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Validation of the Phenomenon and Mechanisms of Negative Feedback in Soil Organic Carbon Turnover Using Computer Models

Ruiqi Wang[1,2], Yuanyuan Cai[1,2], Lili Wang[2], Dianlin Yang[2]*, Huifen Liu[1], Bingchang Tan[2]

[1]College of Agronomy & Resources and Environment, Tianjin Agricultural University, Tianjin 300384, China

[2]Agro-Environmental Protection Institute, Ministry of Agriculture and Rural Affairs, Tianjin 300191, China

***Corresponding author:** Dianlin Yang, yangdianlin@caas.cn

Abstract:

The humification coefficient of input organic material (*h*) and the decomposition rate (*k*) of soil organic carbon (SOC) are two crucial parameters that govern the SOC turnover processes. Numerous prior studies have examined how factors like water and temperature can influence these processes, but the impact of SOC content on its own turnover processes has received limited attention. We have developed computer models to investigate the effect of SOC content on SOC turnover processes and the underlying mechanisms. The findings indicate that regardless of changes in *h* and *k*, the SOC content also varies asymptotically over time, ultimately reaching an equilibrium state. Assuming that these two parameters remain constant with respect to SOC content, the SOC content would increase linearly without any limitation from the C input level. However, when considering that *h* decreases with SOC content and *k* increases simultaneously, the SOC content would increase asymptotically with the C input level. This suggests an asymptotic relationship between SOC content and C input level. The variations in *h* and *k* with SOC content are referred to as negative feedback in SOC turnover. Further examination of the mechanisms behind this negative feedback supports the asymptotic relationship between SOC content and C input level. We propose that the concept of negative feedback in SOC turnover is valid and that it is both necessary and feasible to incorporate this effect into model development.

Keywords:

Soil organic carbon
Saturation
Humification
Decomposition
Turnover process
Negative feedback
Computer model

1. Introduction

Soil organic carbon (SOC) plays a crucial role in enhancing soil fertility and mitigating the greenhouse effect [1,2]. The international soil science community has gradually formed a new discipline called "carbon sequestration soil science" around the issue of soil carbon sequestration [3]. The dynamics of organic carbon are the result of a balance between the processes of organic material humification and organic carbon degradation (this article does not consider organic carbon losses caused by runoff, leaching, etc.). Under relatively stable hydrothermal conditions and management measures, the organic carbon content increases or decreases over time and ultimately reaches an equilibrium state. Simultaneously, the equilibrium value of organic carbon increases with increasing carbon input levels. The first-order kinetic equation proposed by Jenny [4] and Henin and Dupuis [5] shows that organic carbon dynamics are related to the humification coefficient (h) of organic materials and the degradation coefficient (k) of organic carbon. Understanding these two parameters is beneficial for recognizing the organic carbon turnover process and provides a theoretical basis for building computer models.

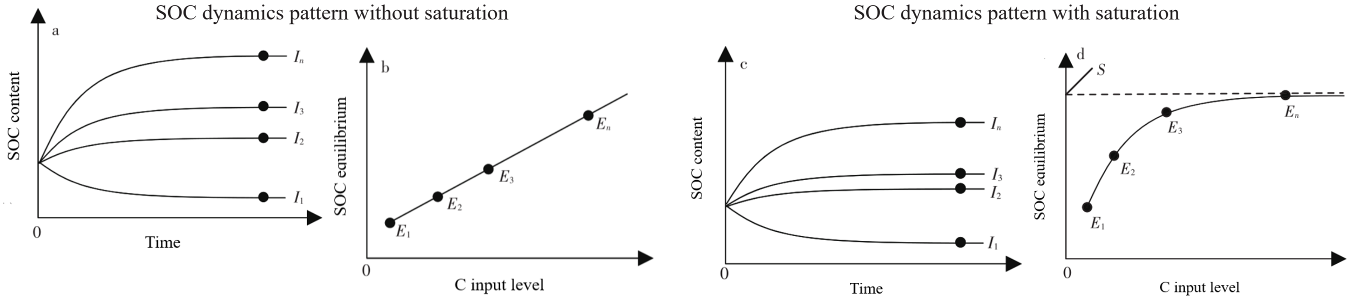
$$\mathrm{d}C/\mathrm{d}t = I_m h - Ck \qquad (1)$$

In the formula, C represents the organic carbon content (g·kg^{-1}); t represents time (a); I_m represents the carbon input level per unit soil mass (g·kg^{-1}·a^{-1}); h represents the humification coefficient of organic materials (dimensionless); k represents the degradation coefficient of organic carbon (a^{-1}).

Previous studies have shown that h and k are affected by the following factors: (1) Environmental factors, such as soil temperature and soil moisture content; (2) Properties of organic materials, such as C/N ratio and lignin content; (3) Soil properties, such as soil pH and soil texture [6]. Additionally, management measures can indirectly affect the soil carbon turnover process by changing the above factors. Therefore, most current organic carbon computer models, such as RothC, CENTURY, DNDC, and Agro-C, consider all or some of the above factors [7-9]. However, apart from the above factors, the organic carbon content is often in dynamic change, and there are few reports on the impact of changes in organic carbon content on the process of organic material humification and organic carbon degradation.

Most previous studies have focused on the influence of environmental factors, properties of organic materials, and soil properties on the organic carbon turnover process. Therefore, in long-term positioning experimental studies, assuming that these three factors are relatively stable, h and k will be quantitative parameters. According to the first-order kinetic equation of organic carbon turnover, when the organic carbon reaches an equilibrium state, $\mathrm{d}C/\mathrm{d}t = I_m h - Ck = 0$, then $C = E$, $E = (h/k) \times I_m$ (E represents the equilibrium value of organic carbon, g·kg^{-1}), and the equilibrium value of organic carbon will increase proportionally and unlimitedly with increasing carbon input levels. This is the reason most current organic carbon model predictions show a linear relationship between the equilibrium value of organic carbon and carbon input levels [10,11]. However, some viewpoints suggest that there is a saturation value for organic carbon, and it cannot increase indefinitely [12-14]. To this end, Stewart *et al.* [10] proposed a dynamic model of organic carbon, which believes that on the one hand, the organic carbon content increases or decreases asymptotically with time and finally reaches an equilibrium state; on the other hand, the equilibrium value of organic carbon also increases asymptotically with increasing carbon input levels, and the maximum equilibrium value reached under sufficient carbon input levels is considered the saturation value of organic carbon (**Figure 1**).

Based on the dynamic model of organic carbon of saturation value theory, Tan *et al.* [15] used mathematical calculations to initially discover that h decreases exponentially as the organic carbon content increases, while k increases exponentially, and vice versa. Ultimately, changes in organic carbon content further inhibit subsequent changes in itself by altering h and k. Therefore, this phenomenon of organic carbon content effect is defined as the negative feedback effect of organic carbon turnover. Tan *et al.* [15] further proposed that the negative feedback effect is formed by three mechanisms: (1) Biological mechanism: As the organic carbon content increases, the driving force for organic carbon degradation, mainly composed of microorganisms, becomes stronger; (2) Chemical mechanism: The soil's ability to protect organic carbon is limited, and a higher proportion of organic carbon is in an unprotected active


SOC dynamics pattern without saturation

SOC dynamics pattern with saturation

Figure 1. Illustration of SOC saturation and SOC dynamics pattern. (a) SOC dynamics pattern without saturation shows that SOC will change over time; (b) SOC equilibrium level will increase linearly as C input level increases; (c) While SOC dynamics pattern with saturation shows that SOC will also change over time; (d) However, the equilibrium value increases asymptotically with increasing carbon input levels, and the equilibrium value at sufficiently high carbon input levels is considered the saturation value.

state; (3) Physical mechanism: The increase in organic carbon content improves the physical environment for organic carbon turnover, promoting the turnover of organic carbon.

Do *h* and *k* relate to organic carbon content? What is the mechanism that causes the negative feedback effect of organic carbon turnover? Computer models can verify scenarios and hypotheses that are difficult to achieve ideal results through experimental means, thus providing a better understanding of the dynamic process of material cycling [7,16]. In this study, organic carbon is treated as a single or double pool. By constructing organic carbon models, the phenomenon and mechanism of the negative feedback effect of organic carbon turnover are verified separately, providing a theoretical basis for better understanding the organic carbon turnover process and optimizing computer models.

2. Materials and methods

The first-order kinetic equation demonstrates that changes in organic carbon content are the result of a balance between organic carbon formation during the humification process of organic materials and organic carbon degradation. The amount of organic carbon formed during humification is the product of the carbon input level and the humification coefficient, while the loss of organic carbon due to degradation is the product of the organic carbon content and the degradation coefficient. In this study, both a conventional model (without considering negative feedback) and a negative feedback model (considering negative feedback effects and mechanisms) were constructed based on this equation. It should be noted that this study only qualitatively verifies the negative feedback effect of organic carbon and related mechanisms. Therefore, the models do not involve common influencing factors such as temperature and moisture, as these factors do not affect the verification process of the negative feedback phenomenon and mechanism.

2.1. Single-pool model to verify negative feedback phenomenon

2.1.1. Conventional model

In the conventional model, both *h* and *k* are independent of organic carbon content (**Figure 2a**). Based on existing research [17], *h* is set to 0.34, *k* is set to 0.177 a^{-1}, resulting in the equation $dC/dt = 0.34I_m - 0.177C$. During the simulation process, the soil bulk density (B) is set to 1.36 $g\cdot cm^{-3}$ [18], and the initial organic carbon content in the 0–20 cm depth (D) soil layer is 4.00 $g\cdot kg^{-1}$. The relationship between the carbon input level per unit area (I, in $kg\cdot hm^{-2}\cdot a^{-1}$) and the carbon input level per unit soil mass (I_m) is $I_m = I / (100DB)$.

2.1.2. Negative feedback model

The difference between the negative feedback model and the conventional model is that both *h* and *k* are related to organic carbon content (**Figure 2b**). Based on the research of Tan *et al.* [15], the relationship between these two parameters and soil organic carbon content is expressed as: $h = \ln(1.39 – 0.0265C)$, $k = 0.00223\ln(C – 3.27)$. The soil bulk density and the initial organic carbon content in the 0–20 cm soil layer are the same as in the conventional model.

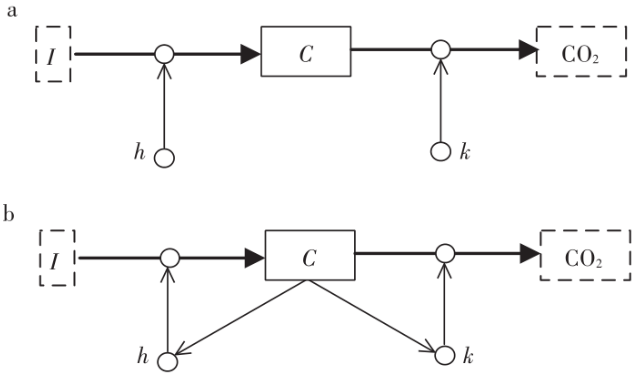


Figure 2. Model structure for normal and negative feedback model. *I* represents the level of carbon input (kg·hm^{-2}·a^{-1}); *h* represents the humification coefficient of organic materials; *C* represents the organic carbon content; *k* represents the organic carbon degradation coefficient. The large arrow indicates the process of organic carbon formation and degradation, while the small arrow indicates a relationship between two variables. The amount of organic carbon formed by humification is the product of *I* and *h*, and the amount of organic carbon degraded is the product of *C* and *k*. In the conventional model, both *h* and *k* are independent of organic carbon content (a); in the negative feedback model, both *h* and *k* are related to organic carbon content (b).

2.2. Verification of negative feedback mechanism using a two-pool model

The aforementioned model assumes organic carbon as a single entity, but organic carbon exhibits high heterogeneity. Currently, most computer models set organic carbon as a two-pool or multi-pool system, and some models also consider the mutual conversion between different organic carbon pools. These models assign corresponding degradation and conversion coefficients to different organic carbon pools. To simplify, this study assumes organic carbon consists of two pools (i.e., active organic carbon and inert organic carbon), without considering the conversion between different organic carbon pools, to verify the mechanism of organic carbon content. The model is expressed as follows:

$$\begin{cases} C = C_1 + C_2 \\ \dfrac{dC_1}{dt} = I_m hp - C_1 k_1 \\ \dfrac{dC_2}{dt} = I_m h(1-p) - C_2 k_2 \end{cases} \tag{2}$$

In the formula: C_1 and C_2 represent the content of active organic carbon and inert organic carbon, respectively. The turnover of the two organic carbon pools follows a first-order kinetic model, where k_1 and k_2 are the degradation coefficients of the two components, respectively. *p* represents the proportion of newly formed organic carbon allocated to the active organic carbon pool. The structures of different models are shown in **Figure 3**.

When the mechanism of organic carbon content is not considered, *h*, *p*, k_1 and k_2 are fixed constants, which can be set as 0.34 [17], 0.46, 0.66, and 0.02 a^{-1} [8],

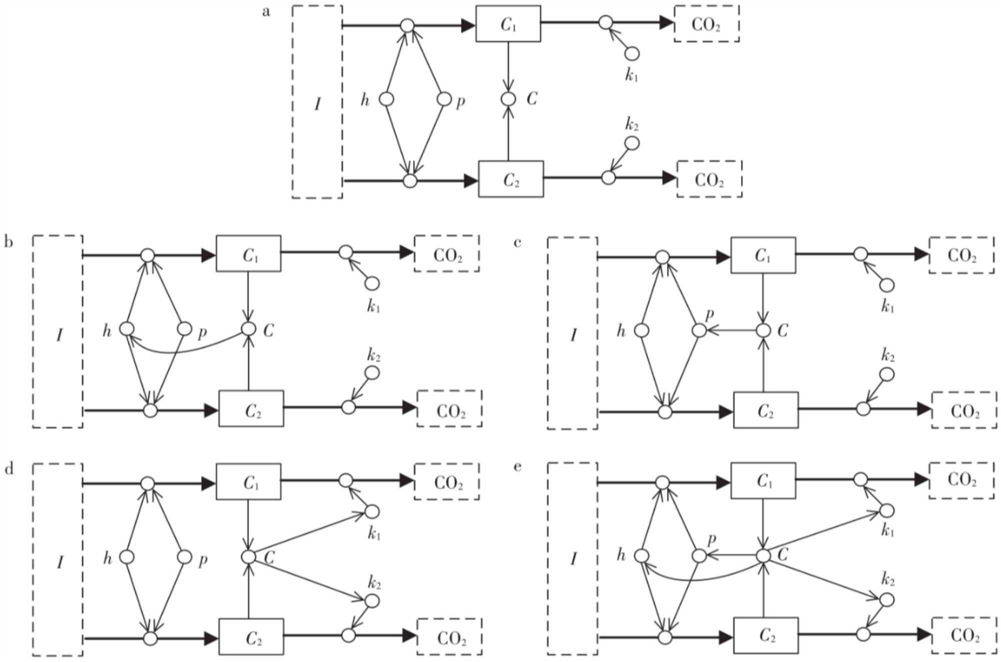


Figure 3. Description of the two-compartment model. (a) The regular model does not consider the mechanism of negative feedback; (b) The humification coefficient decreases with the accumulation of organic carbon; (c) A higher proportion of newly formed organic carbon is allocated to the active organic carbon pool; (d) The degradation coefficient of the two organic carbon components increases; (e) Comprehensively consider the three mechanisms of the action of organic carbon content (ie, b, c, and d).

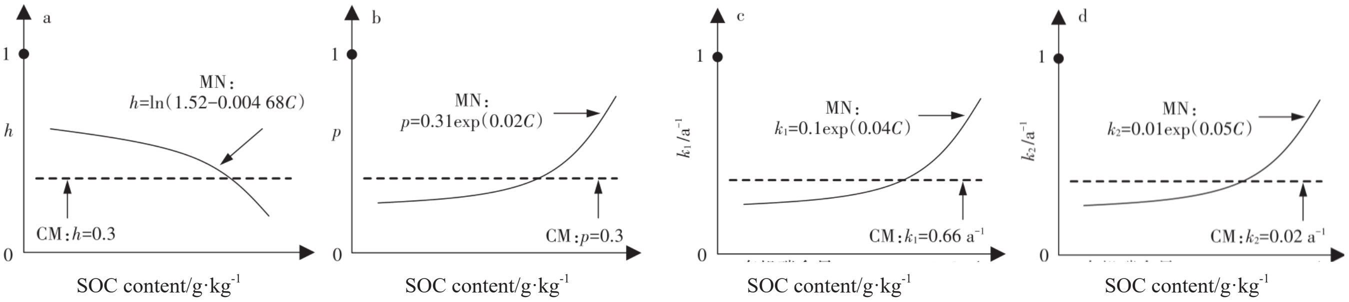


Figure 4. Model parameter assignment. The CM model indicates that the effect of organic carbon content is not considered; MN model indicates the effect of the organic carbon content.

respectively. However, when considering the mechanism of organic carbon content, based on the negative feedback mechanism proposed by Tan *et al.* [15], the parameters can be adjusted according to the above four values, as shown in **Figure 4**. That is, as the organic carbon content increases, h decreases, p increases, and both k_1 and k_2 increase. Theoretically, all parameter values are less than 1. It must be noted that the mathematical relationships between h and C, p and C, as well as k and C set in this study do not reflect precise quantitative relationships but rather simplified qualitative trends. This is because, on one hand, the purpose of this study is to qualitatively verify the mechanism of organic carbon content, and on the other hand, quantitative research on these relationships is currently lacking. Despite this, these simplified relationships do not affect the qualitative verification of the mechanism of organic carbon content in this study.

The study investigates two relationships: (1) the relationship between organic carbon content and time (C-t relationship); (2) the relationship between organic carbon content and carbon input level (C-I relationship).

The study used SELLA software to build a computer model and Origin 8.5 for graphing.

3. Results and analysis

3.1. Verification of negative feedback phenomenon

3.1.1. Dynamic changes of organic carbon with time

As time progresses, under different constant carbon input levels, the organic carbon content simulated by both the conventional model and the negative feedback model asymptotically increases or decreases to a steady state. At the same time point, a higher carbon input level results in a higher organic carbon content. After 50 years of model operation, the organic carbon approaches or reaches a steady state (**Figure 5**).

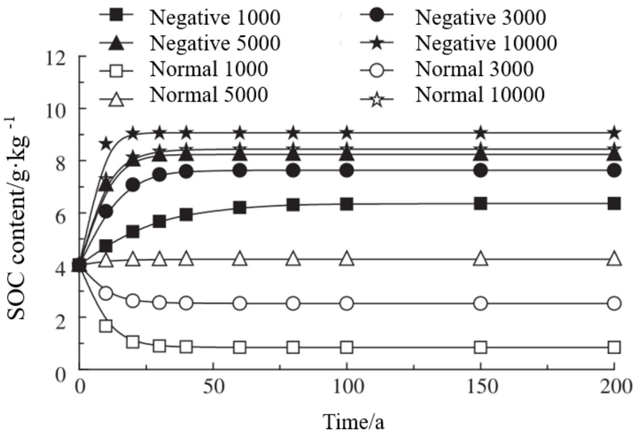


Figure 5. SOC dynamics for different models and C input levels. “Negative” means negative feedback model; “Normal” means regular model; 1000~10000 means different carbon input levels (kg·hm^{-2}·a^{-1}). It is the same below.

3.1.2. Relationship between organic carbon equilibrium values and carbon input levels

Since the organic carbon content in both models fully reaches a steady state after 200 years of operation, we maintained the models’ runtime at 200 years and increased the carbon input level from a constant level to a high level, such as 100,000 kg·hm^{-2}·a^{-1}, to further understand the relationship between organic carbon equilibrium values and carbon input levels at different high carbon input levels. The results showed that as the carbon input level increases, the organic carbon equilibrium value increases (**Figure 6**). The conventional model demonstrated a proportional linear increase in equilibrium values with increasing carbon input levels, indicating no saturation phenomenon of organic carbon. However, the negative feedback model showed an asymptotic increase in equilibrium values with increasing carbon input levels. The organic carbon equilibrium values were basically the same at carbon input levels of 50,000 $kg·hm^{-2}·a^{-1}$ and 100,000 $kg·hm^{-2}·a^{-1}$, indicating the existence of an organic carbon saturation value (**Figure 6**). Additionally, the soil carbon sequestration efficiency (*E/I*, $g·hm^{2}·a·kg^{-2}$) of the conventional model did not change with increasing carbon input levels, while the carbon sequestration efficiency of the negative feedback model decreased with increasing carbon input levels, showing a clear law of diminishing returns (**Figure 7**).

3.1.3. Relationship between non-equilibrium organic carbon content and carbon input levels

In theory, under sufficient time conditions, organic carbon content can ultimately reach a steady state. However, in practice, organic carbon content is often in a dynamic process of approaching equilibrium. Therefore, this study further analyzed the relationship between organic carbon content and carbon input levels after model operation for 10, 20, and 40 years under different carbon input levels, i.e., in a non-equilibrium state. The results showed that in the conventional model, after different years of model operation, the organic carbon content increased linearly with increasing carbon input levels (**Figure 8a**). In the negative feedback model, the organic carbon content increased asymptotically with increasing carbon input levels (**Figure 8b**).

3.2. Verification of negative feedback mechanism

3.2.1. Dynamic changes of organic carbon with time

Taking a carbon input level of 3000 $kg·hm^{-2}·a^{-1}$ as an example to investigate the mechanism that forms negative feedback. After running the model for 200 years, regardless of whether the mechanism of organic carbon content is considered, the organic carbon content asymptotically changes to a steady state over time (**Figure 9**).

3.2.2. Relationship between organic carbon content and carbon input levels

After running the model for 200 years, when considering the mechanism of organic carbon content, both the organic

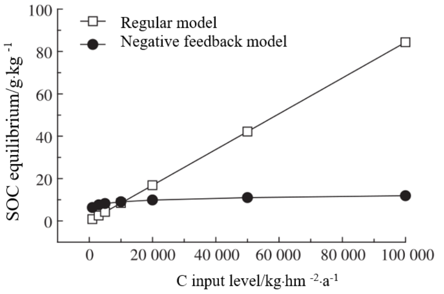


Figure 6. Relationship between SOC equilibrium and C input level

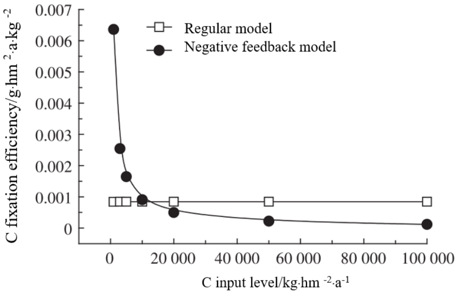


Figure 7. Relationship between C fixation efficiency and C input level

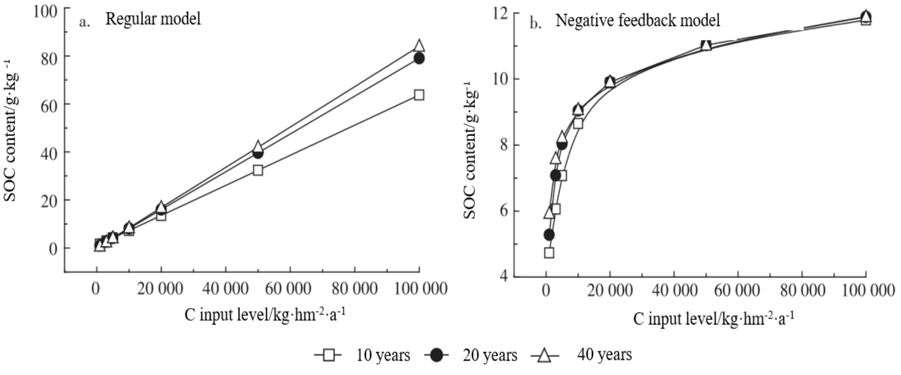


Figure 8. Relationship between SOC content and C input level for different years

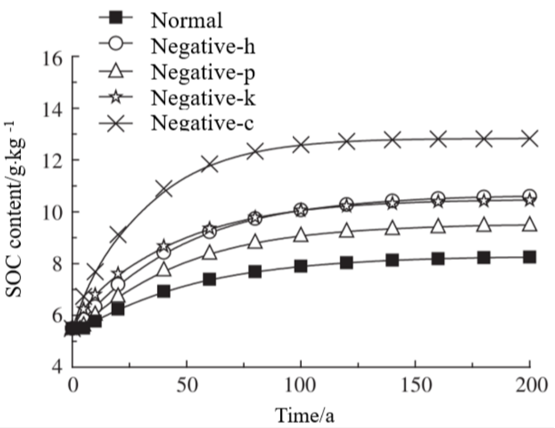


Figure 9. SOC dynamics for the two-compartment models. "Normal" means a regular model that does not consider the negative feedback effect. "Negative-*h,*" "Negative-*p*," and "Negative-*k*" respectively represent a model of the fusion negative feedback mechanism. *h* represents humification coefficient of organic material decreases with the increase of organic carbon. *p* indicates that the proportion of newly formed organic carbon to the active organic carbon component increases as the organic carbon content increases. *k* indicates that the degradation coefficient of the two organic carbon components increases as the organic carbon content increases. "Negative-*c*" means a model that considers three mechanisms simultaneously. It is the same below.

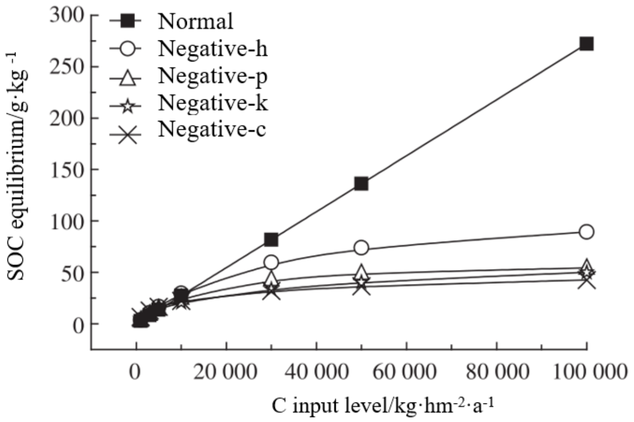


Figure 10 . Relationship between SOC equilibrium and C input level for two-compartment models

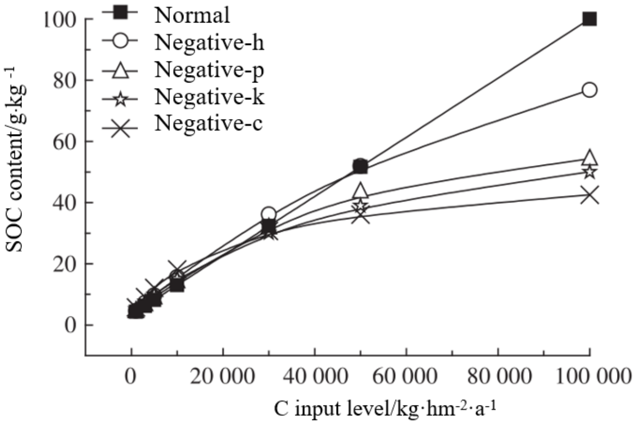


Figure 11. Relationship between SOC content and C input level for two-compartment models

carbon equilibrium value (*E*) and the carbon input level (*I*) show an asymptotic relationship. Conversely, without considering the mechanism of organic carbon content, the two exhibit a linear relationship (**Figure 10**). Further exploration of the relationship between non-equilibrium organic carbon content and carbon input levels simulated by the two types of models revealed that after 20 years of model operation, the relationship between organic carbon content (*C*) and carbon input level (*I*) exhibits a similar phenomenon to the *E-I* relationship: as long as the mechanism of organic carbon content is considered, an asymptotic *C-I* relationship is presented; conversely, without considering the mechanism of organic carbon content, a linear *C-I* relationship is observed (**Figure 11**).

4. Discussion

4.1. Rationality of negative feedback in organic carbon turnover

The changes in organic carbon content with time (*C-t* relationship) and the relationship between organic carbon content and carbon input levels (*C-I* relationship), including the relationship between equilibrium values and carbon input levels (**E-I** relationship), are important aspects of expressing organic carbon dynamics [10]. Previous computer models have primarily focused on simulating the dynamic changes in organic carbon content but have not paid sufficient attention to the simulation results of the *C-I* relationship. However, this relationship can reflect whether organic carbon content affects its own turnover process and intuitively shows the soil's carbon sequestration capacity corresponding to a given carbon input level. Therefore, examining the simulation results of computer models for the *C-I* relationship should receive more attention in model research. Paustian *et al.* [11] pointed out that most current computer models predict a linear *E-I* relationship, regardless of whether organic carbon is treated as a multi-component or single-component system. They attributed this linear relationship to the first-order kinetic equation and fixed *k* parameter values. Bayer *et al.* [19] also demonstrated through mathematical calculations that when *h* and *k* are assumed to be fixed, there is a linear relationship between organic carbon content and carbon input levels. The simulation results of the conventional model in this study show that the relationship between organic carbon content and time cannot reflect whether organic carbon content affects the turnover process of organic carbon. However, the relationship between organic carbon content and carbon input levels can reflect the role of organic carbon content: when negative feedback effects and mechanisms are not considered, the conventional model simulates a linear *C-I* relationship (including the *E-I* relationship), consistent with the above research results (**Figures 6**, **8a**, **10**, and **11**). Due to the limited protective effect of soil on organic carbon, organic carbon content does not increase indefinitely with increasing carbon input levels but eventually reaches a saturation state [12]. Although some long-term experiments show a linear relationship between organic carbon content and carbon input levels, this relationship is attributed to low carbon input levels and a narrow range of input levels, which do not reveal a significant asymptotic relationship [10]. The results of this study also show that when considering negative feedback effects, there is an asymptotic *C-I* relationship. However, the significance of this asymptotic relationship is related to the range of carbon input levels; a smaller range makes it less significant. Additionally, even if the input level range is large, but the content is close to the saturation value, it is not obvious (**Figure 8b**).

Thus, it can be seen that without considering negative feedback effects and mechanisms, computer models will simulate a linear *C-I* relationship (including the *E-I* relationship). When considering negative feedback effects and mechanisms, computer models will simulate an asymptotic *C-I* relationship. Furthermore, the author also found through mathematical derivation that negative feedback effects exhibit an asymptotic *C-I* relationship. Analysis of multiple long-term experimental data in China also revealed that the asymptotic *C-I* relationship is more common than the linear relationship (data not published). Therefore, the negative feedback effect in organic carbon turnover is both reasonable and simulatable. Kemanian *et al.* [20] have already integrated negative feedback effects into the C-farm model and successfully simulated the dynamic process of organic carbon in two long-term experiments in Oregon, USA, and Rothamsted, England.

4.2. Mechanism of negative feedback in organic carbon turnover

The negative feedback effect in organic carbon turnover may be caused by the following biochemical and physical reasons:

(1) Higher degradability of organic carbon: Due to the limited protective capacity of soil for organic carbon, a higher proportion of organic carbon remains in an unprotected and active state as the organic carbon content increases. Studies have shown that the ratio of the light fraction of SOC (soil organic carbon) to the heavy fraction of SOC increases with increasing light fraction content [21]. Since the light fraction of organic carbon is more easily degraded [22], the overall degradability of total organic carbon increases with increasing content.

(2) Stronger degradation driving force: Soil microorganisms are the main drivers of organic carbon turnover, and the most important factor controlling microbial biomass is substrate availability [23]. With increasing organic carbon content, soil microbial biomass and its activity increase, directly promoting the degradation process of organic carbon, whether it is in an active or inert state [24].

(3) Favorable degradation environment: Soil bulk density decreases with increasing organic carbon content [22,25], thereby improving soil ventilation conditions, enhancing oxygen availability, and facilitating the diffusion of soil carbon dioxide. This provides a better external environment for the organic carbon turnover process.

These three reasons result in a higher degradation coefficient for organic carbon at high contents. Simultaneously, the latter two reasons also directly promote the degradation of organic materials. Consequently, only a smaller amount of carbon is converted into organic carbon, leading to a decrease in the humification coefficient of organic materials.

Based on these three mechanisms, this study quantifies them into three methods: (1) As organic carbon content increases, the proportion of newly inputted carbon that forms organic carbon decreases. (2) A higher proportion of newly formed organic carbon enters the easily degradable labile carbon pool and remains unprotected. (3) The degradation rates of different organic carbon pools all increase. The results show that all three expressions exhibit an asymptotic *C-I* relationship (**Figures 10** and **11**), indicating that these three mechanisms are possible. Another phenomenon relates to the proportion of the easily degradable labile organic carbon pool to total organic carbon. Apart from the mechanism where "a higher proportion of newly formed organic carbon enters the easily degradable pool," the "increase in degradation rates of different organic carbon pools" can also lead to an increase in the proportion of the easily degradable organic carbon pool (**Figure 12**). However, neglecting the negative feedback mechanism of organic carbon turnover and the decrease in the proportion of newly inputted carbon forming organic carbon does not change the proportion of the labile organic carbon pool. Evidently, changes in the proportions of different organic carbon pools are the result of a combination of chemical mechanisms (such as adsorption-desorption equilibrium), biological mechanisms (enhanced microbial degradation drive), and physical mechanisms (better external environment). Therefore, apart from the relationship between organic carbon content and carbon input levels, the proportion of different organic carbon pools to total organic carbon content can also reflect the role of organic carbon content in its own turnover.

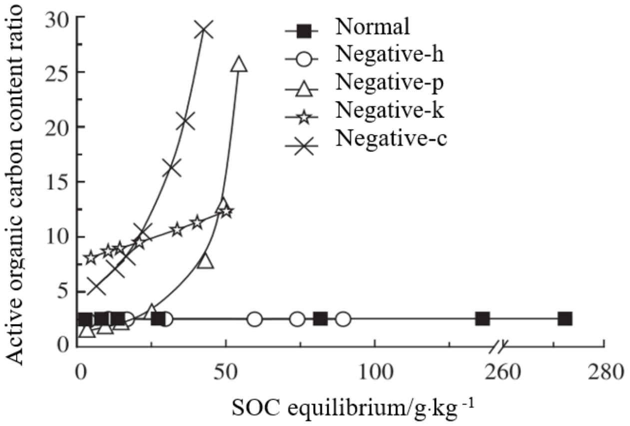


Figure 12. Relationship between active organic carbon ratio and total organic carbon content

4.3. Application of negative feedback in organic carbon turnover

From the perspective of organic carbon protection mechanisms, limited protection capacity is the cause of organic carbon saturation [12]. In terms of factors influencing organic carbon turnover, negative feedback leads to organic carbon saturation, and the soil's limited protection capacity is one of the fundamental reasons for this negative feedback. If computer models do not consider negative feedback, they may overestimate the soil's carbon sequestration capacity at high carbon input levels (such as high organic fertilizer usage or increased terrestrial plant net primary productivity due to elevated atmospheric CO_2 concentrations), or underestimate soil carbon sequestration at low carbon input levels (such as deforestation or lack of organic fertilizer input like straw). Therefore, it is essential to consider negative feedback in organic carbon turnover in computer models. Unlike mature models such as DNDC, RothC, and CENTURY, which treat organic carbon as a multi-component and consider changes in microbial biomass, this study only simulates the phenomenon of negative feedback in organic carbon turnover. When simulating the three mechanisms behind this phenomenon, it only reflects the trend of the mechanisms. Therefore, it is necessary to quantify the three mechanisms that form negative feedback in future organic carbon turnover research. However, as the number of model parameters increases, and some parameters are difficult to obtain, it can lead to parameter error accumulation, which may reduce the usability and accuracy of the model. Hence, a balance between model complexity and accuracy is required [20]. The simulation of organic carbon saturation or negative feedback will be one of the directions of future model research [26].

5. Conclusion

The humification coefficient of organic materials decreases with increasing organic carbon content, while the organic carbon degradation coefficient increases with increasing organic carbon content. This negative feedback further inhibits subsequent changes in organic carbon, meaning when organic carbon content decreases, negative feedback slows down the rate and process of its reduction; similarly, when organic carbon content increases, negative feedback inhibits the speed and process of its increase. This negative feedback not only causes organic carbon content to change asymptotically over time but also makes organic carbon content (including both equilibrium and non-equilibrium states) increase asymptotically with increasing carbon input levels.

The relationship between organic carbon and carbon input levels, as well as the proportion of different organic carbon pools to total organic carbon content, can reflect the negative feedback of organic carbon turnover. These aspects should receive more attention in future organic carbon turnover research.

Considering negative feedback in organic carbon turnover in the construction of organic carbon computer models is not only reasonable and feasible but also necessary.

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Disclosure statement

The authors declare no conflict of interest.

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