RESEARCH REVIEW

Mechanisms of soil organic carbon stability and its response to no-till: A global synthesis and perspective

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Abstract

Mechanisms of soil organic carbon (SOC) stabilization have been widely studied due to their relevance in the global carbon cycle. No-till (NT) has been frequently adopted to sequester SOC; however, limited information is available regarding whether sequestered SOC will be stabilized for long term. Thus, we reviewed the mechanisms affecting SOC stability in NT systems, including the priming effects (PE), molecular structure of SOC, aggregate protection, association with soil minerals, microbial properties, and environmental effects. Although a more steady-state molecular structure of SOC is observed in NT compared with conventional tillage (CT), SOC stability may depend more on physical and chemical protection. On average, NT improves macro-aggregation by 32.7%, and lowers SOC mineralization in macro-aggregates compared with CT. Chemical protection is also important due to the direct adsorption of organic molecules and the enhancement of aggregation by soil minerals. Higher microbial activity in NT could also produce binding agents to promote aggregation and the formation of metal-oxidant organic complexes. Thus, microbial residues could be stabilized in soils over the long term through their attachment to mineral surfaces and entrapment of aggregates under NT. On average, NT reduces SOC mineralization by 18.8% and PE intensities after fresh carbon inputs by 21.0% compared with CT ($p < .05$). Although higher temperature sensitivity (Q_{10}) is observed in NT due to greater Q_{10} in macro-aggregates, an increase of soil moisture regime in NT could potentially constrain the improvement of Q_{10}. This review improves process-based understanding of the physical and chemical mechanism of protection that can act, independently or interactively, to enhance SOC preservation. It is concluded that SOC sequestered in NT systems is likely to be stabilized over the long term.

KEYWORDS
microbial activity, physicochemical protection, priming effects, soil organic matter, soil structure, tillage practices

1 | INTRODUCTION

Mitigation to climate change due to the ever-increasing greenhouse gas (GHG) emissions is a challenging global issue (van Groenigen et al., 2011). Carbon (C) contained in soils to 1 m depth is about three times as much as in the atmosphere. Thus, even a small proportion of soil organic C (SOC) could induce quantitatively relevant variations in atmospheric carbon dioxide (CO_2) and generate positive feedbacks to climate change (Lal, 2004a). Furthermore, SOC plays a key role in determining soil health and agricultural productivity

(Lehmann & Kleber, 2015). Therefore, improving SOC sequestration is an important goal for both scientists and policymakers.

In agro-ecosystem, SOC is sensitive to changes in climate and management practices (e.g., tillage, irrigation, and fertilizer), and thus it is not stable but has high temporal and spatial variabilities (Qi et al., 2019; Xue et al., 2018). For example, higher temporal variation was observed in conventional tillage (CT), with 12.1%–35.3% lower SOC content compared with that under no-till (NT) (Qi et al., 2019). Fertilizer application changed the contributions of wheat and maize to SOC, and caused a spatial variability in wheat–maize cropping systems (Shi et al., 2017; Wang et al., 2015). Nitrogen fertilizer alone could be sufficient to allow maintenance but not build-up of SOC compared with unfertilized soil because mineral fertilizer application increased SOC mineralization rate in aggregates (Collier et al., 2017; Yu et al., 2012). Thus, understanding the processes of SOC stability is crucial to enhancing SOC sequestration.

In the initial stages, more C inputs improve SOC levels during the rapid accumulation stage from time ($T0$) to time ($T1$) (Figure 1). However, no positive linear relationship exists between SOC gained and additional C inputs over time as the soil will eventually become saturated and unable to hold any further SOC (Berhane et al., 2020). This is responsible for the slow fluctuation in SOC content from time ($T1$) to time ($T4$). During the slow fluctuation phase, a recycling process is observed from time ($T1$) to time ($T2$), time ($T2$) to time ($T3$), time ($T3$) to time ($T4$), etc. This trend indicates that SOC saturation is associated with SOC stability, and leads to the prediction that SOC level in the future will be maintained around the saturation point in the topsoil and subsoil layers (Six et al., 2002; Stewart et al., 2007; Zhao et al., 2015). In general, the saturation point in paddy soils is higher than that in upland soils due to the lower decomposition under
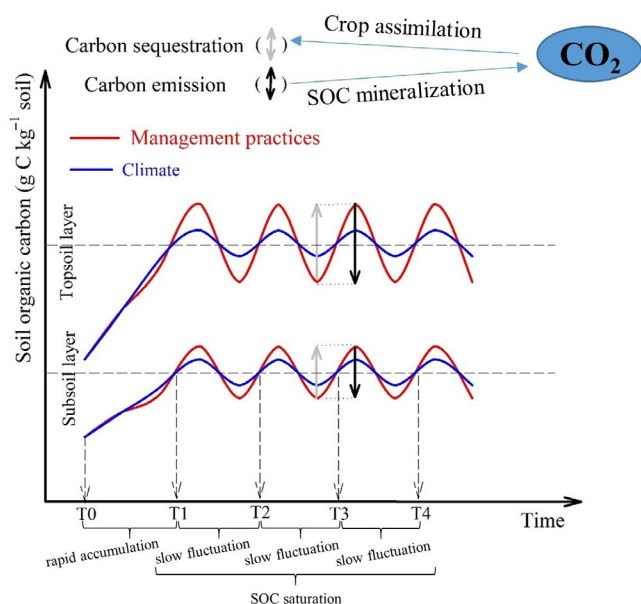
waterlogged condition, and thus the greater capacity for SOC sequestration in paddy soils (Wei et al., 2021). However, the saturation point is also affected by management practices and climate (Qi et al., 2019; Stewart et al., 2007), which causes temporal and spatial fluctuation in SOC stocks. Temporal and spatial fluctuation can cause temporary net SOC loss, which must subsequently be recovered by more C inputs (Qi et al., 2019; Yang et al., 2020). Thus, maintaining the stability (stabilization) of SOC, as important as achieving high SOC, is critical to sustaining the agricultural and environmental benefits of SOC sequestration (Qi et al., 2019). This issue is receiving increasing research attention (Angst et al., 2019; Bai et al., 2020; Mu et al., 2020).

SOC stability and stabilization are both defined as the tendency of SOC to resist loss (Ives & Carpenter, 2007; Yang et al., 2020). SOC stability raises the question of whether it could persist for a long term, and tends to show the change of SOC at a certain moment or period, highlighting the results of SOC stabilization (Angst et al., 2019; Mu et al., 2020). However, SOC stabilization necessitates the understanding of diverse factors influencing its stability comprehensively, such as soil physical, chemical, and biological properties (Plaza et al., 2013). It describes the state of the whole soil-environment system when SOC stabilization is achieved and underscores the entire process of SOC stabilization (Poeplau et al., 2017; von Lützow et al., 2008). The SOC accumulation depends on SOC stability in the long term, while increased SOC levels could maintain the SOC stability because higher SOC contributed to building an eco-enzymatic system in stable C pools (Dai et al., 2017; Menichetti et al., 2015). However, these processes are also regulated by climate and management practices (Reichstein et al., 2013; Xue et al., 2018). Thus, it is not sure whether high SOC content can also enhance its stability.

McCann (2000) summarized SOC stability, as an ecosystem property, which can be viewed from two perspectives: resistance (capacity to resist perturbation) and resilience (capacity to recover from the perturbation). However, previous studies have primarily focused on perturbation from natural disturbance (Chen et al., 2021; Mccann, 2000; Schmidt et al., 2011; Yang et al., 2020). Agricultural soils contain 25%–75% less SOC than undisturbed or natural soils (Lal, 2004b), indicating a large potential for SOC accumulation. However, there is a lack of a strong generalizable understanding of the mechanisms of SOC stability under different agricultural management practices. Yet, improved knowledge is crucial to strengthening predictions of SOC cycle feedbacks to climate change.

In agro-ecosystem, management practices (e.g., tillage, irrigation, and fertilizer) strongly influence physical, chemical, biological, and environmental events that cause successional upset, stress, and disturbance to systems (Yang et al., 2020). Whether SOC can resist these changes and persist in soils is critical to understanding SOC dynamics in agricultural systems (Schmidt et al., 2011). Current thinking suggests that SOC persistence depends not only on the intrinsic properties of the SOC itself, but also on physicochemical and biological effects that lower the probability of its decomposition (Plaza et al., 2013). Building a conceptual framework integrating these factors affecting SOC stability (e.g., physical, chemical, biological, and environmental factors) is

FIGURE 1 Schematic diagram of carbon sequestration and emission (loss) during the processes of soil organic carbon stability (Qi et al., 2019; Yang et al., 2020) [Colour figure can be viewed at wileyonlinelibrary.com]

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important to enhance the prediction of SOC responses to changes in climate and management practices.

It is widely recognized that SOC in the surface soil has lower levels of stability compared with that in the subsoil (Fontaine et al., 2007), and thus it is important to adopt management practices that enhance the stability of SOC in surface soils. One practice that has shown the potential to increase SOC stability in the surface soil is conservation agriculture (CA). It is estimated that 9%–15% of global arable land is currently managed using CA systems, or aspects of CA practice, for example, NT (Kassam et al., 2019; Prestele et al., 2018). Previous studies have primarily focused on the changes in SOC accumulation under NT, but SOC stock is dynamic and SOC stability is a major determinant of the capacity of a soil to sequester atmospheric CO_2 (Poeplau et al., 2018). Greater SOC stability indicates a lower turnover and higher residence time of SOC (Dungait et al., 2012). Understanding the mechanism of SOC stability under NT helps to predict SOC dynamics under changing environments. Nonetheless, limited information is available about the mechanisms of SOC stability under NT. Thus, the objectives of this review are to identify (i) the factors that affect SOC stability, (ii) the mechanisms which stabilize SOC under NT, and (iii) whether the SOC under NT is likely to be preserved in soils over the long term.

2 | FACTORS AFFECTING SOC STABILITY

SOC comprises a range of organic compounds of various molecular sizes and degrees of decomposition that interact with their surroundings (Lehmann & Kleber, 2015). The SOC pools can be divided into different pools that are defined functionally according to their ability to resist mineralization and persist in the soil, with distinct turnover rates for each pool (Zimmermann et al., 2007). Functional systems typically class SOC as labile, slow, and resistant pools based on their turnover time. It is assumed that the labile SOC pool is composed mainly of chemically labile and unprotected compounds and persists for several hours to months. The slow and resistant (stable) SOC pools persist for decades to centuries (Qin et al., 2019). Parton et al. (1987) defined labile SOC as having a mean residence time (MRT) of ~1–5 years, slow SOC as having a MRT of ~20–40 years, and resistant SOC as having a MRT of ~200–1500 years.

Several factors contribute to SOC stability and its MRT (Don et al., 2013; Plaza et al., 2013). For example, SOC accumulation is the balance between C input from plant biomass and C loss from SOC mineralization associated with the stabilization and destabilization processes (Crowther et al., 2016). It is expected that increased assimilation of C by crops will increase C inputs and SOC accumulation, and potentially reduce the increase in atmospheric CO_2 (Dignac et al., 2017). However, fresh C inputs may also increase the existing SOC mineralization and release SOC-derived CO_2, via a phenomenon known as the "priming effect (PE)" (Kuzyakov et al., 2000). Indeed, it has been estimated that, worldwide, positive PE intensities have decreased SOC accumulation by 51% from 1901 to 2010 by increasing native SOC mineralization rates (Guenet et al., 2018).

The C input from crop residues is also one of the most influential factors regulating the chemical composition of organic materials in agricultural soils (He et al., 2018). The decomposition of crop residues initially correlates with its bulk chemical composition, for example, the C:N ratio, lignin, and cellulose contents (Schmidt et al., 2011). Accordingly, the molecular structure of SOC has long been thought to determine SOC mineralization rates and has been regarded as an important factor regulating SOC stability. Indeed. complex chemical molecular characteristics (e.g., aromatic, aliphatic, alkylaryl, and biaryl bonds) can slow SOC decomposition (Yang et al., 2020).

In addition to molecular structure, physical protection of organic material within soil aggregates and the chemical absorption of organic molecules by soil minerals (chemical protection) are also important to SOC stability (Angst et al., 2021; Gao, Wang, Li, Wu, et al., 2019; Zhang et al., 2017). Dead crop material converted into organic products can form intimate associations with soil aggregates and soil minerals through physicochemical and biological transformation (Lehmann & Kleber, 2015; Miller et al., 2019). Soil aggregates are a vital physical property, and nearly 90% of SOC in topsoil exists in aggregates (Jastrow, 1996), which are usually divided into different size classes with different stability (Devine et al., 2014; Modak et al., 2020; Razafimbelo et al., 2008; Six, Bossuyt, et al., 2004; Zhang, Zhu et al., 2018). Miller et al. (2019) concluded that, besides occlusion within soil aggregates, chemical protection through association with soil minerals also determines SOC stability. Thus, interest in SOC stability, mineral-mediated chemical stabilization, has increased considerably in recent years (Patzner et al., 2020). Chemical protection (stabilization) is associated with soil clay content, as well as iron (Fe) and aluminum (Al) oxides, which can trap or adsorb SOC and reduce the degrading capacity of decomposers (Chen et al., 2021). Compared to soil microbial properties and crop growth, physicochemical protection explains more variance in the SOC stability (Chen et al., 2019). However, microbial properties are also important, because microbial activity directly drives the SOC mineralization (Blagodatskaya & Kuzyakov, 2008; Fang et al., 2018), and influences aggregate formation and adsorption by minerals (Six et al., 2002).

SOC dynamics is a function of climate, and particularly the interplay between temperature and moisture regimes (González-Domínguez et al., 2019). Schmidt et al. (2011) indicated that environmental conditions can affect the probability of SOC decomposition and SOC persistence. Warming impacts SOC stability and sequestration because SOC mineralization is temperature dependent (Melillo et al., 2002). Thus, the indicator called "temperature sensitivity (Q_{10})" (the increase in SOC mineralization for every 10 degrees increase in temperature) can be used to predict the fate of SOC under global warming. Lefèvre et al. (2014) reported a general relationship between Q_{10} and SOC stability, with a higher Q_{10} observed for stable compared to labile SOC pools. Labile SOC increases soil microbial activity and macro-aggregate formation under NT, which, in turn, protects the labile C from microbial attack by encapsulation and occlusion (Kan, Ma, et al., 2020; Six, Bossuyt, et al., 2004). Furthermore, stable SOC is as vulnerable to PE as is more labile SOC (Guenet et al., 2012). Thus, labile SOC may not be always

labile, and stable may not be persistently stable. Soil moisture, influenced by climate changes under global warming, regulates the microbial activity and substrate availability for microbial utilization, and thus affects the microbial acclimation to warming and SOC stability (Wang et al., 2006). Hao et al. (2016) and Kan, He, et al. (2020) reported that SOC mineralization rates increased with the increase in soil moisture contents. However, Sun et al. (2016) argued that SOC mineralization was the lowest when the soil moisture regime was at the middle level. Thus, the relationship between soil moisture and SOC stability is unclear, and limited information exists about the interaction effects of temperature and moisture on SOC stability.

In summary, SOC stability is determined by six mechanisms: (1) priming effects after inputs of fresh carbon; (2) molecular structure of SOC compound; (3) physical protection by aggregates; (4) chemical protection through association with soil minerals; (5) microbial properties; and (6) environmental effects (Figure 2). The present study is based on the hypothesis that these six factors govern the SOC stability and preservation independently and interactively.

3 | SOC MINERALIZATION AND ACCUMULATION UNDER NT

The measurement of SOC mineralization rates via laboratory incubation not only reflects the potential of SOC loss, but also correlates with soil physicochemical and biological characteristics, which are widely used to evaluate SOC stability (Balota et al., 2004; Das et al., 2019; Fu et al., 2012; Guo et al., 2016; Jacobs et al., 2010; Kabiri et al., 2016; Kan, Virk, et al., 2020; Liang et al., 2003; Lu et al., 2014; Whitman et al., 2014; Zhang et al., 2010). In general, labile SOC is accessible for microbial decomposition and is depleted faster than recalcitrant SOC over the incubation period (Das et al., 2019; Wei et al., 2019). Thus, laboratory incubation is an effective approach to assess SOC stability and identify factors impacting SOC mineralization and stability.

A global literature review has thus been conducted to examine the SOC mineralization under NT as compared with CT. Overall, the studies were those implemented on a long-term basis (20 years on average). In general, lower mineralization was observed in NT compared with CT in most studies (35 out of 49) (Autret et al., 2020; Kan et al., 2021; Kan, Ma, et al., 2020; Kan, Virk, et al., 2020; Qi et al., 2019; Raiesi & Kabiri, 2017; Sarker, Singh, Cowie, et al., 2018; Sarker, Singh, Dougherty, et al., 2018; Sarker et al., 2019; Watts et al., 2010) (Table 1), although several studies also observed a higher mineralization rate under NT (Dimassi et al., 2014; Fernández et al., 2010; Oorts et al., 2006; Vazquez et al., 2019). On average, SOC mineralization in NT of 33.53 g C kg^{-1} SOC is 18.8% lower than that under CT ($p = .002$; paired t-test) (Figure 3a). Furthermore, a negative correlation exists between SOC mineralization and SOC content in NT ($R^2 = .15$, $p = .006$) and CT ($R^2 = .21$, $p = .001$) (Figure 3c), indicating that lower SOC mineralization is associated with the increase in SOC accumulation. A quadratic relationship is observed between SOC mineralization of NT/CT and SOC content of NT/CT, but most of the data points are in the first quadrant (Figure 4). This trend indicates that lower mineralization but higher SOC content occurs in NT compared with CT. On average, SOC content in NT of 18.96 g kg^{-1} is 19.9% higher than that under CT for the upper soil layer ($p < .001$; paired t-test) (Figure 3b). Thus, it is concluded that NT reduces SOC mineralization, which contributes to the SOC accumulation in upper soil depth. It can also be hypothesized that the reduction in mineralization is due to the enhanced stability of SOC in NT systems.

These results are similar to a number of other studies examining differences in SOC between NT and CT systems at both global and regional scales (Table 2). A global meta-analysis showed that NT could improve SOC stock by 4.90 Mg ha^{-1} at 0–30 cm depth, with a sequestration rate of 0.57 Mg C ha^{-1} year^{-1} (Angers & Eriksen-Hamel, 2008; West & Marland, 2002). Similar findings were also reported by Virto et al. (2012). However, Luo et al. (2010) argued that NT only improved SOC stock at 0–10 cm depth by 3.15 Mg ha^{-1}, and decreased SOC stock by 3.30 Mg ha^{-1} compared with CT for 20–40 cm depth. Thus, no
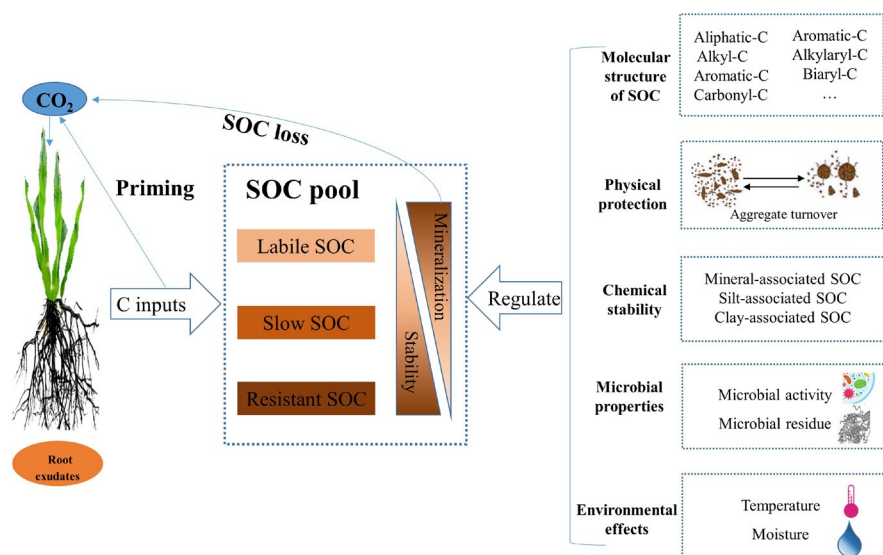

FIGURE 2 Factors affecting soil organic carbon stability and mineralization and their relationship (Chen et al., 2021; Kan, He, et al., 2020; Kuzyakov et al., 2000; Schmidt et al., 2011; Six, Bossuyt, et al., 2004; Yang et al., 2020) [Colour figure can be viewed at wileyonlinelibrary.com]

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significant difference was observed between NT and CT for 0–40 cm depth. Using meta-analysis for China, Du et al. (2017) suggested that NT improved SOC stock at 0–20 cm depth and no change at >30 cm depth. Zhao et al. (2015) reported that NT improved SOC stock at 0–10 cm depth, and improvement could be enhanced when NT is combined with residue retention (RR) compared with CT without RR.

4 | SOC STABILITY UNDER NT

Many studies have reported that NT has the potential to offset some of the anthropogenic emissions of CO_2 through SOC sequestration in upper soil layers. However, limited information is available regarding whether the accumulated SOC under NT would be sequestered for a long time horizon. Thus, we discuss how NT influences SOC stabilization using the mechanisms identified in Section 2 above.

4.1 | Priming effects

The combination of NT with RR has been widely reported to improve SOC accumulation (Dikgwatlhe et al., 2014; Zhao et al., 2020). Nonetheless, RR may also increase SOC mineralization and accelerate SOC loss if it induces a positive PE, and thus the rate of SOC sequestration under NT may not remain constant (Heitkamp et al., 2012; Shahbaz et al., 2017). Greater understanding is required of

TABLE 1 Literatures of SOC mineralization and contents under NT and CT

Country	Experiment duration (years)	Soil depth (cm)	Cumulative SOC mineralization (g CO_2-C kg^{-1} SOC)		SOC content (g kg^{-1})		Note	Reference
			NT	CT	NT	CT		
America	14	0–5	84.23	95.22	11.10	9.00		Watts et al. (2010)
Argentina	14	0–18	17.01	16.00	7.70	6.50		Fernández et al. (2010)
Australia	16	0–10	12.77	17.87	11.90	12.90	2–6.5 mm AS	Sarker, Singh, Cowie, et al. (2018)
	16	0–10	19.79	30.00	12.80	12.80	0.25–2 mm AS	
	16	0–10	14.68	24.26	13.60	14.50	<0.25 mm AS	
	46	0–10	13.33	15.24	20.40	20.70	2–6.5 mm AS	
	46	0–10	25.40	26.03	20.60	21.60	0.25–2 mm AS	
	46	0–10	23.49	24.13	20.60	21.70	<0.25 mm AS	
	16	0–10	16.00	20.00	11.90	12.60		Sarker, Singh, Dougherty, et al. (2018)
	46	0–10	15.20	13.80	17.70	17.75	Stubble burnt 0N	
	46	0–10	17.30	14.00	20.75	19.57	Stubble burnt 90N	
	46	0–10	16.40	20.60	18.54	19.13	Stubble retention 0N	
	46	0–10	18.70	20.20	19.52	20.30	Stubble retention 90N	
	16	0–10	14.70	19.10	18.90	17.60		Sarker et al. (2019)
	46	0–10	17.90	19.60	23.20	22.40		
Brazil	22	0–50	7.57	5.18	20.60	15.30	Soybean–Wheat	Balota et al. (2004)
	22	0–50	3.11	4.90	22.40	14.70	Maize–Wheat	
	22	0–50	2.33	3.45	20.60	13.90	Cotton–Wheat	
Canada	24	0–10	10.56	6.12	29.50	21.50	1–2 mm AS	Zhang et al. (2010)
	24	0–10	11.90	10.12	24.70	20.80	0.25–0.5 mm AS	
	16	0–7.5	6.09	7.04	32.53	29.27		Liang et al. (2003)
	25	0–7.5	5.04	3.39	37.14	33.33		
	8	0–7.5	15.23	14.45	23.83	20.27		

(Continues)

TABLE 1 (Continued)

Country	Experiment duration (years)	Soil depth (cm)	Cumulative SOC mineralization (g CO_2-C kg^{-1} SOC)		SOC content (g kg^{-1})		Note	Reference
			NT	CT	NT	CT		
China	10	0–5	31.21	67.94	14.90	10.20	>2 mm AS	Kan, Ma, et al. (2020)
	10	0–5	34.80	74.96	17.70	11.70	0.25–2 mm AS	
	10	0–5	37.43	68.62	17.10	12.30	0.053–0.2 mm AS	
	10	0–5	31.51	88.17	15.20	8.31	<0.053 mm AS	
	13	0–5	37.19	59.91	44.00	34.60		Qi et al. (2019)
	10	0–5	37.35	65.15	15.76	10.64		Kan, Virk, et al. (2020)
	1	0–5	32.59	34.20	25.50	25.35		Lu et al. (2014)
	31	0–10	42.25	40.76	24.59	18.66	Rhizosphere soil	Fu et al. (2012)
	31	0–10	34.08	56.76	24.15	17.22	Bulk soil	
	5	0–5	36.22	45.69	14.12	12.54		Kan et al. (2021)
	8	0–5	38.75	56.55	15.10	11.57		
	11	0–5	38.37	69.52	15.99	10.51		
France	33	0–5	51.70	27.20	22.10	10.90		Oorts et al. (2006)
	40	0–5	59.90	45.10	18.40	11.80	High nutrient	Dimassi et al. (2014)
		0–5	77.70	44.40	18.40	11.80	Low nutrient	
	18	0–27	23.53	25.17	13.00	10.90		Autret et al. (2020)
Germany	37	0–5	23.84	24.99	15.80	9.30	Macro-aggregates destroyed	Jacobs et al. (2010)
	37	0–5	28.70	19.99	15.80	9.30	Bulk soil <10 mm	
Iran	3	0–20	98.73	115.25	7.09	6.95	Incubation for 11 weeks	Raiesi and Kabiri (2017)
	4	0–20	118.48	148.49	7.09	6.95		
	6	0–20	120.17	151.37	7.09	6.95		
	3	0–20	41.17	53.33	7.09	6.95	Incubation for 3 weeks	Kabiri et al. (2016)
	4	0–20	47.54	64.06	7.09	6.95		
	6	0–20	48.43	65.42	7.09	6.95		
Japan	2	0–15	59.94	61.92	30.33	31.93		Guo et al. (2016)
Spain	10	0–5	22.55	18.18	47.90	35.20		Vazquez et al. (2019)

Abbreviations: AS, aggregate size; CT, conventional tillage; NT, no-till or reduced tillage; SOC, soil organic carbon; 0N, no nitrogen fertilizer applied; 90N, 90 kg N ha^{-1} yr^{-1} of nitrogen fertilizer applied.

how the addition of crop residues will affect the SOC mineralization due to positive PE intensity under NT and CT to better predict the SOC stability. This knowledge would enhance the understanding of mechanisms involved in SOC sequestration under conservation tillage (NT with RR). To achieve this, we reviewed PE intensities measured in five studies after inputs of fresh carbon were added to NT and CT systems (Table 3). In general, lower PE intensities were obtained under NT compared with CT based on long-term field experiments (≥5 years) following the inputs of residues of wheat (Mo et al., 2021; Sarker, Singh, Cowie, et al., 2018; Sauvadet et al., 2018), maize (Kan, Virk, et al., 2020), canola (Sarker, Singh, Cowie, et al., 2018), and cellulose (Dimassi et al., 2014). On average, PE

under NT was 15.17 g C kg^{-1} SOC or about 21.3% lower than that under CT ($p < .05$; paired t-test). Thus, while fresh carbon inputs cause positive PE intensities in both NT and CT, PE is lower in NT than under CT. However, in all the studies reviewed, aboveground parts were used as the fresh C source and belowground roots were ignored. As the contribution of root material to SOC is often higher than residues (Rasse et al., 2005), greater understanding is required of the role that root inputs have on the PE under different tillage practices.

The reason for the lower PE intensity under NT may be related to differences in soil physicochemical properties (i.e., abiotic factors) between tillage systems, as these are one of the main drivers

FIGURE 3 Soil organic carbon (SOC) mineralization (a) and SOC content (b) under NT and CT, as well as their relationship (c). The solid and dashed lines in (a) and (b) are median and mean values, respectively. Gray shading in (c) represents the 95% confidence interval [Colour figure can be viewed at wileyonlinelibrary.com]

In panel (c):
$$Y = 23.19 - 0.13X \quad R^2 = .15 \quad p = .006$$
$$Y = 19.94 - 0.10X \quad R^2 = .21 \quad p = .001$$
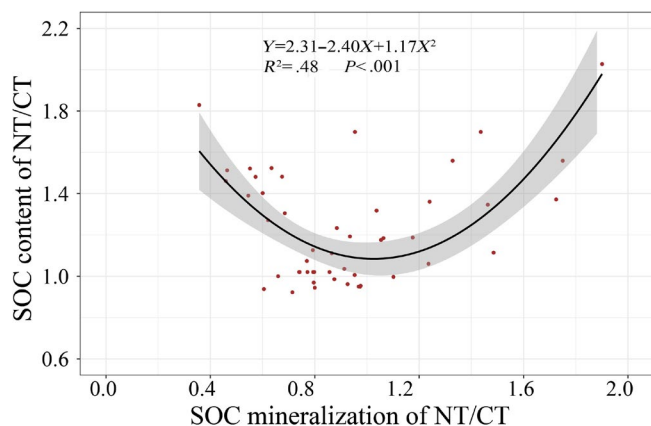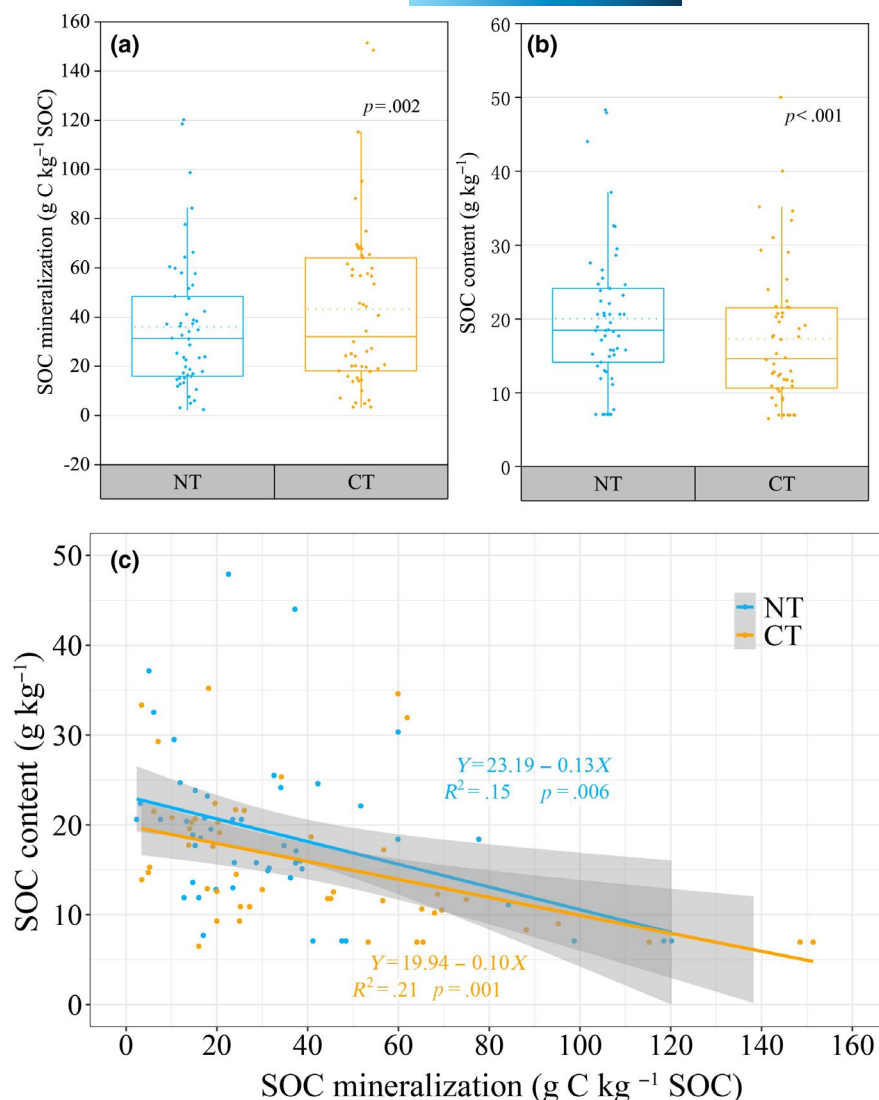
FIGURE 4 The relationship between soil organic carbon (SOC) mineralization of NT/CT and SOC content of NT/CT. Gray shading represents the 95% confidence interval [Colour figure can be viewed at wileyonlinelibrary.com]

In Figure 4:
$$Y = 2.31 - 2.40X + 1.17X^2 \quad R^2 = .48 \quad P < .001$$

of C turnover and PE during the SOC mineralization (Blagodatskaya & Kuzyakov, 2008). For example, Kan, Virk, et al. (2020) reported a negative correlation between soil compaction and PE intensities among different tillage practices, and it has been well established that higher compaction often occurs in NT systems (Bogunovic et al., 2018). In compacted soil, the closer the packing of aggregates can alter soil hydrology (Alesso et al., 2019), and potentially lower aeration, which ultimately impacts aerobic microbial communities, potentially inducing changes in the magnitude of any PE. Furthermore, soil acidification is often observed after the adoption of NT (Li, Li, et al., 2020; Li, Song, et al., 2020), and a positive correlation exists between pH and PE intensities (Kan, Virk, et al., 2020). Soil pH not only affects the stability of aliphatic and long-chain alkyl substances, but also changes the contents of iron (Fe) and aluminum (Al) oxides (Berhe & Kleber, 2013; Bull et al., 2000). Thus, changes in soil pH under NT may affect PE intensities of SOC mineralization. Moreover, greater aggregation under NT was observed compared with CT after residue addition (Kan, Ma, et al., 2020; Wang et al., 2019). Because crop residues could not only provide a C source for microbial growth, but also contribute to the formation of microbial-derived binding agents for aggregation (Six et al., 2000). In this sense, it potentially protects SOC from mineralization induced by the residue addition.

TABLE 2 SOC sequestration (rate) under NT and CT using meta-analysis

Country	Treatment	Control	Soil depth (cm)	SOC sequestration (rate)	Reference
Global	NT	CT	30	+4.90 Mg ha^{-1}	Angers and Eriksen-Hamel (2008)
Global	NT	CT	30	+0.57 Mg ha^{-1} year^{-1}	West and Post (2002)
Global	NT	CT	10	+3.15 Mg ha^{-1}	Luo et al. (2010)
			20–40	−3.30 Mg ha^{-1}	
			40	No change	
Global	NT	CT	30	+3.40 Mg ha^{-1}	Virto et al. (2012)
China	NT	CT	20	+3.8%	Du et al. (2017)
			≥30	No change	
China	NT-RR	CT-RR	5	+0.69 Mg ha^{-1}	Zhao et al. (2015)
			5–10	+0.33 Mg ha^{-1}	
			10–20	No change	
			20–30	No change	
			30–40	No change	
			40–60	No change	
			>60	No change	
	NT+RR	CT-RR	5	+1.63 Mg ha^{-1}	
			5–10	+0.69 Mg ha^{-1}	
			10–20	No change	
			20–30	No change	
			30–40	No change	
			40–60	No change	
			>60	No change	

Abbreviations: +RR, residue returning; CT, conventional tillage; NT, no-till or reduced tillage; −RR, residue removal; SOC, soil organic carbon.

4.2 | Molecular structure of SOC

Characterizing the molecular structure of SOC is crucial to understanding SOC stability and predicting its response to management practices (Gao et al., 2021). Using biomarkers and ^{13}C nuclear magnetic resonance (NMR) has advanced the understanding of stabilization mechanisms of SOC at the molecular composition and functional groups levels, and allowed a greater understanding of SOC genesis and transformation (Gao, Wang, Li, Han, et al., 2019; Gao et al., 2021). These techniques can also be used to quantify changes in the composition of SOC under NT and CT management. For example, SOC in macro-aggregates under NT has a wider shape of aliphatic C (O-alkyl and alkyl C) and aromatic-C region compared with those under CT (Zhao et al., 2012). There are also tillage-induced differences in SOC associated with micro-aggregates. In general, the shape of the alkyl-C, aromatic-C, and carbonyl-C regions is also observed to be broader for NT than that for CT (Zhao et al., 2012). These results indicate that SOC under NT has a more steady-state chemical composition compared with that under CT. However, several studies have reported that aliphatic C is the most dominant functional group, and conversion to NT retains more labile compounds (e.g., n-alkanols, carbohydrates, and aliphatic C) in the 0–10 cm depth than CT (Gao, Wang, Li, Han, et al., 2019; Gao et al., 2021). Despite these differences, it is difficult to deduce that

SOC accumulated under NT is retained and stabilized in soil for the long term. The impact of SOC molecular structure on its stability has been questioned (Schmidt et al., 2011). An inherently "recalcitrant" biomolecule does not necessarily persist, and conversely, "labile" biomolecules do not necessarily readily decompose nor get quickly mineralized (Miltner et al., 2012). Although the increase in SOC under NT consists primarily of compounds from labile C pools, these can be protected against decomposition through interaction with the mineral matrix or by occlusion within aggregates (Gao et al., 2021; Lehmann & Kleber, 2015). Thus, some researchers have argued that SOC stability is caused more by microbial inaccessibility due to mineral interactions and soil aggregation than by structural recalcitrance (Plaza et al., 2013; Schmidt et al., 2011). It can thus be concluded that SOC stability is not controlled just by molecular structure in NT versus CT systems over the long term, but also by the rate of mineralization as influenced by changes in aggregate structure and other mechanisms of chemical protection.

4.3 | Physical protection

The primary mechanism of physical protection of SOC is the enclosure within aggregates. Aggregates form a barrier that restricts decomposers from accessing the organic substrates because of

TABLE 3 Literatures of cumulative PE under NT and CT

Country	Experiment duration	Soil depth (cm)	Carbon addition	Cumulative PE (g CO$_2$-C kg^{-1} SOC)		Percentage change (NT vs. CT) (%)	Note	Reference
				NT	CT			
Australia	16	0–10	Canola residue	2.30	3.52	−34.7	2–6.5 mm	Sarker, Singh, Cowie, et al. (2018)
				2.42	5.34	−54.7	0.25–2 mm	
				2.39	3.95	−39.5	<0.25 mm	
			Wheat residues	1.93	3.02	−36.1	2–6.5 mm	
				2.05	3.94	−48.0	0.25–2 mm	
				1.82	3.48	−47.7	<0.25 mm	
	46	0–10	Canola residue	2.45	2.52	−2.8	2–6.5 mm	
				2.32	2.32	0	0.25–2 mm	
				2.34	2.24	4.5	<0.25 mm	
			Wheat residues	1.13	1.15	−1.7	2–6.5 mm	
				1.06	1.13	−6.2	0.25–2 mm	
				1.08	1.03	4.9	<0.25 mm	
China	9	0–15	Wheat residues	84.42	107.53	−21.5	2–6 mm	Mo et al. (2021)
				86.97	100.62	−13.6	2–0.25 mm	
				59.13	72.60	−18.6	<0.053 mm	
	10	0–5	Maize residues	16.94	25.72	−34.1		Kan, Virk, et al. (2020)
France	5	0–5	Wheat residues	6.68	7.95	−16.0		Sauvadet et al. (2018)
	40	0–5	Cellulose	3.98	6.55	−39.2	High nutrient	Dimassi et al. (2014)
				6.85	11.59	−40.9	Low nutrient	
On average				15.17b	19.27a	−21.3		

Note: Different lowercase letters indicate the $p < .05$ using paired t-test.
Abbreviations: AS, aggregate size; CT, conventional tillage; NT, no-till or reduced tillage; PE, priming effect.

physical occlusion, intercalation, hydrophobicity, and encapsulation interaction with mineral surfaces (Hontoria et al., 2016; Six et al., 2000; Somasundaram et al., 2017; Zhang, Li, et al., 2018; Zheng et al., 2018). Physical protection depends on the level of aggregation and SOC encapsulated within micro-aggregates is more stable than that within macro-aggregates (Pinheiro et al., 2004; Pulleman & Marinissen, 2004; Six, Bossuyt, et al., 2004; Somasundaram et al., 2018). Nonetheless, micro-aggregates are formed within macro-aggregates, and Six et al. (2000) reported that 27% of the macro-aggregate in CT consists of micro-aggregates, whereas this value was 47% in NT. Thus, the dynamics of macro-aggregates are crucial to SOC stability because it influences the micro-aggregation and the sequestration of SOC within these micro-aggregates (Six, et al., 2002; Six, Ogle, et al., 2004). It has been widely documented that NT reduces soil disturbance and increases macro-aggregate formation, in contrast to CT (Six, Bossuyt, et al., 2004; Zhang et al., 2014). A global literature review showed that NT had a higher proportion of macro-aggregates compared with CT, except in paddy soils when the experimental duration was 11 years (Wang et al., 2019). On average, the proportion of macro-aggregates in soil under NT was 55.8%, and 32.7% higher than that under CT ($p < .05$; paired t-test) (Table 4). Furthermore, the soil under NT often had a lower rate of mineralization in macro-aggregates compared with that under CT (Kan, Ma, et al., 2020; Sarker, Singh, Cowie, et al., 2018). As such, the soil under NT is characterized by a lower SOC mineralization compared with that under CT.

4.4 | Chemical protection

Highly reactive mineral surfaces regulate SOC by sorption and desorption reactions and precipitation and dissolution of mineral-SOC associations (e.g., organic bounded mineral Fe/Al oxides [Fep/Alp] and non-crystalline mineral Fe/Al oxides [Feo/Alo]), thus limiting SOC mobilization and degradation (Coward et al., 2017; Nguyen et al., 2019). Interestingly, NT management increases the relative importance of aggregation for stabilization and, in turn, decreases the contribution of mineral associations to the stable pool (von Lützow et al., 2008). Although aggregate turnover is an important process affecting SOC stability, Fe/Al oxides can lead to the formation of soil aggregates through their strong flocculating effect as a dominant binding agent, and in turn increase the protection of SOC by physical protection in aggregates (Asano & Wagai, 2014; Six, Ogle, et al., 2004). In this sense, the chemical protection of Fe/Al may be more important than aggregate protection in SOC stability. Furthermore, the contents of Feo in NT were significantly higher than that under CT, and Feo contents were correlated with SOC content and SOC mineralization (Qi, Zhao, et al., 2021). Similar results were also reported by Inda et al. (2013), Huang et al. (2016), and Xue et al. (2019).

Silt and clay minerals have a strong surface adsorption capacity, and more easily adsorbed hydrophobic SOC has a slow rate of degradation. Alkyl C is considered a particularly recalcitrant form of soil C, and clay size fractions generally show a greater alkyl C content

than the whole soil (Lützow et al., 2006). Six et al. (2000) indicated that SOC in micro-aggregates can be stabilized over the long term compared with mega- or macro-aggregate. Additionally, Sarker, Singh, Cowie, et al. (2018) reported lower SOC mineralization in micro-aggregate compared with macro-aggregate. In general, micro-aggregates contained well-decomposed plant and microbial residues, with the greatest organo-mineral protection against microbial mineralization compared with macro-aggregates (Sarker, Singh, Cowie, et al., 2018; Von Lützow et al., 2008). In contrast, less decomposed organic materials and some free particulate organic matter may be present in macro-aggregates (Sarker, Singh, Cowie, et al., 2018; Six et al., 2002). Nevertheless, some studies also reported that amounts of SOC mineralization in silt + clay fractions were lower than that in micro-aggregates, primarily due to physicochemical protection and high specific surface areas (low microbial accessibility) in silt + clay fractions (Fernández et al., 2010; Kan, Ma, et al., 2020; Sarker, Singh, Cowie, et al., 2018). Specific surface area and swelling–shrinking in silt + clay could stabilize SOC through both polyvalent cations bridging and mineral surface sorption (Kleber et al., 2015; Sarker, Singh, Cowie, et al., 2018). Thus, a positive correlation is often observed between SOC and silt + clay contents (Chung et al., 2010; Gulde et al., 2008). Present studies are typically focused on aggregate turnover, and limited information was available regarding the variations in SOC protection by silt + clay induced by tillage practices. Confusingly, one study found that NT decreased SOC content in silt + clay fractions, although NT decreased the SOC mineralization (Kan, Ma, et al., 2020). Disruption of aggregates is related to a loss of SOC as CO_2 that depends on clay content (Stockmann et al., 2013). Compared to silt and sand contents, clay content can determine fates of SOC with active SOC pool into CO_2 (loss) or labile SOC pool. Thus, soils with higher clay content have a stronger aggregate structure to better resist disturbance from tillage, while soils with higher sand content have poor resistance for stability (Li, Li, et al., 2020; Li, Song, et al., 2020). A higher proportion of clay was observed in soil under NT compared with that under CT (Zhang et al., 2020). Moreover, clay dispersibility is widely used to evaluate soil structural stability. A negative correlation was observed between clay dispersibility and SOC content, and NT (or reduced tillage) reduced the contents of clay dispersibility compared with CT (Gajda et al., 2018, 2021). Thus, it is concluded that NT could increase the clay content and decrease clay dispersibility, and thus promote soil aggregation and benefit SOC stability.

4.5 | Microbial properties

Soil microbes control the C cycling, and SOC mineralization after sterilization can be half as much as in unsterilized soils under different tillage practices (Qi, Jing, et al., 2021). Thus, lower soil microbial activity should reduce the amount of SOC mineralization (CO_2 production) (Blagodatskaya & Kuzyakov, 2008; Qi, Jing, et al., 2021). However, high soil respiration (CO_2 production) is considered a sign of healthy soil. It has been reported that NT increases soil bacterial

TABLE 4 Literatures of macro-aggregate size distribution under NT and CT

Country	Experimental duration (years)	Soil depth (cm)	Macro-aggregate size distribution (>0.25 mm) (%)		Percentage change (NT vs. CT) (%)	Reference
			NT	CT		
Argentina	14	0–6	57.7	52.5	9.9	Fernández et al. (2010)
Australia	47	0–10	76.1	66.4	14.6	Somasundaram et al. (2017)
Brazil	3	0–5	78.2	69.7	12.2	Pinheiro et al. (2004)
China	30	0–10	89.5	66.6	34.4	Zheng et al. (2018)
	12	0–5	46.5	27.0	72.2	Zhang, Li, et al. (2018)
	8	0–5	47.1	26.2	79.8	Zhang et al. (2017)
	16	0–10	25.1	22.0	14.1	Gao, Wang, Li, Wu, et al. (2019)
	2	0–5	73.0	64.0	14.1	Wang et al. (2019)
	11		87.0	88.0	−1.1	
	5	0–5	32.4	21.1	53.6	Kan et al. (2021)
	8		50.7	37.0	37.0	
	11		59.9	37.5	59.7	
	10	0–10	42.5	30.9	37.5	Zhang, Zhu, et al. (2018)
India	9	0–5	27.6	24.7	11.7	Modak et al. (2020)
	4	0–5	77.2	65.9	17.1	Somasundaram et al. (2018)
Madagascar	11	0–5	75.8	64.5	17.5	Razafimbelo et al. (2008)
Spain	1	0–5	26.7	11.6	130.2	Plaza-Bonilla et al. (2010)
	17		49.5	10.3	380.6	
	20		51.2	24.7	107.3	
	6	0–5	42.2	30.4	38.8	Hontoria et al. (2016)
On average			55.8a	42.1b	32.7	

Note: Different lowercase letters indicate the $p < .05$ using paired *t*-test.
Abbreviations: CT, conventional tillage; NT, no-till or reduced tillage.

diversity and microbial biomass (Li, Li, et al., 2020; Li, Song, et al., 2020; Wang et al., 2016), and thus NT could be expected to have a higher rate of SOC mineralization. In contrast, lower SOC mineralization rates were typically observed in NT compared with that of CT reviewed in the current study (Figure 3). Jastrow et al. (2007) suggested that soil respiration (CO_2 production) is mainly induced by intracellular metabolism (microbial pathway) carried out by various enzymes. However, it is widely accepted that soils also generate CO_2 through non-microbial pathways (Wang et al., 2017). Brookes et al. (2017) suggested that SOC mineralization is independent of microbial biomass size and structure. When microorganisms are not able to access SOC, the mineralization rate is actually regulated by the abiotic transformation of SOC into biologically available forms (the "Regulatory Gate Hypothesis") (Brookes et al., 2017). Given that SOC mineralization refers to both microbial and non-microbial CO_2 emissions, it may therefore be possible for NT soil to have higher microbial activity and lower SOC mineralization if NT simultaneously decreases rates of abiotic mineralization. In this regard, Qi, Jing, et al. (2021) evaluated non-microbial CO_2 emissions using sterilized soils, and observed that NT reduced non-microbial CO_2 emissions compared with CT, which can decrease SOC mineralization and lead to more SOC accumulation under NT. However, this is

an under-researched area and our understanding of the mechanisms behind the impact of tillage practices on non-microbial CO_2 emissions is limited. Thus, soil abiotic factors (e.g., aggregate protection and mineral association as described in Sections 4.3 and 4.4) were correlated with the protection of SOC from mineralization under NT. In addition, microbial activity also enhances the protection of soil aggregates and mineral association. For example, the production of microbial-derived binding agents contributes to the formation of macro-aggregates (Six et al., 2000). Similarly, microbial-derived dissolved organic carbon (DOC) can form mineral-associated SOC when it is adsorbed and co-precipitated (Kleber et al., 2015).

Some recent studies have indicated that microbial necromass (after their cell death) is an important source of stable SOC, and its contribution to SOC can be much more important than has been previously thought (Angst et al., 2021; Ma et al., 2018; Miltner et al., 2012). Microbial residues in soils contain components (e.g., murein, chitin, and lipids) specific for microorganisms, and these compounds have been suggested to stabilize in soils (Lützow et al., 2006). Aggregate protection and SOC associated with soil minerals are important to the stability of microbial residues. For example, microbial residues could be entrapped in small pores in aggregates, where decomposers are unable to access them (Angst et al., 2021) (Figure 5). Moreover, microbial

residues could attach to mineral surfaces, and it reduces the distances between microbial necromass and sorption sites (Angst et al., 2021). Plaza et al. (2013) observed that interaction between microbial residues and minerals contributes to long-term SOC stabilization and sequestration under NT systems. Overall, interaction effects exist between aggregate protection, association with minerals, and microbial activity (residues). To date, however, only limited information exists about the contribution of microbial activity (residues) to SOC stability under NT management. Nonetheless, conversion to NT management can enhance aggregate protection (Kan, Ma, et al., 2020) and the formation of Fe/Al oxides (Qi, Zhao et al., 2021), and thus promote the stability of microbial residues under NT (Figure 5).

4.6 | Environmental effects

In general, temperature rise could stimulate microbial activity and improve the contribution of microbial residues to SOC (Ding et al., 2019). In coarser soils, soil moisture content also controls the degradation of lignin and the accumulation of microbial residues, thus affecting SOC mineralization (Ma et al., 2018). As described in Section 4.5, microbial residues play an important role in SOC stability, and thus soil temperature and moisture regimes could affect SOC stability in NT systems. Increases in macro-aggregate formation observed in NT systems are known to help protect SOC from mineralization (Kan, Ma, et al., 2020; Sarker, Singh, Cowie, et al., 2018; Somasundaram et al., 2018). Yet, macro-aggregates have greater Q_{10} values compared with micro-aggregates (Kan, He, et al., 2020). Moinet et al. (2020) postulated that the Q_{10} of SOC mineralization decreases with an increase in SOC stability, and micro-aggregate-associated SOC is stabilized in the long term (Six et al., 2000). Furthermore, NT improves macro-aggregate proportion by 32.7% compared with that under CT; thus, Kan, He, et al. (2020) reported that NT decreased SOC mineralization but increased its Q_{10} (Figure 6). This indicates that while the loss of SOC in NT systems is currently lower relative to CT, it could be vulnerable to loss following the temperature increases expected under future warming.
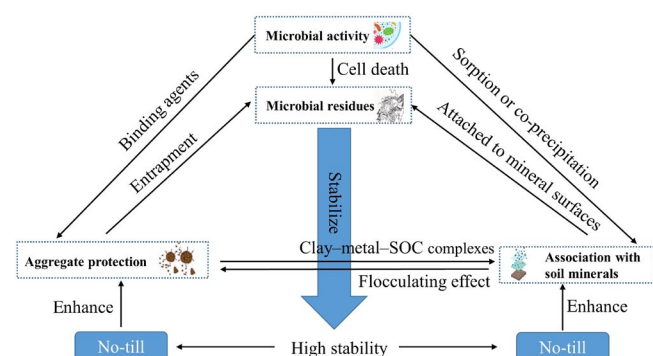
A global meta-analysis showed that soil available moisture capacity may increase by 8.7% under NT compared with CT (Li, Li, et al., 2020; Li, Song, et al., 2020). Kan, He, et al. (2020) indicated that these increased moisture contents could constrain the increase in Q_{10} observed under NT. A reasonable explanation for this finding is that high soil moisture could decrease Q_{10} in macro-aggregates (Kan, He, et al., 2020), and NT supports the formation of macro-aggregates (Table 4). Besides, soil moisture constrains the heterotrophic component of SOC mineralization, inducing changes in the Q_{10} (Hursh et al., 2017; Wang et al., 2021). These findings indicate that physical protection in macro-aggregate could also constrain the accelerated SOC mineralization induced by temperature rise. Apart from temperature and moisture regimes, radiation is also an important factor affecting SOC mineralization through light-induced degradation. Because a system-based NT is adopted with residue mulch, it protects SOC from light-induced degradation (Zhao et al., 2020).

5 | CONCLUSIONS AND FUTURE DIRECTIONS

This review suggests that physical (aggregate protection) and chemical (association with soil minerals) protection plays a larger role in the SOC stability of NT systems compared to the molecular structure of SOC, PE, microbial properties, and environmental effects. The most interesting finding is that chemical protection could be more important than aggregate protection due to the role of Fe/Al oxides and clay contents in flocculating soils and acting as binding agents for aggregation. The Feo and clay contents are significantly correlated with SOC content and mineralization, and Feo and clay contents in NT are significantly higher than those under CT. Higher microbial activity under NT also acted to increase the binding agent for aggregation and promote the association of SOC with soil minerals. Moreover, higher microbial activity in NT contributes to greater microbial residues, which are stabilized in soils over the long term

FIGURE 5 Effects of microbial activity and residues on soil organic carbon stability under NT as compared to CT (Angst et al., 2021; Kan, He, et al., 2020; Plaza et al., 2013; Qi, Zhao, et al., 2021) [Colour figure can be viewed at wileyonlinelibrary.com]
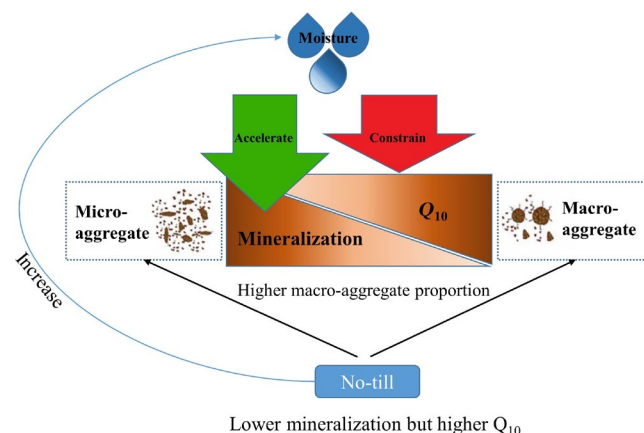

FIGURE 6 The response of soil organic carbon mineralization to temperature and moisture under NT (Kan, He, et al., 2020; Li et al., 2020) [Colour figure can be viewed at wileyonlinelibrary.com]

through their attachment to mineral surfaces and entrapment of SOC within aggregates. Furthermore, NT reduces non-microbial CO_2 emissions through protection by minerals and aggregates. Thus, conversion to NT reduces SOC mineralization and PE intensities after inputs of fresh C compared with CT. Although NT has a higher Q_{10} due to higher magnitude in macro-aggregates, increases in soil moisture under NT can constrain the increase of Q_{10}. This review highlights the crucial role of physical and chemical protection and their interaction in regulating the processes of SOC stability. Our findings enhance the prediction of SOC dynamics under climate change, potentially affecting the carbon-climate feedback.

However, the current research focus has been on the behavior of SOC in the surface soils of NT systems. Reduced SOC sequestration in subsoil under NT limits its potential to mitigate climate change. Global synthesis suggests that microbial-derived residues are crucial to stabilizing SOC in subsoil layers and deep soils can play a decisive role in SOC sequestration. Thus, it is recommended to identify the mechanisms of the microbial-derived C to SOC stability under NT in the future and to enhance the SOC stability and sequestration in subsoil layers.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

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