisation to changes in soil moisture shows considerable variability. Falloon *et al.* (2011) showed that use of moisture response functions from five different soil C models (RothC, TRIFFID, SOILN, Bethy, Sim-Cycle) may result in either large losses or small gains in modelled future global C stocks.

The factors determining the moisture sensitivity of SOM mineralisation are not completely understood. The critical water content for microbial desiccation stress varies between taxa, with fungi being more tolerant of dry conditions than bacteria (Harris 1981; Manzoni *et al.* 2012). However, at water contents between desiccation stress (matric potential \sim –1500 kPa) and field capacity (–10 kPa), the main impacts of soil water content on microbial respiration may be indirect (owing to the influence of water content on diffusion of organic substrates), rather than a direct physiological response of microorganisms to water stress (Linn and Doran 1984; Davidson *et al.* 2000; Schjønning *et al.* 2003).

Based on a meta-analysis of 12 published laboratory incubation studies, Paul *et al.* (2003) evaluated ways of expressing soil water status with respect to its influence on N mineralisation. From the wide range of soil water descriptors evaluated (including gravimetric and volumetric water content; water-filled pore space; soil water potential), relative water content (RWC) was selected as providing a robust relationship with net N mineralisation. One objective of our study was to assess whether RWC (i.e. available water as a proportion of available water holding capacity) could be successfully used to describe the relationships of soil water content with C respiration and N mineralisation in New Zealand soils.

Mineralisation pulses often occur when dry soils are wetted by rainfall or irrigation, a phenomenon commonly known as the ‘Birch effect’ (Birch 1958). In locations where alternating wet–dry conditions are common, these pulses may account for a significant portion of the total mineralisation. Substrates fuelling these re-wetting pulses may include osmo-regulatory compounds, synthesised by the microbial community to protect against osmotic stress in dry soil, and SOM solubilised as a result of soil drying/re-wetting (Slessarev and Schimel 2020). The intensity and duration of dry conditions determine the magnitude of the response to re-wetting (Barnard *et al.* 2020). However, the moisture threshold at which a mineralisation pulse is triggered has not been well defined, even though such information is important to assess the potential significance of the Birch effect in a given environment. A second objective was to identify the critical soil water content below which there is a mineralisation pulse upon re-wetting.

Materials and methods

Soil types, physical and chemical properties

Three soil types that are common in the Canterbury region of New Zealand were selected for this study: (1) Temuka clay loam (Mollic Endoaquept, United States Department of Agriculture (USDA) Soil Classification System); (2) Templeton silt loam (Udic Haplustept); and (3) Waimakariri silt loam (Typic Ustorthents). All three soils were under grass (predominantly perennial ryegrass); long-term (>25 years) at

the Temuka and Waimakariri sites and short-term (\sim 5 years) at the Templeton site. The soils differed in texture, organic matter content, and water holding capacity (Table 1). These soils, which are derived from sedimentary parent materials, were sampled in winter when they had been at, or close to, field capacity for some weeks. At each site, several sub-samples (0–15 cm) were taken using a spade and combined. In the laboratory, the soils were sieved through a 4-mm mesh in field-moist condition. Each soil was split in two parts: one part was air-dried, and the other part was maintained field-moist in a cold room at \sim 4°C prior to the incubation studies.

Physical and chemical properties were determined using the air-dried soils. Texture was assessed by the sieving-sedimentation method (Gee and Or 2002). Water content at field capacity was determined using a tension table at –10 kPa and wilting point of the soils was measured at –1500 kPa using pressure plates. Total carbon (TC) and nitrogen (TN) were determined using Dumas combustion (LECO TruMac, Leco Corporation, St. Joseph, MI, USA). Hot water extractable C (HWEC), a measure of labile C, was extracted at 80°C as described by Ghani *et al.* (2003). Soil pH was determined at a soil:water ratio of 1:2 using a glass electrode. The ammonium acetate method was used to measure cation exchange capacity (CEC) (Thomas 1982).

The soils, which were sampled at sites with little or no input of fertiliser N for several years, were low in mineral N (Table 1). All three soils were acidic (pH 5.3–5.9). The Waimakariri and Temuka soils had higher SOM content (43 and 37 g C kg^{–1}, respectively) than the Templeton soil (23 g C kg^{–1}). HWEC followed the same order as total C in the three soils (range 1222–2362 mg kg^{–1}). The Temuka soil had higher clay content and CEC than the other soils (Table 1).

Table 1. Physical and chemical properties of the study soils.

Property	Soil		
	Temuka	Templeton	Waimakariri
Sand (%)	9.5	37.2	19.6
Silt (%)	61.9	46.3	64
Clay (%)	28.6	16.5	15.4
Field capacity (w/w, %)	39	26	40
Wilting point (w/w, %)	11.4	7.8	9.9
Total carbon (g kg ^{–1})	36.5	23.2	42.9
Total nitrogen (g kg ^{–1})	3.2	1.9	3.5
C:N	11.5	12.2	12.3
pH	5.9	5.3	5.7
Hot water extractable carbon (mg C kg ^{–1})	2031	1222	2362
Mineral N (mg kg ^{–1})	15.7	6.7	10.5
Cation exchange capacity (cmol(+) kg ^{–1})	18	11	12

Texture was expressed as sand (0.053–4 mm), silt (0.002–0.053 mm) and clay (<0.002 mm).

Experimental treatments

There were seven (Temuka and Templeton soils) or eight (Waimakariri soil) moisture treatments, with RWC ranging from 1.0 (field capacity) to -0.04 (below wilting point). The RWC was computed as soil available water content relative to the available water capacity, defined in terms of an upper (i.e. -10 kPa; field capacity) and lower (-1500 kPa; wilting point) limit:

$$\text{RWC} = (\theta_a - \theta_{-1500}) / (\theta_{-10} - \theta_{-1500}) \quad (1)$$

where θ_a is actual soil water content (w/w, %), and θ_{-10} and θ_{-1500} are field capacity (w/w, %) and wilting point (w/w, %), respectively. On average, the RWC increment between successive moisture treatments was 0.15.

Soil preparation

Field-moist soil (the three soils were at field capacity when sampled) was spread thinly on plastic trays on a laboratory bench (20°C) and carefully dried to achieve different target water contents (soils were turned frequently to ensure that they were drying uniformly and avoiding excessive drying at the edges of the soil pile). Once soil had reached the first RWC target (0.84–0.87; Table 2), enough soil was removed for the incubations and other measurements. The drying process then continued with soil samples sequentially removed for the progressively decreasing RWC target values (Table 2). The moisture-adjusted soils were placed in sealed plastic bags and stored in a cold room prior to incubation. For each soil, the entire moisture adjustment procedure was completed within 24 h.

Mineralisation of N and C in aerobic incubation

The moisture-adjusted soils were incubated at 20°C for 8 weeks to measure C and N mineralisation (three replicates of each moisture treatment). To measure C mineralisation, samples of the moisture-adjusted soils (equivalent to 25-g of oven-dry soil) were weighed into 50-mL vials (covered

by Parafilm with punctured holes), which were placed in 1-L air-tight jars (fitted with rubber septa to facilitate headspace gas sampling). The jars were incubated at 20°C for 8 weeks. A sample of headspace air (~ 20 mL) was periodically collected (total of 11 samplings over the 8-week incubation period) with a Hamilton syringe for CO_2 measurement using an infra-red gas analyser (LI-COR, Lincoln, Nebraska, USA). After CO_2 measurement, each jar was flushed with fresh air to bring CO_2 concentration back to the ambient level. De-ionised water was added to the soils to maintain constant water content during the incubation.

After 4 weeks, a subset of samples from each treatment was re-wetted to field capacity to identify the water content threshold below which a respiration flush occurs upon re-wetting. These soils were kept at field capacity for a further 4-week period to quantify the respiration response to re-wetting (headspace CO_2 was measured seven times during the 4-week incubation).

For the N mineralisation study, moisture-adjusted soil samples (equivalent to 25 g of oven-dry soil) were weighed into plastic vials (50 mL) and incubated at 20°C . All vials were covered with Parafilm (holes were punctured in the film to facilitate aeration) to minimise moisture loss; water was added at weekly intervals to offset any water lost by evaporation. Mineral N (NO_3^- -N and NH_4^+ -N) was extracted using 2 M KCl after 2, 4 and 8 weeks of incubation (enough samples were incubated to allow sacrificial sampling at each time point) and determined using an automated colorimeter (QuickChem 8000 FIA+, Lachat Instruments, Loveland, CO, USA) (Keeney and Nelson 1983). Net N mineralisation was calculated by subtracting mineral N at the establishment of the incubation from the amount determined at each sampling point.

Data analysis

Analysis of variance (ANOVA) and the least significant differences (l.s.d.) at the 5% level were performed using the R package ‘agricolae’ (ver. 4.0.5).

Table 2. Moisture treatments imposed on three soils in the incubation experiments.

Gravimetric water content (%)			Relative water content		
Temuka	Templeton	Waimakariri	Temuka	Templeton	Waimakariri
39	26	40	1.00	1.00	1.00
35	23	36	0.86	0.84	0.87
31	20	32	0.71	0.67	0.73
27	16	28	0.57	0.45	0.60
23	13	24	0.42	0.29	0.47
19	10	20	0.28	0.12	0.34
15	7	16	0.13	-0.04	0.20
		12			0.07

Note: relative water content was calculated using Eqn 1.

Results and discussion

Effect of water content on C mineralisation in 8-week incubation

In all three soils, the amount of C respired during the 8-week incubation increased systematically as water content increased (Fig. 1). The cumulative amount of C mineralised in 8 weeks at field capacity (RWC 1.0) was greatest ($P < 0.05$) for Waimakariri soil (1158 mg kg⁻¹), followed by the Temuka soil (958 mg kg⁻¹), with the Templeton soil having the lowest value of 466 mg kg⁻¹. These respiration values are directly in line with the amounts of total and hot water-extractable C in the soils (Table 1).

To compare the C mineralisation vs RWC relationship across the three soils, we normalised mineralisation values measured at all RWCs to mineralisation at field capacity

(RWC = 1.0), which our results confirmed to produce the highest mineralisation rates over the range of volumetric water contents measured (Fig. 1). For all three soils, there was a linear ($R^2 = 0.98$) relationship between relative C mineralisation (8-week) and RWC (Fig. 2). The relationship was similar across soils, but especially so for the Temuka and Waimakariri soils. For those two soils, C mineralisation at wilting point (i.e. RWC = 0) was 25–26% of that at field capacity. Mineralisation appeared to be slightly less sensitive to water content in the Templeton soil, where mineralisation at wilting point was 32% of that at field capacity.

For shorter incubation periods, respiration also exhibited a linear relationship with RWC (results for the first week of incubation shown in Fig. 2). However, respiration in the Temuka and Waimakariri soils appeared slower to adjust to lowered soil moisture than in the Templeton soil. Thus, in the first week of incubation, the estimated amount of

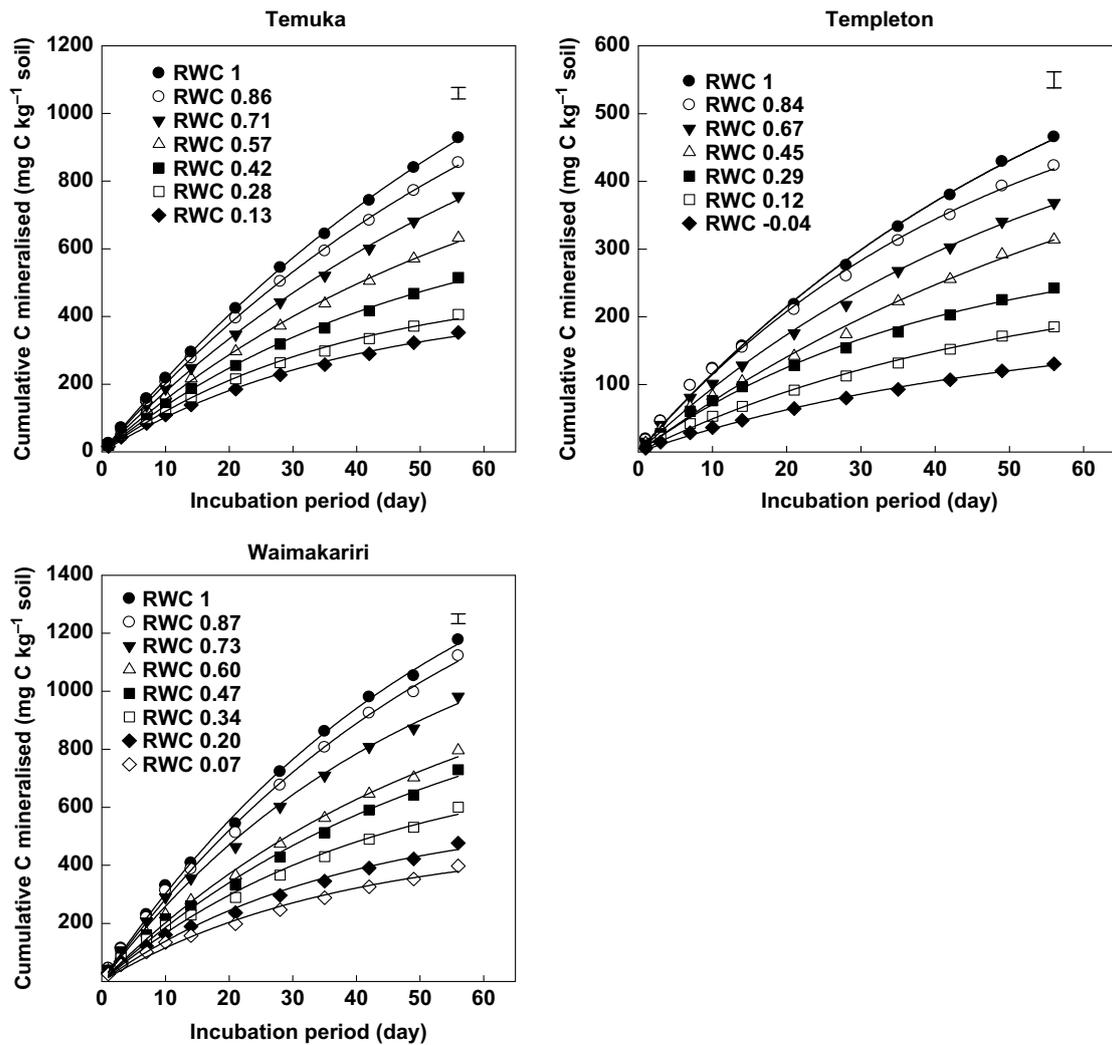


Fig. 1. Carbon (C) mineralisation in three soils at different relative water contents (RWC) during an 8-week incubation at 20°C. The lines were obtained by fitting a first-order kinetic model (Eqn 2) to the data points (vertical bars indicate l.s.d. (5%)).

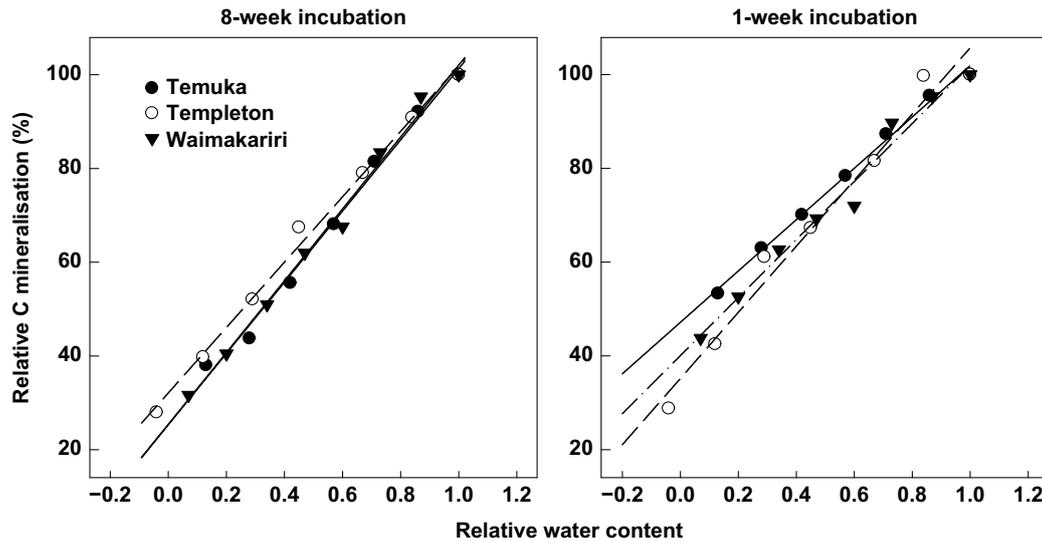


Fig. 2. Relationship between soil relative water content and relative carbon (C) mineralisation in the first week and in the full (8 weeks) incubation (C mineralisation expressed as a percentage of mineralisation at field capacity, RWC 1.0).

respiration at wilting point, as a proportion of that at field capacity, was 40–47% for these soils (vs 25–26% for the full 8-week incubation) (Fig. 2). This observation may suggest that there was a lag period (or equilibration period) during which the microbial population did not experience the full impact of the lowered moisture status. Drying will concentrate dissolved microbial substrate (dissolved organic matter, DOM) and this could temporarily buffer the effect of drying in decreasing solute diffusion. This lag period was relatively brief and respiration data for the second week of incubation had a similar relationship with RWC as data for the full 8-week incubation (data not shown).

Pool size and respiration kinetics

The C mineralisation data were fitted to a single-pool, first-order model of the form:

$$C_{\min} = C_0(1 - e^{-kt}) \quad (2)$$

where C_{\min} is cumulative C mineralised in time t , C_0 is potentially mineralisable C, and k is the mineralisation rate constant. Values of C_0 and k were estimated by least square iteration using SigmaPlot 14.0.

The single-pool model provided a good fit to the experimental data for all soils and RWC treatments ($R^2 > 0.98$) (Fig. 1). We hypothesised that the pool of mineralisable C (C_0) would be independent of the water treatment, whereas the rate constant (k) would increase as water content increases, with a maximum at about field capacity. However, in all three soils, C_0 increased as RWC increased, while the rate constant tended to decrease as RWC increased (Fig. 3).

The largest value of C_0 was always observed in the field capacity treatment and the lowest value in the driest treatment; C_0 in the field capacity treatment was about three times greater than that of the driest treatment. In keeping with total C and HWEC, C_0 values of Temuka and Waimakariri soils (RWC 1.0 treatment) were ~ 2.5 times that of the Templeton soil (Fig. 3a). Although, in all soils, the rate constant tended to decrease as RWC increased (Fig. 3b), the relationship with RWC was not as close as that between RWC and C_0 .

Caution is required in interpreting these model results, given the relatively short duration of the incubation (8 weeks). Nevertheless, there are reports in the literature that mineralisable C may increase with increase in soil moisture (Zak *et al.* 1999; Curtin *et al.* 2012). Whereas some studies have shown that microbial biomass is positively related to water-filled pore volume when substrate supply is held constant (Rakhsh *et al.* 2020), there is also evidence that the mineralisation of native soil organic matter is not necessarily regulated by the size or composition of the soil microbial biomass (Kemmitt *et al.* 2008). Zak *et al.* (1999) hypothesised that the effect of moisture on the pool size could be a reflection of the positive influence of moisture on the flux of organic substrates to microbial cells via diffusion (discussed further below). The Mineralisable C pool (C_0) at field capacity, estimated from the first-order model, represented less than 5% of total C and was less than the amount of HWEC in the soils. This is consistent with the results of McNally *et al.* (2018) who reported that the mineralisable C pool (C_0) predicted from short-term static incubation data underestimates the amount of C that can be lost from soils following conversion of long-term pastures to continuous cropping.

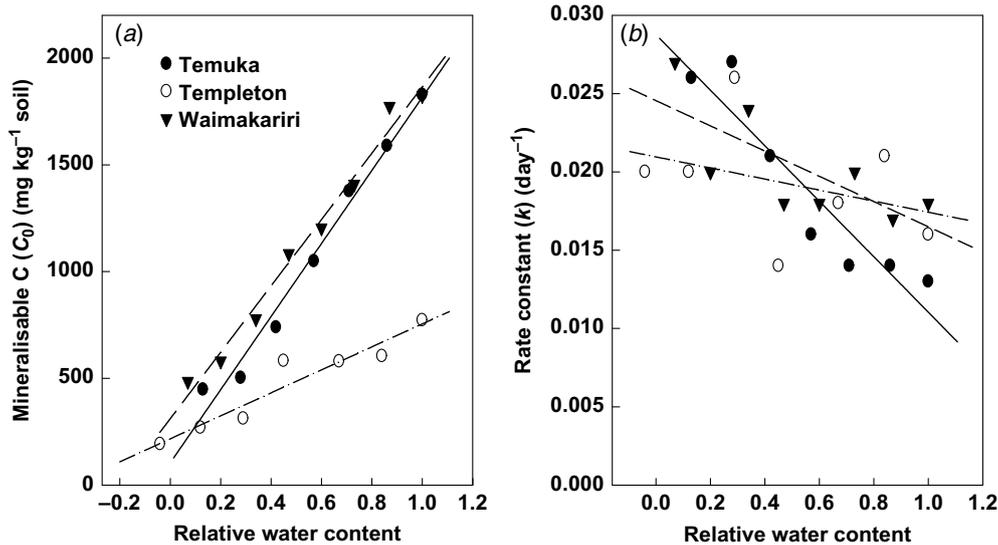


Fig. 3. Relationship of soil relative water content with (a) potentially mineralisable carbon (C_0) and (b) the mineralisation rate constant (k). Values of C_0 and k obtained by fitting C mineralisation data to a first-order model (Eqn 2).

Respiration–moisture relationship

Our results suggest that there was a consistent and robust relationship between respiration (a measure of microbial activity) and soil moisture, expressed as relative water content, that allows for differences in soil water holding capacity that are associated with differences in the texture and SOM content of the three soils investigated in this study. Respiration at wilting point was substantial (~one-quarter to one-third of that at field capacity), confirming that at least some soil microorganisms are more tolerant of moisture stress than are plants. However, even relatively small reductions in the moisture content of wet soil (a decrease in RWC from 1.0 to 0.84–0.87) resulted in a significant decrease in respiration. These apparently contradictory observations can probably be explained in terms of the influence of substrate supply on the respiration rate. Dissolved organic matter (DOM), considered to be the immediate substrate for soil microorganisms (Marschner and Kalbitz 2003; Kemmitt *et al.* 2008), is transported to microbial cells by diffusion. The observed relationship between respiration and RWC may reflect the fact that solute diffusivity is a function of moisture content, provided that the moisture content is above the threshold at which diffusion ceases (the point at which water films on soil particles becomes discontinuous). Solute diffusivity in the three experimental soils was calculated using the model developed by Moldrup *et al.* (2007) and Schjønning *et al.* (2003):

$$D_{S,l}/D_{0,l} = 1.1 \theta_v (\theta_v - \theta_{v,th}) \quad (3)$$

$$\theta_{v,th} = \mathcal{P}(C_{clay}/d_{cl} + OM/d_{om}) \quad (4)$$

where $D_{S,l}$ represents the diffusion coefficient of a solute (DOM in this study) in soil, and $D_{0,l}$ is the diffusion coefficient of that solute in free water (i.e. $D_{S,l}/D_{0,l}$ is relative solute diffusivity, Eqn 3). θ_v is volumetric water content, and $\theta_{v,th}$ is the threshold water content at which solute diffusion ceases. $\theta_{v,th}$ was calculated from Eqn 4. In Eqn 4, \mathcal{P} , C_{clay} , and OM represent the soil bulk density, clay and the organic matter content, respectively, while d_{cl} and d_{om} are the particle densities of clay and organic matter assumed equal to 2.7 and 1.0 g cm^{-3} (Moldrup *et al.* 2007). Fig. 4a shows that solute diffusivity ($\text{m}^2 \text{s}^{-1}$) declined in a non-linear manner as RWC decreased. The soils had very low diffusivity rates (i.e. 0.003, 0.0001 and 0.006 $\text{m}^2 \text{s}^{-1}$ for Temuka, Templeton and Waimakariri soils, respectively) at the wilting point. At field capacity, the solute diffusivity rate in the Templeton soil was about half that in the other two soils. When solute diffusivity was plotted as a proportion of that at field capacity, the relationship with RWC was similar for the three soils (Fig. 4b). These results support the suggestions that reduced substrate supply, owing to slowed diffusion, may be an important cause of the decline in respiration in response to declining soil moisture. However, the response of solute diffusivity to RWC showed some differences from that observed between respiration and RWC; i.e. the solute diffusion relationship was curvilinear (polynomial relationship), rather than the linear relationship observed for respiration vs RWC. Also, solute diffusivity appeared to be more sensitive to low water content than was respiration (diffusivity rate at wilting point was estimated to be 2–6% of that at field capacity vs ~25–30% for respiration).

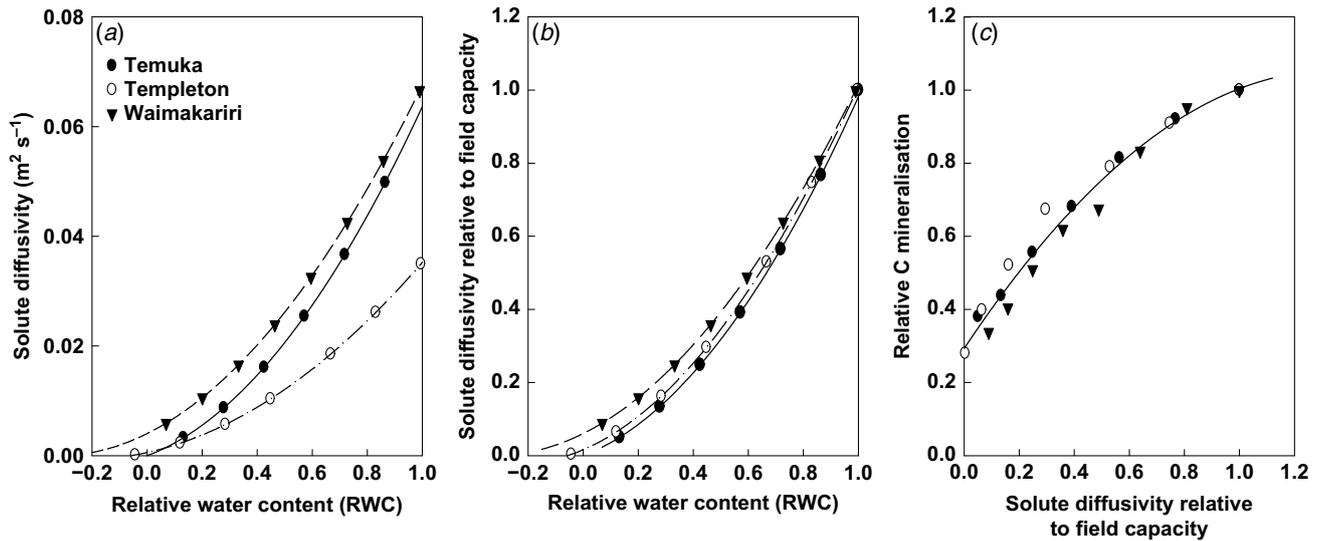


Fig. 4. Relationship of soil relative water content with (a) solute diffusivity, expressed in $\text{m}^2 \text{s}^{-1}$ and (b) relative solute diffusivity; i.e. solute diffusivity relative to that at field capacity (RWC = 1.0). (c) Relationship between C mineralisation and solute diffusivity (both expressed relative to values at field capacity).

Higher water contents would result in a larger interconnected water-filled pore network, enabling microorganisms or enzymes to easily utilise diffusing organic substrates (Franzluebbers 1999; Arnold *et al.* 2015). Conversely, substrate diffusivity and nutrient availability to soil microbes in dry treatments will be retarded at low water content because the channels connecting capillary water are disrupted as the soil dries (Moldrup *et al.* 2001; Manzoni *et al.* 2012). However, the results in Fig. 4c show that significant mineralisation occurred in dry soils (~wilting point) when solute diffusion had effectively ceased. At this point, only DOM that is co-located with microorganisms (and therefore can be degraded locally without significant diffusion) will be mineralised.

In soil, capillary force forms a thin meniscal water film surrounding individual microorganisms, and the curvature radius of the meniscal film has an inverse relation with water potential (Ilstedt *et al.* 2000). When a larger meniscus covers soil microorganisms, more substrate (DOM) is available for microbial decomposers to utilise. Change in the size of water filled-pores in response to changes in RWC may be another important factor affecting the respiration-moisture relationship. The field capacity treatment (-10 kPa, $30\text{-}\mu\text{m}$ water-filled pore size diameter) in this study maintained a ratio of air-filled and water-filled pores that provided an adequate oxygen and solute supply for microbes to metabolise organic matter. Thus, the greatest microbial respiration rates were observed at field capacity. In the intermediate or low RWC treatments, water was mainly contained in medium and small pores (ranging from <0.2 μm to <30 μm). These pores may be uninhabitable by large microorganisms (mostly, bacteria and enzymes will be active) (Van der Linden *et al.* 1989; Sleutel *et al.* 2012). As

such, the large C decomposers may suffer water/substrate stress and enter a dormant stage (or die if they succumb to the stress).

C mineralisation after soil re-wetting

After 4 weeks, a set of soils that had been incubated at the range of RWCs described above (Table 2) was re-wetted to field capacity and respiration measured for a further 4-week period. The intent was to address the question of how dry soil must be to induce the 'Birch effect' (pulse of respiration after re-wetting dry soil). There was no evidence of a flush of C mineralisation when these soils were re-wetted to field capacity, even when soil water content was close to wilting point when re-wetting occurred (Fig. 5). The amounts of C mineralised post re-wetting (data for the first week and the 2-week post-wetting incubation periods in Fig. 5a, b) were similar ($P > 0.05$) regardless of the antecedent water content (i.e. water content prior to wetting to field capacity).

These results would suggest that a flush of mineralisation may not occur if soil water content at the time of re-wetting is above the wilting point. However, this seems to be at variance with the results of Harrison-Kirk *et al.* (2013) who observed a respiration flush after re-wetting moderately dry soils (i.e. soils that had been maintained at 120% of wilting point water content prior to re-wetting).

We confirmed that a flush of respiration occurred when air-dried samples of our three soils (gravimetric water content 2–3%) were wetted to field capacity. In the day after re-wetting, the soils respired 2.9–4.6 times as much $\text{CO}_2\text{-C}$ as the control soils (soils that had been maintained at field capacity, not dried) (Fig. 6a). However, the flush was short-lived. In the second and third days post-re-wetting, the

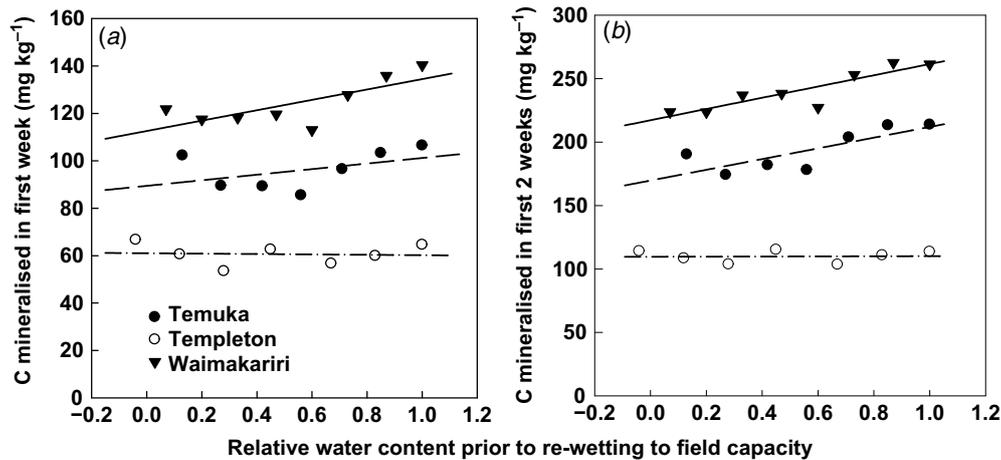


Fig. 5. Carbon mineralised in the first week (a) and first 2 weeks (b) of incubations after re-wetting (to field capacity) of soils with a range of pre-wetting water contents.

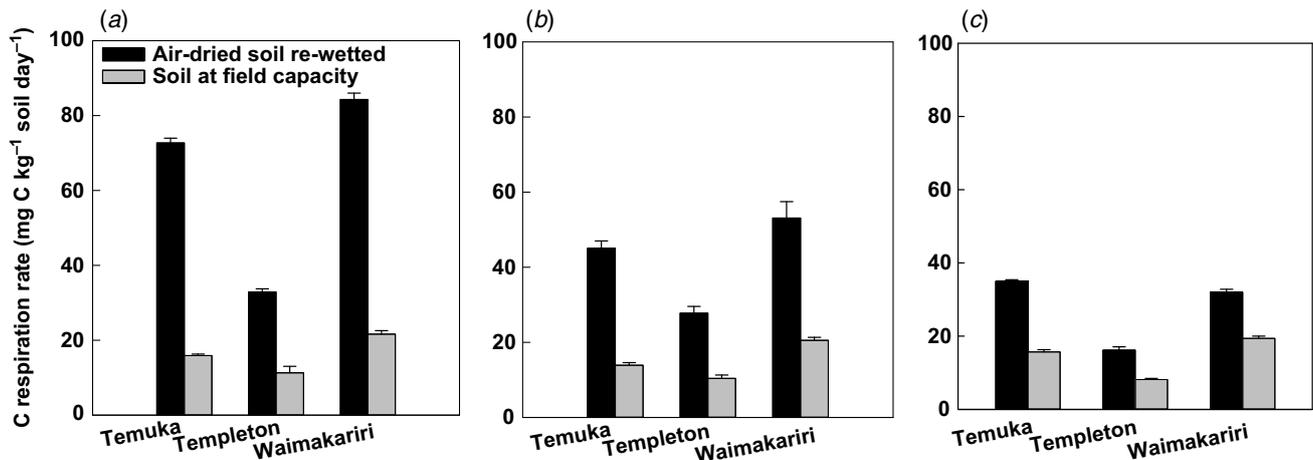


Fig. 6. Carbon (C) respiration rate on the first day (a) and Days 2 and 3 (b) and Days 3–7 days (c) after re-wetting air-dry soils compared with respiration from soils maintained at field capacity prior to incubation.

wetted soil respired 2.6–3.3 times as much $\text{CO}_2\text{-C}$ as the control soils (Fig. 6b), and the respiration rates in re-wetted soils were 1.6–2.2 times those of control soils in the 3–7 day period (Fig. 6c).

The intensity of the respiration flush is likely to be inversely related to soil water content at the time of re-wetting (Fierer and Schimel 2003). A hypothesised/hypothetical relationship between the flush size and RWC at time of re-wetting is in Fig. 7 for soils producing either a large or a small respiration flush (large or small Birch effect). We assume a linear increase in flush size as RWC decreases, with the slope of the relationship between flush size and RWC being the same for both soils. If this model is correct, the RWC required to initiate a respiration flush upon re-wetting would be lower for soils exhibiting a small Birch effect (Fig. 7). This model might explain why our soils, where the Birch effect was apparently relatively small, did not exhibit a respiration flush when

RWC at re-wetting was ≥ -0.04 (slightly below wilting point; Fig. 6) whereas other workers have reported a respiration pulse after re-wetting relatively moist soil (Harrison-Kirk et al. 2013). The magnitude of the Birch effect has been shown to vary depending on physico-chemical characteristics (e.g. texture, compaction) as well as on the quantity and composition of organic matter in the soil (Beare et al. 2009; Butterly et al. 2010). Work is needed to determine if the relationship depicted in Fig. 7 between drying intensity and the size of the respiration flush after re-wetting is valid for soils exhibiting the Birch effect to different degrees.

Relationship between net N mineralisation and relative water content

Nitrogen mineralisation, measured over an 8-week incubation period, decreased in the three soils as water content

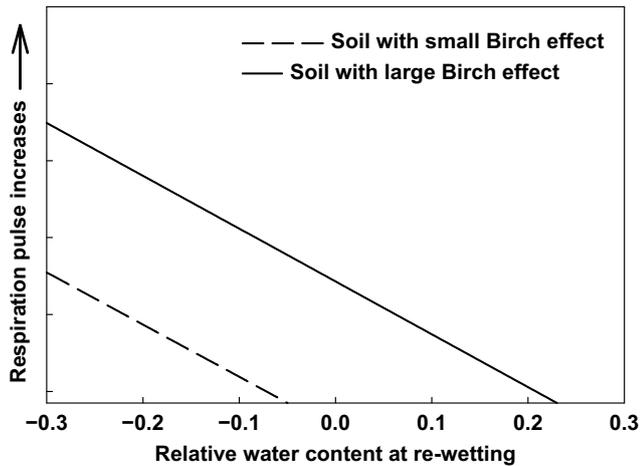


Fig. 7. Hypothetical relationship between relative water content at re-wetting and the size of respiration pulse post re-wetting for soils exhibiting either a small or large Birch effect.

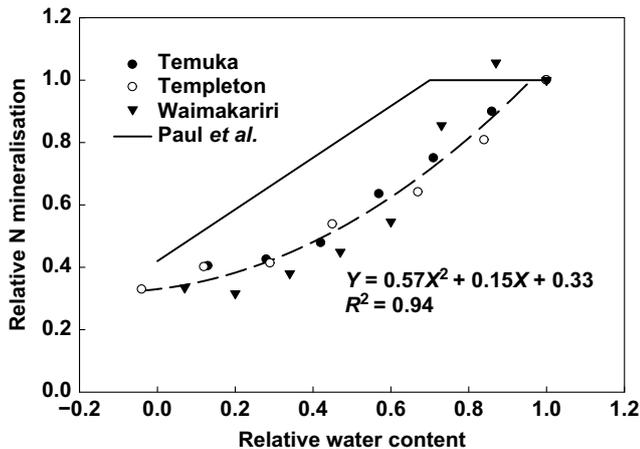


Fig. 8. Relationship (dashed line, fitted) between relative water content and N mineralisation in Temuka, Templeton and Waimakariri soils during an 8-week incubation (N mineralisation at each relative water content expressed as a proportion of mineralisation at field capacity). The solid lines represent the best-fit regression line from the study of Paul *et al.* (2003).

decreased (Fig. 8). Relative mineralisation (N mineralised as a proportion of mineralisation at field capacity) was non-linearly related to RWC; i.e. small decreases in RWC from 1.0 (field capacity) resulted in significant decline in N mineralisation. The relationship of N mineralisation with RWC thus differed from the linear relationship observed between C mineralisation and RWC. The water content where N mineralisation was at its maximum in this study was at field capacity; on average, N mineralisation at wilting point (RWC 0) was estimated to be 33% of that at field capacity.

In all three soils, N mineralisation was low relative to C mineralisation: the mean ratio of mineralised C to mineralised

N (\pm s.d.) being 18.1 (\pm 1.9), 17.7 (\pm 3.2), and 16.5 (\pm 2.7) in the Temuka, Waimakariri and Templeton soils, respectively. Low N mineralisation may be a reflection of the historically low fertiliser N inputs to the three soils.

Our N mineralisation vs RWC relationship showed some significant differences to that reported by Paul *et al.* (2003), based on their meta-analysis. They found that optimal RWC for N mineralisation is ≥ 0.7 , with N mineralisation at wilting point being 42% of that at field capacity. Overall, our study indicated that N mineralisation is more sensitive to soil drying than the meta analysis of Paul *et al.* (2003) would suggest. Use of our mineralisation vs RWC equation (Fig. 8) may result in predictions of net N mineralisation that are somewhat lower than those obtained using the Paul *et al.* (2003) function. Even so, our data support their conclusion that RWC may be a reliable (and practical) ‘water modifier’ to describe the influence of soil moisture on N mineralisation.

Conclusions

The results indicate that the response of C mineralisation to soil water content can be predicted as a simple function of RWC. Changes in solute diffusivity (substrate accessibility) and size characteristics of the water-filled soil pores are main driving factors underpinning the SOM moisture–mineralisation relationship. Physical characteristics required to estimate RWC (upper and lower limit of available water content) are available for many soils (or approximate values can be estimated). Therefore, RWC provides a practical index for moisture-adjustment of N mineralisation values. However, N mineralisation appeared more sensitive than C mineralisation to declining soil water content. Further work is needed to extend our findings to other soil types and to verify the observation that a flush of mineralisation does not occur if soil water content at the time of re-wetting is above the wilting point.

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Data availability. The data that support our findings are available from the corresponding author upon reasonable request.

Conflicts of interest. The authors declare no conflicts of interest.

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