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Sequestration of soil carbon by burying it deeper within the profile: A theoretical exploration of three possible mechanisms

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ABSTRACT

Subsoil carbon is generally older and decomposes more slowly than topsoil carbon. It has, therefore, been suggested that carbon stocks could be increased by burying carbon-rich topsoil at depth to slow its decomposition. This has been supported by recent experiments that showed that buried topsoil carbon indeed decomposed more slowly, but the mechanisms causing the reduction have not yet been identified. We investigated three theoretical mechanisms that may explain reduced decomposition rates at depth: (1) lower soil-temperature variability, (2) lower oxygen concentrations/redox potential and (3) less priming (biological synergy). Temperature variability decreases with soil depth. As decomposition rates vary non-linearly with temperature, reduced temperature variability should, therefore, reduce annual decomposition rates. However, detailed simulations showed that it changed annual decomposition rates by only a few percent. Maximal decomposition rates also require adequate oxygen, but our simulations showed that oxygen diffusion rates would need to be reduced 1000 to 10 000-fold compared to the topsoil for it to protect buried soil carbon. Oxygen limitation is, therefore, likely to be confined to soils that are water-logged for extended periods. Priming (or biological synergy) is assumed to be the stimulation of decomposition rates by the availability of labile organic carbon. Our simulations showed that lower labile carbon inputs could reduce priming and potentially preserve up to half of buried carbon for centuries. If experimental work can further substantiate the role of this mechanism, carbon burial at depth could become a practical and useful climate-change mitigation option.

1. Introduction

To prevent ongoing and accelerating climate change, it is necessary to decrease net greenhouse gas emissions to the atmosphere. This can be helped by sequestering atmospheric carbon (C) in soils (e.g. Paustian et al., 2016; Smith, 2016; Whitehead et al., 2018). Soil C contents generally decrease with depth (e.g. Jobbagy and Jackson, 2000), which suggests that subsoils could potentially store more C than they currently do. Subsoil C is also usually older than topsoil C (e.g. Rumpel and Kögel-Knabner, 2011; Mathieu et al., 2015; Shi et al., 2020), which indicates that soil depth, or a factor associated with it, could determine the persistence of soil organic C (SOC).

Thomsen et al. (2008), for example, found high C contents in a 3000-year old bronze-age burial mound. C contents were particularly

high in an anaerobic zone $[18 \text{ gC} (\text{kg soil})^{-1}]$, but under aerobic conditions at 3–5 m depth, C contents were also still about 6 gC (kg soil)⁻¹. Upon excavation and sample preparation, all samples respired C, indicating that buried C was not inherently recalcitrant but some aspect of burial had prevented decomposition for 3000 years (Thomsen et al., 2008).

These observations, therefore, suggest that soil C stocks could be increased by simply transferring topsoil C to the subsoil, provided that new topsoils can rebuild their C stocks to levels similar to those of the original topsoils for an overall C gain. This has been supported by recent observations, such as Alcantara et al. (2016), who observed that deep tillage (>60 cm depth) that had been carried out more 40 years earlier in northern Germany had increased SOC stocks by 43%. Buried topsoil C was preserved while the new topsoil had accumulated new SOC. In New

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Received 11 May 2021; Received in revised form 20 September 2021; Accepted 21 September 2021 Available online 23 September 2021 0038-0717/© 2021 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licensex/by-nc-nd/4.0/). Zealand, some highly podzolised sandy soils under grasslands are managed by one-time full inversion of soils (soil "flipping") to a depth of 1–3 m to eliminate water-logging, and Schiedung et al. (2019) showed that flipping had buried 160 ± 14 tC ha⁻¹ of topsoil C at 30–150 cm depth where most of it had persisted for at least 20 years.

Recent work has, therefore, investigated whether C stocks could be increased by burying soil C below 30 cm through full-inversion tillage during pasture renewal (Calvelo Pereira et al., 2018, 2020; Beare et al., 2020; Lawrence-Smith et al., 2021). Topsoil C would be buried to slow its decomposition while low-C subsoil would be brought to the surface to receive fresh C inputs from pasture growth and re-build new topsoil C (Lawrence-Smith et al., 2021). Early results from these studies have been promising, with Calvelo Pereira et al. (2018) reporting that full-inversion tillage increased C stocks by about 14 tC ha⁻¹ 4 years after pasture renewal. Additional on-farm trials are further testing this potential for extra C storage and ascertain the generality and persistence of the response (e.g. Beare et al., 2020; Calvelo Pereira et al., 2020). Vos et al. (2020), however, found in a study of German soils that shallow ploughing to 25 cm did not lead to the protection of buried C. That suggests that the details of ploughing, especially the depth of inversion, may be critically important for determining the persistence of buried C.

In general, it is not clear what factors could account for the observed persistence of SOC at depth, and whether the persistence is restricted to particular soil or environmental conditions, or whether it is an inherent property of the organic matter that forms naturally at depth. In particular, it is not clear whether the empirically observed enhanced C storage is likely to be a general phenomenon or restricted to special circumstances. Radiocarbon analyses have shown that subsoil C is typically older than topsoil C (Rumpel and Kögel-Knabner, 2011; Mathieu et al., 2015; Shi et al., 2020). If that persistence is related to some aspect of the conditions in the subsoil, then any C deposited at depth may similarly resist decomposition under those subsoil conditions. In support of that notion, Wordell-Dietrich et al. (2017) found that added root litter decomposed faster in topsoil than subsoil samples. Newey (2005) and Solly et al. (2015), however, found that, litter decomposition rates were similar at all depths once differences in temperature and water contents had been accounted for. Hicks Pries et al. (2018) provided a detailed temporal analysis and found that litter buried at different depths decomposed at similar rates over the first year, but after three years, decomposition rates were much slower at 95 cm depth than near the soil surface.

It is known that decomposition is enhanced when temperature (e.g. Kirschbaum, 2000; Tomczyk et al., 2020), soil moisture (Moyano et al., 2012, 2013) and oxygen (O_2) concentration (LaRowe and Van Cappellen, 2011) are favourable. It is also possible that decomposition of SOC is synergistically enhanced when there are greater inputs of labile SOC (Fontaine et al., 2007; Don et al., 2013), which is also described as 'priming' (e.g. Kuzyakov et al., 2000). If any of these conditions are less favourable at depth, then simple inversion of the soil could slow decomposition rates by moving SOC from favourable to unfavourable conditions. Here, we have explored three specific processes that could potentially affect the decomposition rate with soil depth: temperature, O_2 availability and priming.

1.1. Soil temperature

Decomposition rates generally increase strongly with increasing temperature (e.g. Lloyd and Taylor, 1994; Kirschbaum, 2000), and temperatures tend to vary with soil depth. While annual mean temperatures remain invariant with depth, temperatures near the surface are much more variable than deeper in the soil (e.g. Smerdon et al., 2003). Greater temperature variability could then lead to higher annual organic C decomposition rates simply because more activity could be gained when temperatures are below the mean (e.g. Tomczyk et al., 2020). This could lead to higher decomposition rates in the topsoil than in the subsoil.

1.2. Oxygen

Full decomposition of reduced C compounds to CO_2 requires O_2 (LaRowe and Van Cappellen, 2011), and rates could, in principle, be limited if O_2 availability were limited at depth. The effect of O_2 limitation is clearly apparent under permanently wet conditions, such as in peat bogs (e.g. Kuhry and Vitt, 1996). Such peat deposits show that extreme O_2 limitation can prevent organic matter decomposition and lead to increasing C stocks. However, the role of O_2 under less extreme conditions is not clear as the O_2 requirement of decomposition varies with the chemical composition of different compounds (LaRowe and Van Cappellen, 2011), and the draw-down in oxygen concentrations is a function of decomposition rates.

1.3. Priming (biological synergy)

Decomposition of organic C might also be enhanced simply by an increase in the overall decomposer activity in the soil. The topsoil receives ongoing inputs of fresh and readily decomposable organic C from plant roots, animal dung and above ground litter. That can support high decomposer activity and may facilitate the decomposition of more resistant organic C fractions (Fontaine and Barot, 2005; Fontaine et al., 2007; Wutzler and Reichstein, 2013). Organic C in the subsoil will receive fewer inputs of fresh and highly decomposable organic C. The subsoil, therefore, cannot support a very active decomposer community, which could reduce the specific decomposition rate of less labile organic C compounds.

Here, we have conducted a theoretical analysis to explore the potential effect of these three mechanisms on C decomposition rates. We try to understand the conditions under which each of these processes may be more or less important, and what contribution each process could make towards protecting C in the subsoil.

2. Materials and methods

2.1. Soil organic matter model

We used a simple SOC model, essentially a simplified version of the well-established CENTURY model (Parton et al., 1987; Kirschbaum and Paul, 2002), consisting of three organic C pools with different turnover rates, designated, in line with the terminology used by Kirschbaum and Paul (2002), as active, slow and resistant organic C:

$$O_t = O_a + O_s + O_r \tag{1}$$

where O_t is total SOC, O_a is active, O_s is slow and O_r is resistant organic C. The daily change in the size of each pool was calculated as:

$$dO_p/dt = C_{p(in)} - C_{p(out)}$$
⁽²⁾

where O_p is the quantity of C in pool p (to represent active, a, slow, s, and resistant, r, C, respectively), t is time, and $C_{p(in)}$ and $C_{p(out)}$ are the rates of C influx and efflux into and out of pool p.

C input into each pool was described as:

$$C_{p(in)} = f_p \left(C_{tot} \,/\, 365 \right) \tag{3}$$

where f_p is the fraction of fresh C moving to pool p, and C_{tot} is the annual quantity of fresh C from senescence and plant death to become new organic C. That was divided by 365 here to provide daily values.

C efflux from each pool was calculated as:

$$C_{p(out)} = O_p r_p l_t l_{o,p} l_b \tag{4}$$

where r_p is a basic turn-over rate of each pool, and l_t , $l_{o,p}$, and l_b are limitation terms by temperature, O_2 and priming, respectively. For temperature and priming limitations, the same limitation terms were used for all three pools, but for O_2 limitations, $l_{o,p}$, different limitations were assumed for each pool as described in detail in Section 2.3.

Calculations of the different limitation terms are described below. Limitation values were generally in the range from 0 to 1, but for O_2 limitations, the upper range was not formally limited to 1, but varied with the setting of K_m values (see below) for the different SOC pools. When investigating the effect of each of these, the other limitation terms were set to non-limiting values. The parameter r_p was adjusted for different simulations with different sets of limitations so that under the starting conditions for each pool, $C_{p(in)} = C_{p(out)}$.

2.2. Temperature limitations

For calculating soil temperature, the soil was sub-divided into 10-cm layers down to a depth of 10 m. While the deeper layers were not directly relevant for C dynamics, they all contributed to the temperature profile over relevant shallower soil depths.

Temperature changes were then calculated at an hourly time step, with temperature change of each layer, dT_i/dt , calculated as:

$$dT_i / dt = (T_{i-1} + T_{i+1} - 2T_i) / \tau \quad \text{if } i > 1$$
(5a)

$$dT_1 / dt = (T_a + R + T_2 - 2T_1) / \tau$$
 if $i = 1$ (5b)

where T_i is the temperature of layer *i*, T_{i-1} the temperature of the layer above, and T_{i+1} the temperature of the layer below, *t* is temperature, here calculated at hourly intervals, and τ a time constant of change. This equation assumes layers to be of constant thickness throughout and ignores any differences through different thermal properties of different layers due to different mineralogy, porosity or water contents (e.g. Tarnawski et al., 2012).

 T_a is daily mean air temperature and *R* a factor that describes the elevation of average soil temperature above average air temperature as a result of direct radiation input that changes as a function of vegetative cover (Paul et al., 2004). Mean air temperature was estimated as the mean of daily minimum and maximum temperatures. The model was parameterised and tested against daily observed temperatures from a study site in Mehrstedt, Germany (Don et al., 2009) as described below.

Once patterns of temperature change had been calculated for each layer, decomposition activity was calculated hourly over a whole year, D_{i_i} as:

$$D_j = l_{t,i} \tag{6}$$

where $l_{t,i}$ is the temperature limitation term, calculated following Kirschbaum (2000) as:

$$l_{t,i} = e^{[3.36(T_i - 40)/(T_i + 31.79)]}$$
⁽⁷⁾

Annual decomposition activity for each soil layer, D_i , was then calculated as:

$$D_i = \sum_{j=1}^{365^+24} \left(D_{i,j} \right)$$
(8)

where $D_{i,j}$ is the decomposition activity calculated for each hour of each day, *j*, and each soil layer, *i*. Normalised results for each layer, *d_i*, relative to the topsoil, designated as layer '1', were then calculated as:

$$d_i = D_i / D_1 \tag{9}$$

2.3. Oxygen limitation

 O_2 diffusion in the soil can be modelled with different models of varying complexity (e.g. Neira et al., 2015). Here, we used a simple modelling approach (see Cook, 1995), focused primarily on the potential differences in O_2 limitation between different depths in the soil. To calculate the effect of O_2 concentration on decomposition activity, we followed the decomposition of a unit of organic C placed at different

depths in the soil with different ease of access to O₂. Over time, the quantity of C was reduced through ongoing decomposition and its average quality declined as active C decomposed first and slow and resistant fractions remained.

The O_2 concentration at the sites of decomposition, O_d , was calculated, following Cook (1995), as:

$$O_{d,1} = \frac{21 - (D_1 + R_1)}{r_1} \tag{10a}$$

$$O_{d,s} = \frac{O_{d,1} - (D_s + R_s)}{r_s}$$
(10b)

where the subscripts 1 and *s* refer to the topsoil and subsoil, respectively, *D* is the O₂ consumption rate by daily decomposition activity of all three organic C pools combined, *R* is the oxygen demand by root respiration at the respective layer, $r_{o,1}$ and $r_{o,s}$ is the O₂ diffusion resistance from the atmosphere to the site of decomposition, and '21' represents the normal atmospheric O₂ concentration in percent. Calculations for the subsoil were based on the O₂ concentration calculated for the topsoil as the starting condition.

Daily decomposition rate, D, was calculated as:

$$D = d_a + d_s + d_r \tag{11}$$

where d_a , d_s and d_r are the decomposition rates of the active, slow and resistant pools, respectively.

The root distribution in the soil was assumed to decrease exponentially with depth as well as depending on O_2 concentration so that:

$$R_i = \frac{O_d}{(O_d + K_r)} R_{tot} e^{-dk}$$
(12)

where R_{tot} is the respiration rate from the total root system, d is the depth in the soil, k is a parameter to describe the rate of exponential decrease of root density with depth, and K_r is a Michaelis-Menten constant for the dependence of root respiration on O₂ concentration. For these calculations, the topsoil was assumed to be at 5 cm depth and the subsoil at 45 cm. The fraction of total root mass was then integrated for 10-cm intervals around each specified root depth.

For specific simulations, the diffusion resistance was calculated as:

$$r_o = r_{base} r_m \tag{13}$$

where r_{base} is the minimal base diffusion resistance near the soil surface, which was also used for calculating diffusion resistances for the topsoil. The term, and r_m is a multiplier of that diffusion resistance used in our scenarios to represent conditions deeper in the soil after soil inversion with diffusion paths that led to a range of diffusion resistances. The O₂ limitation to decomposition rate was then calculated in dependence on O₂ concentration as:

$$l_{o,p} = O_d / (O_d + K_{o,p}) \tag{14}$$

where $K_{o, p}$ is Michael-Menten constant for the dependence of decomposition rate on O₂ concentration, with different O₂ sensitivities assumed for pools with different recalcitrance. While it is known that the decomposition of labile C compounds has a lower dependence on O₂ concentration than that of more recalcitrant compounds (LaRowe and Van Cappellen, 2011), we could not find any experimental work that quantified the O₂ requirements of different organic C fractions in the soil. The parameters used here were, therefore, only indicative.

2.4. Priming (biological synergy)

The biological limitation term, l_b , was calculated as:

$$l_b = (1 - s) + s \ a_b \tag{15}$$

where s is the priming requirement of decomposition (0–1.0). If respiration could proceed without requiring any priming, this term

would be set to 0, and if decomposition were totally reliant on priming, it would be set to 1. In essence, the part in brackets describes the component of respiration that is independent of priming, and the term *s* a_b describes the component reliant on priming.

The term a_b is the normalised total biological decomposer activity, calculated as:

$$a_b = 1 - e^{-k_b D}$$
(16)

where k_b is a priming scalar to quantify the dependence of biological decomposer activity on priming, and D is the total daily decomposition rate as defined above.

2.5. Observational data

To parameterise the soil temperature model, we used data from Mehrstedt in Thuringia in Central Germany (10.65° E; 51.28° N). It was a pasture site that was compared with afforestation to study land use change effects on C fluxes and SOC (Don et al., 2009) and included detailed half-hourly weather observations sampled over a period of more than 3 years. That included measurements of air temperature and soil temperatures at 2, 4, 8, 16, 32 and 64 cm depth. A fit to the data is given in the On-line Supplemental Information.

2.6. General modelling protocols

We could find no published literature that would have allowed detailed parameterisation of the model described here. Parameterisation therefore had to be confined to a range of plausible values. The parameters used to run these simulations are given in Table 1. The value of k_b was set to a value of 500 d ha tC⁻¹. This meant that priming was essentially non-limiting as long as any active SOC was present in the soil, but reduced to a value of zero when active SOC was exhausted after some time following soil inversion. Slow and resistant SOC could therefore not decompose at all without the priming engine provided by active SOC. Base conditions for O₂ limitations were set to $r_{base} = 10$ which led to an O₂ concentration in the topsoil of about 20.67%, which is about 1.5% below atmospheric O₂ and constitutes a typical concentration observed in soils without special impedance (e.g. Song et al., 2019).

Total C input rate was set to 10 tC ha^{-1} yr⁻¹, with decomposition rates of the three SOC pools set to achieve initial pool sizes of 5, 50 and 50 tC ha^{-1} for the active, slow and resistant pools, respectively. The

Table 1

Parameters used for the simulations shown in this work. Other specific details are given in respective sections.

		Units	Value
Topsoil		cm	5
Subsoil		cm	45
Active pool	O_a	$tC ha^{-1}$	5
Slow pool	O_s	$tC ha^{-1}$	50
Resistant pool	O_r	$tC ha^{-1}$	50
New C to active	f_a		0.89
New C to slow	f_s		0.1
New C to resistant	f_r		0.01
Time constant for T change	τ_i	hr	6.4
Temperature elevation of soil relative to air	R	°C	0.85
temperature			
Annual C input to the soil	C_{tot}	$tC ha^{-1} yr^{-1}$	10
Annual C release through root respn.	R _{tot}	$tC ha^{-1} yr^{-1}$	5
Root depth distribution	k	$\rm cm^{-1}$	0.1
O2 diffusion resistance to topsoil	r_{base}	% m ² s	0.104
		μ mol ⁻¹	
K _m of O ₂ dependence of active pool respn	K _{o,a}	%	0.1
K _m of O ₂ dependence of slow pool respn	$K_{o,s}$	%	1
Km of O2 dependence of resistant pool respn	$K_{o,r}$	%	10
Km of O2 dependence of root respiration	K_r	%	10
Priming scalar	k_b	d ha t C^{-1}	500

topsoil was modelled to receive all regular new C inputs so that all SOC pools reached their set initial sizes. The subsoil, on the other hand, was assumed to initially receive no C inputs so that no organic C was formed. This was an extreme simulation that made it easier to follow the patterns after soil inversion. Normally, some C is present even in subsoils, supported by a small quantity of fresh C inputs from deep roots or leaching of dissolved organic C. However, these small quantities of C only dilute the patterns seen after soil inversion, but do not fundamentally alter them. To make the patterns clearer, we, therefore, focused on the more extreme scenario described here.

For given environmental conditions and a set of parameters, set pool sizes under equilibrium conditions could be obtained by selecting appropriate $r_{a\nu}$ r_s , and r_r parameters. Different 'r' values were needed when different sets of limitations were included. To model the patterns after soil inversion, the established pools were simply swapped, so that the new topsoil started with zero pool sizes, while the new subsoil started with large pools. After inversion, the new topsoil received all subsequent fresh C inputs at the same rates as before inversion, whereas the buried topsoil received no further C additions.

3. Results

3.1. Temperature variability

We compared our simple soil-temperature model with measurements taken at 6 depths down to 64 cm. The model was generally consistent with the observations, with Nash-Sutcliffe (Nash and Sutcliffe, 1970) model efficiencies ranging from 0.93 near the surface to 0.98 at 64 cm depth (Fig. S1). The discrepancies were most significant near 0 °C when the simple model did not adequately capture the complex temperature patterns associated with ice-water phase shifts or the variable insulating properties of a snow layer. However, across the full temperature range, the overall model efficiency of 0.93 was still acceptably high. Periods with low temperatures were also of limited importance for overall decomposition activity so that small temperature errors would have only marginally affected annually summed decomposition activity. We, therefore, regard our model as appropriate for the present purpose.

Temperatures generally fluctuated more nearer the soil surface than at depth where temperatures were more stable (Fig. 1a). Without interactions with soil moisture, decomposition activity was calculated to be highest in the topsoil because of the stimulation of decomposition rates when temperatures exceeded average temperatures (Fig. 1b). This caused the depth differences in calculated decomposition activity (Fig. 1c) to be more pronounced than the differences in the underlying temperatures (Fig. 1a). When we summed total decomposition activity over the whole measurement period, it showed a clear trend of decreasing decomposition activity with soil depth (Fig. 1d). However, while the depth trend was clear, it was quantitatively small so that down to a depth of 50 cm, relative decomposition rates fell by less than 10% from its peak near the soil surface. The temperature effect became more pronounced deeper into the soil, but that was of little practical importance because there is normally very little SOC at those depths.

The quantitative significance of the temperature effect was further explored by running simulations under observed annual weather sequences from across New Zealand (Fig. 2). These runs were used to further elucidate the quantitative significance of temperature variability under different mean temperatures and patterns of temperature variation from different sites. Reduced temperature variations at depth reduced annual decomposition activity at both 25– and 55–cm depths. However, at 25 cm, decomposition was reduced by only 1–4% compared with that at 5 cm (Fig. 2a), and by 1–8% at 55 cm (Fig. 2b), with the reduced decomposition activity being more pronounced at lower mean temperatures. There was also much site-to-site variability, especially at intermediate temperatures. This mostly reflected the extent of interseasonal temperature variations, with sites with more even temperatures throughout the year showing lesser reductions in decomposition



Fig. 1. The interaction between soil depth and decomposition activity, showing (a) the seasonal temperature cycle at different depths in the soil and (b) the response of decomposition activity to temperature (after Kirschbaum, 2000), derived relative decomposition activity as a function of soil depth for the temperatures shown in panel (a) and (d) normalised annual decomposition activity as a function of depth for the soil shown here. Temperatures in (a) at 4, 32 and 64 cm were the temperatures observed at Mehrstedt, Germany (Don et al., 2009), and temperatures deeper in the soil (shown as dashed lines) were modelled.



Fig. 2. Reduction in annual decomposition activity relative to the top-5 cm at depths of (a) 25 cm or (b) 55 cm in the soil. Data at lower depths are expressed as a percentage of expected decomposition activity at 5 cm. Simulations were conducted for temperature data from 10 491 specific locations from all of New Zealand, with error bars showing the standard deviations of data binned at one-degree intervals.

rates with depth (data not shown).

While the simulations showed a reduction in decomposition activity with soil depth, the effect was numerically small, suggesting that the temperature effect on its own is unlikely to greatly enhance the persistence of buried C in the short term. Based on our simple SOC model, a 5% reduction in total decomposer activity increased SOC by only about 2.5 tC ha⁻¹ (about 2.4%) over 10 years (Fig. 3a). When the soil was first inverted, decomposition of buried active SOC slowed under the more even temperatures at depth. However, as the amount of buried active SOC decreased while a new active pool formed in the topsoil, temperature variations gradually became less effective, and after 5 years, the

size of new active pool in the topsoil was similar to the size of the active pool before burial, while nearly all C in the buried active pool had decomposed. With the sizes of the active pool in topsoil and subsoil being close to what they had been before burial, temperature variations ceased to have any effect on decomposition rates.

The slow pool followed the same pattern but over a much longer time frame, and it was even slower for the resistant pool (Fig. 3b). That meant that temperature effects on the decomposition of the active pool led to a short-term C gain that was completely reversed within a few years (Fig. 3a). The slow pool reached a peak after about 50 years before partial reversal. Overall, burial of SOC under more even temperatures



Fig. 3. Changes in the active (red), slow (blue) and resistant (green) SOC pools and total SOC (black) after full-inversion tillage, considering only temperature variability as a mechanism for C protection. The graph shows total C stocks combined for both topsoil and the subsoil. This is shown for (a) 10 years and (b) 200 years. Full-inversion tillage was simulated here by swapping C in the topsoil at 5 cm, and subsoil at 55 cm depth. All other factors, such as C input rates, remained the same. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

led to a slight SOC gain of about 7 tC ha⁻¹ that peaked about 75 years after burial before gradual reversal thereafter (Fig. 3b).

3.2. Oxygen limitations

In principle, O_2 deprivation could also play a role under fullinversion tillage. The inversion of soils could take SOC from an aerobic zone near the soil surface (Fig. 4a) and deposit it deeper within the soil where O_2 supply might be more limited (Fig. 4b), especially in soils with restricted drainage, a high ground-water table, or if frequent rainfall leads to water saturated conditions in deeper soil horizons for at least part of the year.

This is explored here by considering the fate of SOC with varying access to O_2 . We quantified O_2 supply by relative O_2 diffusion resistances as they may change in different soils through lengthened diffusion paths deeper into the soil, possibly further increased through soil compaction or a layer of water. The extent of O_2 draw-down between the atmosphere and the sites of decomposition is determined by both the rate of decomposition and the diffusion resistance. The simulations showed that O_2 concentrations could potentially vary considerably with different diffusion resistances over both the short (Fig. 5a) and long term (Fig. 5b), but when diffusion resistances were increased less than 1000-fold over default values, they still had little effect on decomposition rates (Fig. 5c and d) and remaining SOC stocks (Fig. 5e and f). Diffusion resistance had to increase at least 500-fold to make any noticeable



Water-saturated or compacted soil

Fig. 4. Diagrammatic presentation of O_2 limitations to decomposition, showing (a) a normal soil with organic C (black circles) near the soil surface with good access by O_2 and (b) a soil that has been inverted. Soil inversion transfers organic C to deeper layers in the soil where O_2 supply can become restricted through water-saturation or soil compaction. Larger light brown circles represent soil mineral particles, smaller black circles represent organic C and the blue area represents a part of the soil filled with water. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

difference to decomposition rates and SOC over the short term (Fig. 5c, e) and more than 1000-fold to make a difference over the longer term (Fig. 5d, f).

These patterns were largely caused by the interplay between decomposition rates that drove the draw-down in O_2 concentration and the relative O_2 sensitivities of organic matter fractions with different lability. Initial decomposition rates were fast and could cause a significant draw down in O_2 concentration with even moderate increases in diffusion resistances, but, because the decomposition of labile C was assumed to be fairly insensitive to O_2 concentration, its decomposition rates remained unimpeded with even greatly reduced O_2 concentrations.

These simulations, therefore, suggested that moderate increases in diffusion resistances would be unlikely to significantly protect buried soil C after full-inversion tillage. Increases in diffusion resistances up to 100-fold resulted in barely noticeable changes in SOC, and even increases in diffusion resistances up to 1000-fold were still of only minor importance (Fig. 5e and f). Diffusion resistances would have to increase more than 1000-fold to significantly affect the trajectories of C losses. Such increases in diffusion resistance could be found under permanent water saturation, such as in peat bogs, but they are unlikely to be found without water as a diffusion barrier, not even in severely compacted soils.

3.3. Priming (biological synergy)

Priming was simulated here through our simple conceptual SOC model with active, slow and resistant SOC pools. The slow and resistant pools typically contain most SOC, illustrated here through the size of the boxes (Fig. 6) whereas the predominant C flows move through the active pool, with lower flux rates through the slow pool and resistant pool, illustrated by the thickness of the arrows.

Decomposition rates were assumed to be proportional to the sizes of respective pools, illustrated by the red dotted lines, and by additional biophysical factors, such as temperature, that are not shown here. Decomposition rates were thus assumed to follow simple first order decay dynamics. In addition, we assumed an interaction between these pathways, illustrated by the green dashed lines. It meant that decomposition depended not only on external factors and their own pool sizes but also on the decomposition rate of the active pool, essentially equating to the activity of the decomposer community (priming).

The consequences of a possible priming effect are illustrated here for two soil layers, a topsoil that receives ongoing C inputs and a subsoil with no fresh C inputs. The soil was then inverted at year 0 (Fig. 7). We assumed that before inversion, all carbon pools in the topsoil had reached steady state with inputs equal to outputs, and all subsoil pools were set to zero. After inversion, the pools in the subsoil were assumed to receive no further C inputs, leading to gradual C loss from those pools.



Fig. 5. Interactions between O_2 concentration and organic C decomposition. Simulations are shown for different O_2 diffusion resistances relative to the diffusion resistance to organic matter placed near the soil surface (multiples, x). Relative diffusion resistances up to 100-fold (100x) generally made little difference in the simulations and are represented by lines superimposed on each other. The figure shows (a, b) O_2 concentration over time and with different diffusion resistances, (c, d) resultant decomposition rates, and (e, f) remaining organic C over time. That is shown over (a, c, e) 10 or (b, d, f) 1000 years. Note that panel (d) uses a logarithmic scale while all other panels use linear scales.



Fig. 6. Conceptual 3-pool SOC model. Red dotted lines represent the standard formulation of organic C models, illustrating the first-order dependence of organic C degradation on the size of pools. Dashed green lines illustrate additional priming effects. The size of the boxes illustrates the relative sizes of different pools and the thickness of black arrows illustrates relative flux rates. The green circle represents the activity of the decomposer community which then synergistically affects the flux through other decomposition pathways. Additional biophysical controls on decomposition rates have been omitted from this diagram. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The new topsoil received the same input of fresh C as the original topsoil before inversion which allowed a gradual build-up of new respective pools, starting from zero pool sizes in the subsoil brought up from depth through soil inversion. Without considering priming (or the effects of temperature or O₂ concentration), gains would have matched losses perfectly, with no overall change in total SOC stocks, but a dependence on priming created an asymmetry in their trajectories after inversion.

For the active pools, there was only a slight asymmetry (Fig. 7a), with the build-up of a new active pool slightly faster than the loss of buried active C. Changes in the sizes of the slow and resistant pools were numerically much more important, however, especially those of the slow pool (Fig. 7b and c). It was a large pool that could lose or gain a substantial quantity of C over decades, but when decomposition of the buried slow pool was no longer stimulated by priming, its C loss rate slowed significantly. The size of the slow pool in the newly exposed soil meanwhile increased more quickly to almost reach its steady-state size within 100 years. For the resistant pool, too, the formation of a new resistant pool in the newly exposed topsoil was faster than the loss of the buried resistant pool. However, both gains and losses were so slow that even after 100 years, the new resistant pool still contained less than 10 tC ha⁻¹, making its asymmetric changes quantitatively not as important as those of the slow pool.

Summing C in all SOC pools then yielded an overall increase in total C stocks from the initial 105 to over 140 tC ha^{-1} within 100 years



Fig. 7. Illustrating the effect of priming on SOC, following full-inversion tillage that buries a former topsoil, and exposes a former subsoil to fresh C inputs at the soil surface. Shown are (a) active SOC in the exposed and buried soil layers over the first 5 years, (b) slow and resistant SOC in the same layers over 100 years, (c) the same pools as in (b) plus total SOC stocks summed over the two layers and (d) the total quantity of SOC over 500 years with different priming requirements, which describe the extents of the dependence of decomposition rates on priming.

(Fig. 7c) as buried C was protected from decomposition through the cessation of priming while the newly exposed subsoil could build sizeable new pools through ongoing inputs of fresh C. Overall C gains depended on the extent of the dependence on priming (Fig. 7d). If decomposition rates were only partly stimulated through priming, the overall C gains through soil inversion would also be only partly realised. With full priming requirement (which implies complete cessation of decomposition activity without stimulation by some decomposition activity), C stocks over the first few decades after soil inversion increased by about 1 tC ha⁻¹ yr⁻¹, which then gradually diminished as the soil approached new steady-state condition with carbon stocks reaching about 150 tC ha⁻¹ after 200 years (Fig. 7d). The benefit of soil inversion diminished with reducing priming requirement (if other possible mechanisms were ignored). Obviously, if decomposition did not require

any priming, then there would be no C benefit if that priming effect were removed through soil inversion. Persistent C gains were only realised if there were near total dependence on priming (Fig. 7d). If there remained even slight ongoing decomposition activity without priming (priming requirement <1), it would lead to the eventual loss of buried C as well.

Overall, these stimulations clearly illustrate how resistant C in the soil could be protected and remain in the soil for hundreds of years if the decomposition engine provided through priming is lost. This would happen through soil inversion and burial of C at depth where the ongoing stimulation through fresh C inputs would be lost.



Fig. 8. Simulated extra soil carbon benefit of soil inversion under different combinations of the three mechanisms investigated here shown for (a) the first 10 years after inversion and (b) for 250 years. All simulations included the effect of different temperature profiles at depth and near the soil surface. This was combined with the effects of 10 000-fold increases in O_2 diffusion resistance and priming and with both effects included together. In an extra simulation, the 10 000-fold increase in diffusion resistance was applied for only 6 months of the year.

3.4. The effect of soil inversion under different protective mechanisms at depth

Finally, we assessed the C storage potential through full-inversion tillage under different potential protective mechanisms at depth in the soil (Fig. 8). If only the more even temperature at depth acted as a C stabilising factor, it could still lead to some increase in C stocks, but by only a few tC ha⁻¹. Other mechanisms would have to be involved to achieve more substantial storage benefits.

If the soil at depth was permanently water-logged, it could prevent the decomposition of SOC and lead to substantial savings of almost 15 tC ha^{-1} after 10 years that eventually stabilised after 250 years with a gain of more than 50 tC ha^{-1} in the soil. The savings could be enhanced even more if priming further added to C protection, especially at later stages of decomposition. When soils were assumed to be water-logged for only half the year, however, there was little ongoing benefit in the long term as the aerobic conditions for half the year could still lead to the eventual decomposition of all C deposited at depth. This pattern could be seen clearly over the first few years (Fig. 8a) as decomposition rates, and consequent C storage, zig-zagged between higher and lower rates in summer and winter, respectively, but after 250 years, little benefit remained (Fig. 8b).

Priming alone led to similar extra C storage as O_2 deprivation, but with a delay of a few years. For the first few years after soil inversion, decomposition at depth could still continue at high rates as the buried active C could initially provide the synergistic stimulus needed for high decomposition rates. After a few years, however, that stimulatory effect disappeared with the decomposition and loss of the active C pool, leading to a substantial reduction in the decomposition rates of slow and resistant C. The remaining C was then protected from further loss.

4. Discussion

Previous studies showed that large quantities of soil organic C buried at depth can persist for many decades (e.g. Alcantara et al., 2016; Schiedung et al., 2018). This has led to growing interest in applying one-off full inversion tillage during pasture renewal to bury topsoil C at depth to increase overall soil C storage by slowing the decomposition of buried C while allowing the new topsoil to accumulate C in the soil brought up from depth (e.g. Lawrence-Smith et al., 2021). While most initial observations have shown promising results (e.g. Calvelo Pereira et al., 2018; 2020; Beare et al., 2020), Vos et al. (2020) had found that traditional shallow ploughing to a depth of less than 30 cm had not protected buried C from decomposition. That finding showed that C protection at depth is not ubiquitous and points to the need to develop a better understanding of the mechanisms that could possibly protect SOC at depth.

4.1. Temperature variability

The most certain benefit of C burial lies in reducing temperature variability with depth (Fig. 1), with the consequence of slowing decomposition rate under more constant temperatures (Fig. 2). Our simulations showed that temperatures fluctuated more nearer the soil surface, while temperatures were more stable at depth (Fig. 1a) which has also been observed in the annual cycle (Smerdon et al., 2003; Tomczyk et al., 2020). Decomposition is generally held to be a strongly non-linear function of temperature (e.g. Lloyd and Taylor, 1994; Kirschbaum, 2000, Fig. 1b). This implies that overall decomposition activity could be increased with increasing temperature variations around mean temperatures (Kirschbaum, 2010). It arises because more activity can be gained when temperatures exceed average temperatures than is lost when temperatures are below average because the temperature response curve is steeper at higher than lower temperatures (Tomczyk et al., 2020). The extent of temperature variations can, therefore, have important implications for the inferred temperature

response of soil respiration (Ågren and Axelsson, 1980; Graf et al., 2008; Kirschbaum, 2010; Tomczyk et al., 2020). Our detailed simulations showed, however, that this is likely to slow annual decomposition rates only marginally (Fig. 3) and, while some gain in C stocks can be expected, it is unlikely to lead to large C gains through full inversion tillage (Fig. 8). Over longer time scales, even these small temperature-related differences in decomposition rates could make a quantitatively larger contribution to C storage (Fig. 3b). Over the time scale of centuries, C storage could, therefore, be increased through reduced decomposition rates, but even that small gain was not permanent but was lost again over even longer times scales.

There could also be complex interactions between temperature and moisture limitations (e.g. Moyano et al., 2012, 2013). Highest summer temperatures often coincide with times with greatest moisture limitations (Davidson et al., 1998; Rey et al., 2002), and the question arises whether moisture limitations may be more or less pronounced at greater depth. This can differ between sites based on rainfall, soil properties and rooting and drainage patterns. Topsoils are likely to go through repeated wetting and drying cycles. Deeper soil layers could be predominantly too dry (at dry sites) or remain mostly free of moisture limitations (at sites with high and regular rainfall) or intermediate for soils with preferential flow paths that allows deeper soil layers to be rewetted occasionally. It is, therefore, difficult to establish general patterns of the conditions under which changes in relative moisture limitations could make conditions more, or less, favourable for C storage at depth.

4.2. Oxygen requirements

If the temperature effect alone can only marginally contribute to protection of SOC at depth, it requires other explanations for the observed SOC differences after full-inversion tillage (e.g. Alcatara et al., 2016; Calvelo Pereira et al., 2018). Organic C decomposition also requires adequate availability of O2 as the electron acceptor although some, but less energetically beneficial, decomposition is also possible under anaerobic conditions with CH₄ or other possible compounds instead of CO₂ as the final product (LaRowe and Van Cappellen, 2011; Neira et al., 2015; Huang et al., 2020). When O₂ supply is severely curtailed, C can continue to accumulate, as in anaerobic peat bogs (e.g. Kuhry and Vitt, 1996). The decomposition of more recalcitrant C compounds depends even more strongly on O2 than the decomposition of more labile C compounds (LaRowe and Van Cappellen, 2011) so that the relative proportion of recalcitrant compounds tends to increase under anaerobic conditions (e.g. Tambone et al., 2013). In line with the different O2 requirements of the break-down of different compounds reported by LaRowe and Van Cappellen (2011), we assumed O₂ requirements of decomposition to be lower for active than resistant C (see Eq. (14) and Table 1).

Near the soil surface, the O_2 concentration is usually close to 21% (e. g. Owens et al., 2016), but deeper in the soil, the O_2 concentration can be a few percent lower (e.g. Song et al., 2019), especially after periods with heavy rainfall (e.g. Silver et al., 1999). Actual O2 concentrations reflect the proximity to the soil surface and the presence of any soil layers that impede O2 diffusion, with a continuous water layer being the most common cause of strong impedance of O2 diffusion. It also depends on the O2 demand through the decomposition of SOC and root respiration that provides the driving force for lowering subsoil O₂ concentrations. Different plants show quite different sensitivity to O₂ limitations around their roots (Fukao and Bailey-Serres, 2004) before plants become either unable to function in an anoxic environment or shift to meeting their energy requirements through fermentation and glycolysis (Nakamura and Noguchi, 2020). That diversity between plants makes it difficult to provide generalisation. The contribution of roots was modelled here assuming quite O2-sensitive root systems. Root respiration through O2 consumption was, therefore, curtailed under even moderate O₂ limitations which limited the role of roots in drawing down subsoil O2 concentrations.

Our results suggested that O₂ limitations could only protect significant quantities of C at depth if O2 diffusion is severely restricted, which normally requires water-logged conditions. We found that even 1000- to 3000-fold increases in diffusion resistances had little effect on the decomposition of active soil C (Fig. 5) because it could be decomposed effectively even at very low O2 concentrations. The decomposition of slow C, however, required higher O2 concentrations (LaRowe and Van Cappellen, 2011) and could, indeed, be inhibited effectively through oxygen limitations. That limitation was even more pronounced for the decomposition of resistant C. However, because of the slow decomposition rate of these pools, it provided only a weak driving force to draw down O₂ in the soil so that substantial reductions in O₂ concentrations required very large increases in diffusion resistances. With the eventual loss of slow C after hundreds of years, and the consequent further decrease in decomposition rates, O2 concentrations could rise again and allow the eventual decomposition of resistant C as well.

Simple soil compaction, or the lengthening of diffusion paths deeper into the soil, are, therefore, unlikely to induce sufficient O_2 limitations, but a layer of stagnant water could reduce O_2 diffusion rates sufficiently for O_2 to become limiting. If water-logging occurs for only part of the year, it could reduce decomposition rates in proportion to the time that water seals the soil and prevents O_2 access, but it would only slow, but not prevent, ultimate SOC loss, which could still occur at times when drier conditions would allow O_2 access (see Fig. 8). If C were buried under such O_2 limited conditions, it could, however, potentially lead to the release of C as methane with overall unfavourable net climatechange consequences.

4.3. Priming (biological synergy)

Finally, we investigated the possible role of 'priming' (or biological synergy), which we consider to be the enhancement of the decomposition of recalcitrant organic C by increased overall soil biological activity through the availability of fresh labile organic C. Our simulations suggested that the absence of priming could well explain the persistence of organic C at depth for long periods of time. If an ongoing supply of fresh organic C is needed to synergistically enhance the decomposition of recalcitrant C, then its decomposition will be reduced or eliminated when ongoing supplies cease (Fig. 7). Initial decomposition rates right after soil inversion may not change because some labile C will be buried along with more recalcitrant fractions. As that pool of labile C is exhausted and fresh supplies do not reach the deeper layers in the soil, however, the gradual loss of this synergistic stimulation may become progressively more important and slow the rate of decomposition of more resistant SOC fractions.

SOC models, such as CENTURY (Parton et al., 1987; Kirschbaum and Paul, 2002) and RothC (Jenkinson and Rayner, 1977), consider the decomposition of organic C in specified pools to follow simple first-order decay kinetics that depend on the size of those pools and biophysical factors such as temperature, soil moisture and soil texture. These models have been successful for most data sets against which they have been tested, but it is not certain whether they can also correctly describe the patterns under the unique condition of C buried deep within the soil profile.

Some buried SOC has been preserved for thousands of years (Thomsen et al., 2008), and ¹⁴C analyses of subsoil C have shown that it can be thousands of years old (Rumpel and Kögel-Knabner, 2011; Mathieu et al., 2015; Shi et al., 2020). This longevity is typically ascribed to either biochemical recalcitrance or protection through the formation of organo-mineral complexes (Kögel-Knabner et al., 2008; Kleber et al., 2015). However, Fontaine et al. (2007) found that old C could be made available to microbes if fresh and labile C were added to the soil. This supported the notion that a supply of metabolisable energy is an essential pre-requisite to facilitate the decomposition of resistant organic matter by an active decomposer community (Fontaine and Barot, 2005; Wutzler and Reichstein, 2013).

Similarly, Hicks Pries et al. (2018) found that litter buried at different soil depths decomposed at similar rates over the first year, but over the subsequent two years, decomposition rates were significantly higher in shallower than deeper soils. Hicks Pries et al. (2018) interpreted that to mean that over the first year, the added litter itself provided the labile C to establish a flourishing decomposer community. When the labile C in fresh litter had been exhausted, the decomposer community at a shallow depth could be sustained through new C inputs from root exudates and decaying roots while those inputs were absent or minimal at 95 cm depth. This then led to the observed differences in decomposition rates whereas the similar decomposition rates over the first year showed that other differences in the soil, such as temperature variability or O_2 concentrations, did not significantly affect decomposition rates at the different depths.

Don et al. (2013) also showed that soil decomposition rates can be more rapid when organic C becomes more concentrated, and Kuzyakov et al. (2000) and Kuzyakov (2010) described a range of observations, collectively termed 'priming effects', that showed that the decomposition of SOC can be synergistically enhanced by the presence of additional easily decomposable C sources. In essence, the concept of priming postulates that fresh labile organic material in the soil creates a micro-environment replete with microbes and extracellular enzymes that primarily process the fresh available C sources, but that could also degrade older and less readily available SOC. With lower availability of labile C, the abundance of exo-enzymes, decomposer diversity and mesofauna would be reduced, and, with reduced facilitation by these agents, decomposition rates would inevitably slow down (Ekschmitt et al., 2005). Dignac et al. (2017) considered priming to operate firstly by simply creating a more active decomposer community, secondly through the break-down of recalcitrant compounds by specific enzymes to effectively mine organic matter for required nutrients, and thirdly through exudates released by roots and decomposers in the soil. If sufficient exudates are released, they can modify the pH and other properties in the soil environment to disrupt and break open existing organo-mineral complexes to enable the decomposition of protected organic molecules.

While the potential stimulatory effect of increased biological decomposer activity has been demonstrated through a range of manipulative experiments (e.g. Kuzyakov et al., 2000; Fontaine et al., 2007; Don et al., 2013), its role under actual field conditions is more difficult to establish. However, a simple extrapolation from these experimental findings to field conditions would make it likely that it could play an important stimulatory role in the field as well. Topsoils receive the greatest share of fresh C inputs and can thereby develop the conditions that favour decomposition of older C as well. In contrast, fresh C inputs at depth are sparse, thus providing no stimulation of biological activity through fresh C inputs. Calvelo Pereira et al. (2018), for example, reported a 100-fold difference in root C inputs between the 0–5 cm and 25–30 cm layers under a permanent sheep pasture. Consequently, some researchers (e.g. Fontaine et al., 2007; Hicks Pries et al., 2018) have attributed the stability of C in subsoils to the lack of such fresh C inputs.

Because of a scarcity of empirical observations, it is not known how decomposition rates at depth might respond to intermediate supplies of labile carbon. In particular, it is not known what root density might be sufficient to provide enough labile C for the eventual loss of stable C. Would a small amount of C influx from root exudates or root decay have a positive or negative effect on SOC at depth? Would a small C addition add to C stocks at depth, or would the addition of labile root C add as a catalyst to lead to a greater loss of resistant C than the amount added through C turn-over? We do not know the answers to those questions, but they would have a strong bearing on the usefulness of adding C to the subsoil through deep-rooted plant species. This would also be important for determining the depth required for full-inversion tillage to prevent C gains to be lost over time through the influence of any labile-C inputs from roots.

4.4. The use of full-inversion tillage

If future research can demonstrate that a lack of priming operates as a general mechanism to inhibit SOC decomposition at depth, fullinversion tillage could be used as a general mechanism for enhancing SOC storage irrespective of the properties or conditions of specific sites or soils. C storage at depth would also remain fairly secure with C only becoming vulnerable if new fresh C sources reached the stored C at depth. This would not normally happen unless the soil were inverted again, but we would need to better understand whether small C additions through dissolved DOC or some root growth could provide enough labile carbon for priming the decomposition of more resistant C. Fullinversion tillage could, then become a practical management option to enhance soil C stocks to make a significant contribution to climatechange mitigation on grasslands. If full-inversion tillage can be applied more widely, it could result in substantial extra C storage. For New Zealand alone, Lawrence-Smith et al. (2021) identified 2.6 Mha of pastoral soils as suitable for full-inversion tillage and estimated, using fairly conservative assumptions, that this could sequester an additional 36 MtC (0.7 tC ha⁻¹ yr⁻¹) over 20 years.

However, additional factors need to be considered before advocating wide-spread adoption of full-inversion tillage. It would be likely to be more beneficial in cold and wet locations where temperature variations (Fig. 2) and possible O₂ limitations through water logging (Fig. 5) could contribute to the overall benefit. There is still only little known about priming in normal soils under natural conditions, and it is not known under what conditions it might play a greater or lesser role in enhancing C storage at depth. For practical operational reasons, full inversion tillage will also be limited to reasonably flat sites with low to moderate stone content and of sufficient depth to bed rock to allow meaningful inversion may also depend on soil type and the extent of vertical stratification of SOC in different soils (Hedley et al., 2020; Lawrence-Smith et al., 2021).

The overall usefulness of full-inversion tillage as a negative greenhouse gas emission technology for grasslands must also consider associated fossil-fuel emissions from the use of farm machinery for ploughing the soil and any net changes in herbage production. Analysis of the factors from the initial trials have been promising, with relatively minor additional production costs and greenhouse gas emissions from farm machinery. Herbage production was even increased in most studies to add to the overall benefits of full-inversion tillage (Beare et al., 2020; Calvelo Pereira et al., 2020).

An assessment of overall greenhouse gas benefits must also consider any potential changes in methane or nitrous oxide fluxes following fullinversion tillage. McNally et al. (2020) reported that N₂O emissions from livestock urine were reduced by up to 56% over the first 1-2 years following full-inversion tillage at two different experimental sites compared to permanent pasture (Control) plots. Calvelo Pereira et al. (2020) similarly observed reduced nitrate leaching following full-inversion tillage, particularly where a forage crop was grown as a break between old and new pastures to encourage high plant uptake of mineralised nitrogen (Malcolm et al., 2019). Provided there is timely inclusion of a crop phase, spring pasture renewal with full inversion tillage can then provide additional agronomic (higher yields of quality summer forage) and environmental (reduced N leaching) benefits (Calvelo Pereira et al., 2020). The development of appropriate site-specific agronomic practices is, therefore, critical for maximising the potential benefits of full-inversion tillage and minimising potential risks. As long as appropriate protocols are being followed, work to date suggests there is good potential for full-inversion tillage to contribute to reductions of net greenhouse emissions during pasture renewal.

Declaration of competing interest

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

- Ågren, G.I., Axelsson, B., 1980. Population respiration: a theoretical approach. Ecological Modelling 11, 39–54.
- Alcantara, V., Don, A., Well, R., Nieder, R., 2016. Deep ploughing increases agricultural soil organic matter stocks. Global Change Biology 22, 2939–2956.
- Beare, M., McNally, S., Calvelo Pereira, R., Tregurtha, C., Gillespie, R., van der Klei, G., Hedley, M., 2020. The agronomic and environmental benefits and risks of autumn pasture renewal with full inversion tillage. In: Christensen, C.L., Horne, D.J., Singh, R. (Eds.), Nutrient Management in Farmed Landscapes. Occasional Report No. 33. Farmed Landscapes Research Centre, Massey University, Palmerston North, New Zealand, p. 6.
- Calvelo Pereira, R.C., Hedley, M.J., Arbestain, M.C., Bishop, P., Enongene, K.E., Otene, I. J.J., 2018. Evidence for soil carbon enhancement through deeper mouldboard ploughing at pasture renovation on a Typic Fragiaqualf. Soil Research 56, 182–191.
- Calvelo Pereira, R., Hedley, M.J., Hanly, J., Osborne, M., McNally, S.R., Beare, M.H., 2020. The agronomic and environmental benefits and risks of spring pasture renewal with full inversion tillage. In: Christensen, C.L., Horne, D.J., Singh, R. (Eds.), Nutrient Management in Farmed Landscapes. Occasional Report No. 33. Farmed Landscapes Research Centre, Massey University, Palmerston North, New Zealand, p. 9.
- Cook, F.J., 1995. One-dimensional oxygen diffusion into soil with exponential
- respiration analytical and numerical-solutions. Ecological Modelling 78, 277–283. Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as
- independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biology 4, 217–227. Dignac, M.F., Derrien, D., Barre, P., Barot, S., Cecillon, L., Chenu, C., Chevallier, T.,
- Freschet, G.T., Garnier, P., Guenet, B., Hedde, M., Klumpp, K., Lashermes, G., Maron, P.A., Nunan, N., Roumet, C., Basile-Doelsch, I., 2017. Increasing soil carbon storage: mechanisms, effects of agricultural practices and proxies. A review. Agronomy for Sustainable Development 37. Article #14.
- Don, A., Rebmann, C., Kolle, O., Scherer-Lorenzen, M., Schulze, E.D., 2009. Impact of afforestation-associated management changes on the carbon balance of grassland. Global Change Biology 15, 1990–2002.
- Don, A., Rodenbeck, C., Gleixner, G., 2013. Unexpected control of soil carbon turnover by soil carbon concentration. Environmental Chemistry Letters 11, 407–413.
- Ekschmitt, K., Liu, M., Vettera, S., Fox, O., Wolters, V., 2005. Strategies used by soil biota to overcome soil organic matter stability — why is dead organic matter left over in the soil? Geoderma 128, 167–176.
- Fontaine, S., Barot, S., 2005. Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. Ecology Letters 8, 1075–1087.
- Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450, 277–280.
- Fukao, T., Bailey-Serres, J., 2004. Plant responses to hypoxia is survival a balancing act? Plant Science 9, 449–456.
- Graf, A., Weihermüller, L., Huisman, J.A., Herbst, M., Bauer, J., Vereecken, H., 2008. Measurement depth effects on the apparent temperature sensitivity of soil respiration in field studies. Biogeosciences 5, 1175–1188.
- Hedley, M.J., Beare, M.H., Calvelo Pereira, R., McNally, S.R., Lawrence-Smith, E.J., Tregurtha, C.S., Osborne, M.A., Gillespie, R.N., Van der Klei, G., Thomas, S.M., 2020. Where, when and how - practise guidelines for successful introduction of full inversion tillage to increase soil carbon stocks under pasture. In: Christensen, C.L., Horne, D.J., Singh, R. (Eds.), Nutrient Management in Farmed Landscapes. Occasional Report No. 33. Farmed Landscapes Research Centre, Massey University, Palmerston North, New Zealand, p. 9.
- Hicks Pries, C.E., Sulman, B.N., West, C., O'Neill, C., Poppleton, E., Porras, R.C., Castanha, C., Zhu, B., Wiedemeier, D.B., Torn, M.S., 2018. Root litter decomposition slows with soil depth. Soil Biology and Biochemistry 125, 103–114.
 Huang, W.J., Ye, C.L., Hockaday, W.C., Hall, S.J., 2020. Trade-offs in soil carbon
- Huang, W.J., Ye, C.L., Hockaday, W.C., Hall, S.J., 2020. Trade-offs in soil carbon protection mechanisms under aerobic and anaerobic conditions. Global Change Biology 26, 3726–3737.

The authors declare that they have no known competing financial

- Jenkinson, D.S., Rayner, J.H., 1977. Turnover of soil organic-matter in some of Rothamsted classical experiments. Soil Science 123, 298–305.
- Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436.
- Kirschbaum, M.U.F., 2000. Will changes in soil organic matter act as a positive or negative feedback on global warming? Biogeochemistry 48, 21–51.
- Kirschbaum, M.U.F., 2010. The temperature dependence of organic matter decomposition: seasonal temperature variations turn a sharp short-term temperature response into a more moderate annually-averaged response. Global Change Biology 16, 2117–2129.
- Kirschbaum, M.U.F., Paul, K.I., 2002. Modelling carbon and nitrogen dynamics in forest soils with a modified version of the CENTURY model. Soil Biology and Biochemistry 34, 341–354.
- Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., Nico, P.S., 2015. Mineral-organic associations: formation, properties, and relevance in soil environments. Advances in Agronomy 130, 1–140.
- Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., Leinweber, P., 2008. Organo-mineral associations in temperate soils: integrating biology, mineralogy, and organic matter chemistry. Journal of Plant Nutrition and Soil Science 171, 61–82.
- Kuhry, P., Vitt, D.H., 1996. Fossil carbon/nitrogen ratios as a measure of peat decomposition. Ecology 77, 271–275.
- Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. Soil Biology and Biochemistry 42, 1363–1371.
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry 32, 1485–1498.
- LaRowe, D.E., Van Cappellen, P., 2011. Degradation of natural organic matter: a thermodynamic analysis. Geochimica et Cosmochimica Acta 75, 2030–2042.
- Lawrence-Smith, E.J., Curtin, D., Beare, M.H., McNally, S.R., Kelliher, F.M., Calvelo Pereira, R., Hedley, M.J., 2021. Full inversion tillage during pasture renewal to increase soil carbon storage: a New Zealand case study. Global Change Biology 27, 1998–2010.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315–323.
- Malcolm, B.J., de Ruiter, J.M., Dalley, D.E., Carrick, S., Waugh, D., Arnold, N.P., Dellow, S.J., Beare, M.H., Johnstone, P.R., Wholer, M., Brown, H., Welten, B., Horrocks, A.J., 2019. Catch crops and feeding strategy can reduce the risk of nitrogen leaching in late lactation fodder beet systems. New Zealand Journal of Agricultural Research.
- Mathieu, J.A., Hatté, C., Balesdent, J., Parent, É., 2015. Deep soil carbon dynamics are driven more by soil type than by climate: a worldwide meta-analysis of radiocarbon profiles. Global Change Biology 21, 4278–4292.
- McNally, S.R., van der Klei, G., Calvelo Pereira, R., Thomas, S., Beare, M.H., Hedley, M. J., 2020. Nitrous oxide emissions from fertiliser and urine following full inversion tillage autumn pasture renewal. In: Christensen, C.L., Horne, D.J., Singh, R. (Eds.), Nutrient Management in Farmed Landscapes. Occasional Report No. 33. Farmed Landscapes Research Centre, Massey University, Palmerston North, New Zealand, p. 9.
- Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biology and Biochemistry 59, 72–85.
- Moyano, F.E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Yuste, J.C., Don, A., Epron, D., Formanek, P., Franzluebbers, A., Ilstedt, U., Kätterer, T., Orchard, V., Reichstein, M., Rey, A., Ruamps, L., Subke, J.A., Thomsen, I.K., Chenu, C., 2012. The moisture response of soil heterotrophic respiration: interaction with soil properties. Biogeosciences 9, 1173–1182.
- Nakamura, M., Noguchi, K., 2020. Tolerant mechanisms to O₂ deficiency under submergence conditions in plants. Journal of Plant Research 133, 343–371.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models. Part I: a discussion of principles. Journal of Hydrology 10, 282–290.
- Neira, J., Ortiz, M., Morales, L., Acevedo, E., 2015. Oxygen diffusion in soils: understanding the factors and processes needed for modelling. Chilean Journal of Agricultural Research 75, 35–44.
- Newey, A., 2005. Decomposition of Plant Litter and Carbon Turnover as a Function of Soil Depth. Australian National University, p. 203. Ph.D. thesis.

- Owens, J., Clough, T.J., Laubach, J., Hunt, J.E., Venterea, R.T., Phillips, R.L., 2016. Nitrous oxide fluxes, soil oxygen, and denitrification potential of urine- and nonurine-treated soil under different irrigation frequencies. Journal of Environmental Quality 45, 1169–1177.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic-matter levels in great-plains grasslands. Soil Science Society of America Journal 51, 1173–1179.
- Paul, K.I., Polglase, P.J., Smethurst, P.J., O'Connell, A.M., Carlyle, C.J., Khanna, P.K., 2004. Soil temperature under forests: a simple model for predicting soil temperature under a range of forest types. Agricultural and Forest Meteorology 121, 167–182.
- Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G.P., Smith, P., 2016. Climatesmart soils. Nature 532, 49–57.
- Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Global Change Biology 8, 851–866.
- Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter-a key but poorly understood component of terrestrial C cycle. Plant and Soil 338, 143–158.
- Schiedung, M., Tregurtha, C.S., Beare, M.H., Thomas, S.M., Don, A., 2019. Deep soil flipping increases carbon stocks of New Zealand grasslands. Global Change Biology 25, 2296–2309.
- Shi, Z., Allison, S.D., He, Y.J., Levine, P.A., Hoyt, A.M., Beem-Miller, J., Zhu, Q., Wieder, W.R., Trumbore, S., Randerson, J.T., 2020. The age distribution of global soil carbon inferred from radiocarbon measurements. Nature Geoscience 13, 555–559.
- Silver, W.L., Lugo, A.E., Keller, M., 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44, 301–328.
- Smerdon, J.E., Pollack, H.N., Enz, J.W., Lewis, M.J., 2003. Conduction-dominated heat transport of the annual temperature signal in soil. Journal of Geophysical Research -Solid Earth 108. Article #2431.
- Smith, P., 2016. Soil carbon sequestration and biochar as negative emission technologies. Global Change Biology 22, 1315–1324.
- Solly, E.F., Schöning, I., Herold, N., Trumbore, S.E., Schrumpf, M., 2015. No depthdependence of fine root litter decomposition in temperate beech forest soils. Plant and Soil 393, 273–282.
- Song, X.T., Ju, X.T., Topp, C.F.E., Rees, R.M., 2019. Oxygen regulates nitrous oxide production directly in agricultural soils. Environmental Science & Technology 53, 12539–12547.
- Tambone, F., Adani, F., Gigliotti, G., Volpe, D., Fabbri, C., Provenzano, M.R., 2013. Organic matter characterization during the anaerobic digestion of different biomasses by means of CPMAS ¹³C NMR spectroscopy. Biomass and Bioenergy 48, 111–120.
- Tarnawski, V.R., McCombie, M.L., Leong, W.H., Wagner, B., Momose, T., Schönenberger, J., 2012. Canadian field soils II. Modeling of quartz occurrence. International Journal of Thermophysics 33, 843–863.
- Thomsen, I.K., Kruse, T., Bruun, S., Kristiansen, S.M., Knicker, H., Petersen, S.O., Jensen, L.S., Holst, M.K., Christensen, B.T., 2008. Characteristics of soil carbon buried for 3300 years in a bronze age burial mound. Soil Science Society of America Journal 72, 1292–1298.
- Tomczyk, N.J., Rosemond, A.D., Bumpers, P.M., Cummins, C.S., Wenger, S.J., Benstead, J.P., 2020. Ignoring temperature variation leads to underestimation of the temperature sensitivity of plant litter decomposition. Ecosphere 11. Article# e03050.
- Vos, C., Reinsch, T., Schneider, F., Don, A., 2020. Does Grassland Renovation Increase Soil Organic Carbon Stocks? Results of a Long-Term Experiment. Report by the Thünen Institute of Climate-Smart Agriculture, Braunschweig, Germany, p. 29.
- Whitehead, D., Schipper, L.A., Pronger, J., Moinet, G.Y.K., Mudge, P.L., Pereira, R.C., Kirschbaum, M.U.F., McNally, S.R., Beare, M.H., Camps-Arbestain, M., 2018. Management practices to reduce losses or increase soil carbon stocks in temperate grazed grasslands: New Zealand as a case study. Agriculture, Ecosystems & Environment 265, 432–443.
- Wordell-Dietrich, P., Don, A., Helfrich, M., 2017. Controlling factors for the stability of subsoil carbon in a Dystric Cambisol. Geoderma 304, 40–48.
- Wutzler, T., Reichstein, M., 2013. Priming and substrate quality interactions in soil organic matter models. Biogeosciences 10, 2089–2103.