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Forest Soil C: Stock and Stability under Global Change

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Abstract

Both plant biomass and soil C are potential to C sequestration by offsetting atmospheric CO₂. In forest, aboveground and root biomass are the major sources of soil C. Estimation of biomass is challenging due to methodological uncertainty at different spatial scale. The role of root-mycorrhizal symbiosis on long-term C storage in soil is yet to be established. Microbial biomass and community structure are crucial for C regulating processes in soil, and the genomic approach is promising for insights of soil microbial processes in relation to C stock and stability. The dynamics of dissolved organic C (DOC) in soil is extremely complex as many biotic and abiotic factors are involved in the release and flux of DOC in soil solution. Typically, the stability of soil organic C refers to recalcitrant, humified substances and physically protected materials, having the residence time of decadal to millennium scale; however, recent studies showed that microbial inaccessibility and physical protection are the dominant mechanisms. Priming is a potential process of decomposing old C and may have an antagonistic impact on soil C stock, particularly stable C in deep soil. Coupling the C pools with the stability processes is necessary for assessment of forest C balance.

Keywords: soil C stock, biomass, soil microbes, C stability, C fractionation, priming effect

1. Introduction

Carbon dioxide (CO₂) is one of the major greenhouse gases (approximately 72% of the total anthropogenic greenhouse gases) and considered as a primary agent of global warming [1]. It has been estimated that CO₂ is responsible for about 9–26% of the global greenhouse effects [2]. The concentration of carbon dioxide in the atmosphere has increased from 280 ppm of the pre-industrial era (1750) to 408.84 ppm in July 2017 with increasing rate of 2.11 ppm per year [3]. The dramatic rise of CO₂ concentration is attributed largely to human activities, and since soil is the second largest reservoir of C in the terrestrial ecosystems, there is a strong link

between soil and atmospheric C through C cycle. Globally, the soil C pool is about four times larger than the atmospheric pool, and consequently, any change in the flux of CO₂ from soil to atmosphere has paramount importance in the balance of atmospheric CO₂ [4]. Among different terrestrial ecosystems, forest soil contains more than two third of the global soil organic C reserve, although forest occupies only 30% land of the earth surface, creating the highest carbon-rich domain among different land use-based ecosystems. Atmospheric C, once fixed into plant tissues through photosynthesis, is transferred to the soil as plant litter. Part of this C is stored in soils, and the major portion is released to the atmosphere through soil respiration. Some of the stored C in soil can be sequestered as soil organic matter and/or humus for as long as a million years [5]. As such, the potentiality of forest soil for long-term C sequestration is instrumental to many research efforts worldwide. In forest, soil C stock mostly derives from decaying above and belowground plant tissues and root exudates; however, the relative contribution of fine root and accompanying mycorrhizal turnover on soil C storage are considering more vital than the C in aboveground litter [6]. Microbial biomass and the community structure of bacteria, archaea and mycorrhizal fungi contribute to soil organic C stock through biomass production at one hand and releasing stored C through decomposition and respiration processes on the other. Dissolved organic carbon (DOC) is an impotrant C pool in forest soil ecosystems, which considered as a labile and more easily degradable substrates that influence the storage of C in forest soil.

There are several mechanisms of C stability in soil such as formation of humus and other recalcitrant C, formation of organo-mineral complexes, accumulation of C in deep soil layers, etc. Many studies revealed that the considerable amounts of C are in deep soil layers. These C are considered more resistant to microbial degradation due to physical protection, chemical recalcitrance

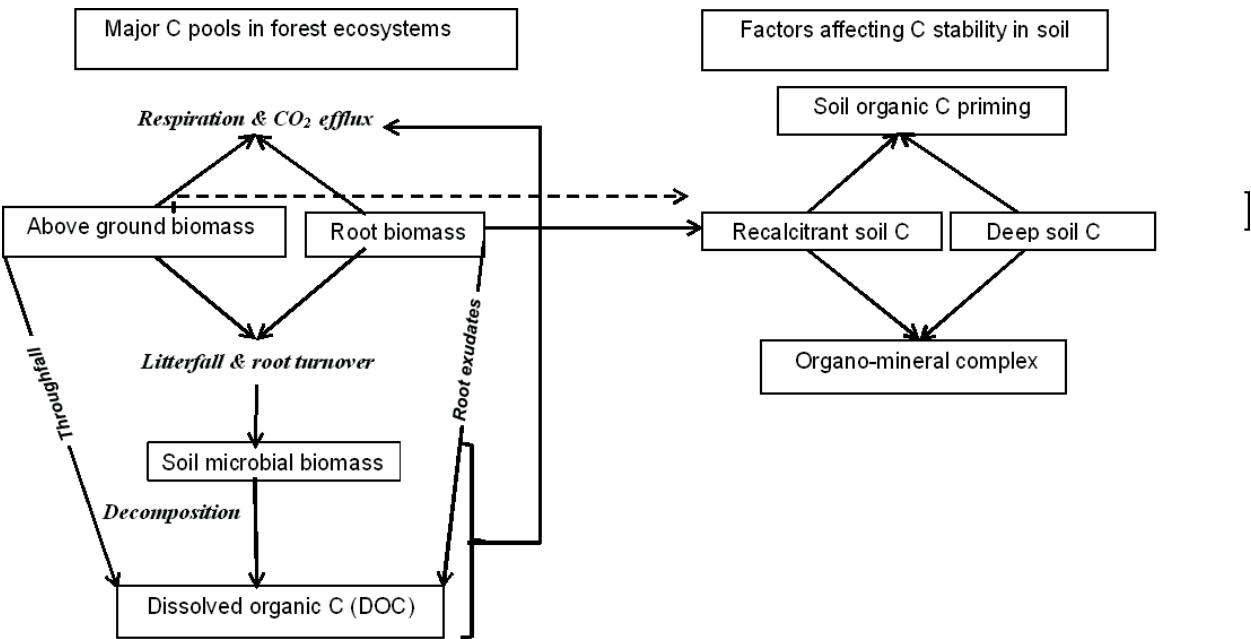


Figure 1. Link between various C pools and stability processes in forest ecosystems. Aboveground biomass and root biomass are the primary source of recalcitrant C; however, root biomass C is considered as more potential than the aboveground biomass (shown as broken line) from soil C stability perspective.

and limited microbial activity [7]. On the other hand, priming is a C unstabling process in which old soil C is decomposed in the presence of new fresh C. The process has been receiving much attention as a potential mechanism of degradation of stable soil organic matter. Our mechanistic understanding of these processes is still unclear, because the heterogeneity of soil and climatic conditions influences the processes considerably. This chapter includes the in-depth discussions on the conceptual basis and functional significance of these major aspects regarding storage and stability of soil C. The C stock part of this chapter includes the following topics: (1) contribution of aboveground plant biomass on storage of soil C, (2) fine root and mycorrhizal biomass production and turnover, (3) soil microbial biomass and community structure and (4) dissolved organic C in forest soil. The stability-related issues are as follows: (1) formation of recalcitrant C pool and C fractionation, (2) organo-mineral complexes and physical protection to soil C, (3) protected C in deep soil and (4) priming—a potential mechanism of destabilizing soil C. The relationships between C pools and stability processes are shown in **Figure 1**.

2. Storage of C in forest soil

In the soil ecosystems, C generally exists in two major forms depending on the soil type: a relatively dynamic organic pool as soil organic matter (SOM) and the inorganic forms mainly as carbonates, both are linked to atmospheric CO₂ through the processes of C cycle. Among different land use-based ecosystems, forest soil contains about one third of soil organic carbon [8]. The accumulation of organic C in forest soils depends on a number of factors such as plant biomass (above and belowground), litter quality and soil microbial activities, management practices and climatic factors such as temperature, precipitation and fire. Plant biomass C and soil C are the two C pools that constitute major part of the ecosystem C reserve [9]. Other pools are forest litter, decomposed detritus, microbial biomass, dissolved organic materials and humus. Among different processes, photosynthesis, canopy respiration, litter flux, litter decomposition, soil respiration, SOC sequestration etc. play important roles in forest C cycle. Thus, the storage of soil C is continuously influenced by dynamics of forest ecosystems and also by many biotic and abiotic factors including climate changes [10]. Because of the interdependency of these carbon pools, it is imperative to evaluate ecosystem C in an integrated approach rather than assessing any pool individually. It is worthwhile to study the controlling elements of C storage mechanisms in addition to stock size for in-depth knowledge of the processes. The factors that affecting the nature and properties of forest soil are quality and quantity of litter, soil nutrient status, root activities, interception of atmospheric deposition, canopy interactions, leaching and microbial activities [11]. C stock in soils of the three major forest biomes follows the order tropical < boreal < temperate and collectively constitutes the largest C sink in terrestrial ecosystems [9]. The quantities of C stock in major global forest biomes are shown in **Table 1**. These huge organic C pools are however not constant over time. The size of the C-stock is related to the quality of soil organic matter in relation to biodegradation and subsequent inorganic C efflux from soil and supply of fresh organic material to the soil. Therefore, the balance between input of organic matter mainly from vegetation in the forest ecosystem, and losses mainly due to decomposition-respiration and leaching, determines the net C storage potential in the soil [12].

Components	Major forest biomes of the world			Total	Proportion
	Boreal	Temperate	Tropical		
Forest area (million hectare)	1135	767	1949	3851	31% of global ice-free land
Forest C stock (including living and dead biomass and soil) (Pg C)	271.5	118.6	471.0	861.1	46% of terrestrial biosphere C stock
Forest biomass density (Mg h ⁻¹ dry mass)	95	121.5	268.9	188.3	–
Total plant biomass forest (Pg C)	53.9	46.6	262.1	362.6	42% of global forest C reserve
Aboveground biomass (Pg C)	43.8	38.8	206.4	289	80% of forest biomass C
Root biomass (Pg C)	10.1	7.8	55.7	73.6	20% of forest biomass C
Litter + dead wood (Pg)	43.1	15.4	57.6	116.1	13% of global forest C reserve
Soil organic C stock (Pg)	174.5	56.7	151.3	382.5	44% of global forest C reserve

*Pg (Peta gram) = 10¹⁵ g

Biomass C was estimated as 50% of dry mass. Aboveground and root biomass fractions were calculated by using root: shoot ratio of 0.23, 0.20 and 0.27 for boreal, temperate and tropical biomes, respectively [119].

Table 1. C stock in various components of forest ecosystems under different forest biomes [24].

Both natural and human induced factors can influence the concentration and stock of soil C in the forest ecosystems. The natural factors are climate, vegetation, soil quality, soil microbial populations, and forest fire, and anthropogenic factors are forest management, afforestation, deforestation, etc. [9]. Tree species (or species composition) is the single most important factor that influences SOC storage in the forest. Most of the forest ecosystem processes are generally controlled by the plant's functional traits in a species-specific way. Litter quality from broadleaved trees is generally higher than that from coniferous tree [13], but differences between broadleaved species and even between genotypes were also observed. Species-specific root turnover rate contributes to soil C dynamics in association with ecto- and arbuscular mycorrhizal fungi in temperate broadleaved forests [14, 15]. The broadleaved trees are particularly important for its higher contribution to carbon sequestration than the narrow leaved coniferous plants. The efficiency of CO₂ uptake is higher in broadleaved species than coniferous because of the low leaf area of coniferous species [16]. Forest management activities that affects SOC stocks includes thinning, harvesting, site preparation and maintaining continuous canopy cover [17], fertilization and liming [18]. Thinning practice can affect soil C storage negatively in several ways: thinning causes changing the stand microclimate by reducing evapotranspiration and increasing soil temperature and can stimulate the decomposition of the forest floor resulting a decrease in soil C pool. In addition, litterfall can be lowered in heavily thinned stands and thus decrease SOC stocks [19]. In contrast, enhanced growth of the understory vegetation due to thinning measures was observed in an experimental site in Finland which ultimately compensated for the reduction of C from tree biomass [20]. Harvesting can affect soil C storage positively or negatively. Removal of whole trees reduces seasonal litter inputs and disturbance affects forest floor and mineral soils leading to soil C loss. In addition, harvesting

causes decrease in photosynthesis and can turn the forest into a C source condition [21]. The consequences of harvesting can persist for variable time frames. For example, measurement of net ecosystem C exchange showed that the increased rates of soil respiration due to harvesting continued for at least 14 years after logging [22, 23]. However, other research has shown that harvest residues left on the forest floor can also increase C stocks on mineral soils [19]. As clear cut harvesting decreases SOC stocks, continuous cover forestry may be an effective option for reduction of soil C losses following selective harvesting and thinning operations. Fire is another major disturbance that can impact soil C stocks in forest ecosystems and may have a long-term impact on C stock in soils of the boreal regions. The impact of fire on SOC stock depends on fire temperature and duration, existing SOC stock and its distribution in the soil profile and the changes in the decomposition rate of SOC following the fire event. It is obvious that most of the forest management interventions have negative impacts on the storage of soil C; however, minimizing the disturbance to soil and stand structure can reduce possibility of C loss [19]. From the above discussions, it is obvious that the nature and properties of soil organic C are highly dynamic and depend on many abiotic and biotic factors within ecosystem. In the following sections, we discuss the significance and mechanistic link of four major C pools with soil C storage in relation to climate change.

2.1. Aboveground biomass and soil C

Two major compounds that are involved in the immediate release of CO₂ to atmosphere and that are boosted by human activities are simple carbohydrates and hydrocarbons (fossil fuel). Carbohydrates in plant biomass are synthesized photosynthetically by fixing atmospheric CO₂; therefore, forest biomass has a potential for reduction of atmospheric CO₂ to some extent, and thus the higher production of biomass through afforestation/reforestation has been recognized as an effective, low cost option for mitigation of climate change impacts [1]. Globally forests possess 86 ± 66 Pg of C and the biomass of living trees contributes 42% of this stock [24]. Expanding tree biomass may also increase the carbon stock in soil as 70% of soil organic C derives from plant biomass [25, 26]. Estimation of biomass is important for many purposes. At a national or regional level, when biomass is considered as a raw materials or energy source, it is necessary for planners and policy makers to know how much timber or fuel wood is available for national consumption. From an environmental management point of view, biomass quantification is important to assess the productivity and sustainability of the forest [27]. Biomass is also an important indicator of carbon sequestration, as forest biomass absorbs C from the atmosphere and stores it in the plant tissue [28].

Generally, the biomass of forest stands can be defined as the quantity of dry materials or sometimes expressed as the amount of carbon contained in woody plants (trees and shrubs) and understory vegetation per unit area (gm⁻²). According to FAO [29], biomass is “organic material both aboveground and belowground, and both living and dead, e.g., trees, crops, grasses, stem, stump, branches, bark, seeds, and foliage.” Aboveground biomass is the total amount of biological material present above the soil surface over a specified area [30]. Tree biomass is generally divided into different components such as foliage, branches, stem, stump, etc. on the basis of physiological functions. As atmospheric CO₂ sequesters in the plant biomass through photosynthesis processes, the quantification of the vegetative biomass is essential in forest ecosystem studies in order to estimate carbon pools at multiple scales [31].

2.1.1. *Forest biomass and climate change*

Net primary production (NPP) is the annual plant biomass that remains in the woodland ecosystem after release of CO₂ as autotrophic respiration. Part of this NPP is subjected to another two processes, viz., decomposition and heterotrophic respiration, when biomass transfers to the forest floor as litter. These ecosystem processes are generally controlled by the plant's functional traits in a species-specific pattern [32]. Tree biomass is analogous to primary production as biomass accumulates atmospheric carbon through photosynthesis. Therefore, the net primary production (NPP) is generally estimated by measuring plant biomass and thus considered as a basic parameter in ecosystem research [33]. However, estimation of forests biomass has received much attention in recent years because of firstly, anthropogenic emissions of CO₂ are thought to be partially offset by increasing forest biomass [34] and secondly, a change in biomass regionally is associated with important components of climate change [35]. Therefore, accurate estimation of biomass is necessary for better understanding of deforestation impacts on global warming and environmental degradation at one hand and ecosystem C sequestration and storage on the other. Woody biomass is particularly important for long-term C sequestration. Generally, as a rule of thumb, 1 m³ wood stores ~0.92 t CO₂ and the woody biomass fixes C depending on its maturity and post-harvesting use [34]. Although the use of wood product as biofuels results in the release of stored C immediately, it provides sustainable C benefits as a substitute of fossil fuel. Alternatively C may be fixed for hundreds of years if it is used for houses or furniture [34].

Deforestation is the human-induced conversion of forest to non-forest land use and causes immediate emission of huge forest carbon stocks through land clearing [1]. Due to deforestation, C is released from both plant biomass and emission of soil C due to disturbance. Forest degradation, especially nonsustainable harvesting, anthropogenic disturbance and collection of fuel wood, causes substantial reduction in forest C stock. Thus, the destruction of forest biomass has raised concerns over global warming and climate changes at a global scale. Conversely, sustainable forest management measures and preventing deforestation can play key role in mitigation of climate change [1]. As the most widely distributed terrestrial ecosystems on earth, forest contains huge C stock in living biomass (in 2005, it was equivalent to more than 1 million metric tons of CO₂ [34]) resulting the uptake of atmospheric carbon and the conversion of greenhouse gases to biomass. Therefore, forests play a significant role in the global climate change, through both CO₂ absorption and emission.

2.1.2. *Estimation of forest biomass*

To fulfill the requirements of the Kyoto protocol, it is necessary to estimate the removal and accumulation of C in forest biomass. The field measurement is considered to be accurate but proves to be very costly and time consuming [35]. The conventional method of biomass estimation is based on field measurements. However, this approach is time consuming, labor intensive and difficult to implement in remote areas [35]. For small-scale studies, the conventional method may be appropriate; but for studying the area of wider spatial scale or the issue of studying carbon sequestration, the use of the field measurement approach is much more challenging. The most common approach to estimate the aboveground biomass includes harvesting and measuring the dry mass of sample trees and use of allometric regression functions [36]. Allometric functions established in one area are often expected to be applicable to an areas

with a similar climate and other conditions, e.g. site conditions, silvicultural measures, etc.; therefore, species-specific equations are getting wide acceptance globally. The role of remote sensing technologies for forest biomass assessment has also been recognized [37], and many studies had been conducted for this purpose worldwide. Forest information, including species, crown closure, age, height and volume, can usually be acquired through aerial photo interpretation [38]. In this technique, multiple regression models are developed based on integration of satellite images and vegetation inventory data and thus provide a method for biomass estimation. Geographic information systems (GIS) is recognized as a powerful tool for ecological studies and combination of GIS data and modeling techniques can improve the model performance. Lidar (light detection and ranging) technology is an active remote sensing tool that provides three-dimensional vertical measurement of ground target and thus can be quantified certain forest attributes such as mean stand height, horizontal and vertical crown dimensions, etc. Using such attribute data, forest characteristics like stem diameter, basal area and aboveground biomass can be calculated from allometric relationships [39]. Although remote sensing techniques provides information on stand-related parameters, Franklin and McDermid [40] pointed out that most of the orbital sensors are inadequate to fully capture forest stand parameters with high level of confidence.

2.2. Fine root and mycorrhiza

Most studies on the role of species traits in C cycling have focused on aboveground biomass, while only recently the importance of root litter for soil C cycling in forest has become apparent [41, 42]. Belowground tree biomass includes all structural coarse roots, fine roots, mycorrhizal fine roots and the mycorrhizal hyphal mycelium [43]. The contribution of coarse roots is mainly as support organs and as long-distance transport pathways, and the fine roots in association with mycorrhizal fungi facilitates nutrient and water uptake, and the uptake of nutrients often involves secretion of root exudates [44]. Although aboveground forest biomass accounts for the majority of the total accumulated biomass in the forest ecosystem, recently research studies on the functions and ecological role of root biomass have been receiving more attention, realizing the fact that root production contributes about 33% of the global annual net primary production [45]. In forest ecosystems, fine root production and turnover represent a considerable proportion of C flux, which transfers to soil organic matter pool through root decomposition and rhizodeposition [42, 46]. In general, root derived C is recognized as more recalcitrant than leaf C. In a decomposition experiment of fresh leaf and root litter from Norway spruce (*Picea abies*), Hansson et al. [47] found that roots decompose more slowly than needles due to litter quality, especially higher lignin content in spruce root (35–37%) compared with needles (15%), suggesting significant contribution of root-derived C to soil organic C storage.

A symbiotic association between mycorrhizal fungi and plant root systems is extremely important in nutrient acquisition and soil C storing and more than 90% of plant species form this mutualistic association. Fungi colonize in the root systems of plants and develops a network of filaments to absorb the soil nutrients which are not available to plants and make it accessible to plants; in return, fungus obtains C sources (energy) from the host plant. Godbold et al. [48] reported the mycorrhizal external mycelium as dominant pathway through which plant photosynthetic C compounds are transferred to soil organic matter. A study with different tree species showed that up to 60% of plant photosynthates C are transferred to soil by

mycorrhizal hyphae [48]. Thus, mycorrhiza plays an important role in plant growth and root development. The biomass and products of mycorrhiza make a significant contribution to soil C and N pool. Rillig et al. [49] found that the quantity of mycorrhiza can be more than free living soil microbial biomass in some tropical forest (0.08–0.2% of total C in old forest). In addition, ectomycorrhizal and ericoid mycorrhizal fungi can produce N degrading enzymes and thus allowing them greater access to organic N sources than arbuscular mycorrhizal fungi. Therefore, soil ecosystems, dominated by ectomycorrhizal and ericoid fungi might have higher soil organic C stock than the arbuscular mycorrhiza due to greater N availability [50].

2.2.1. *Measurement of fine root*

The relationship between global climate change and plant growth and the role of forests as C sequester have encouraged the refinement of the estimates of root biomass and production. In comparison to aboveground biomass, the estimation of belowground biomass is more complicated and laborious. As a result, fewer case studies have been conducted to investigate tree root biomass at a stand level, and more uncertainties exist in belowground biomass estimation on a large scale. Different procedures and techniques have been followed to study the fine root biomass and turnover in the field. However, so far no one technique has been recognized as the best universally. The direct approaches are sequential soil coring, ingrowth cores, minirhizotrons and root mesh, while the indirect methods include carbon fluxes or nitrogen budget approaches and correlations of root biomass or production to pools or fluxes of limiting abiotic resources [43, 51].

Sequential soil coring: The sequential coring method is the most common approach to estimate fine root biomass and turnover in the field and thus the estimation of belowground NPP. The coring depth depends on the age and type of forest species but typically 0–30 cm depth is employed for estimating root biomass, as coring to this depth has been shown to capture a high percentage of the total fine biomass [52]. The difference between biomass estimates at each sampling date is used to estimate the fine root production. Among the different approaches of data analysis, estimating fine root NPP is the most commonly used approach where the differences in biomass between the maximum and minimum fine root biomass measured during a year [51]. A second approach, introduced by Santantonio and Grace [53], includes the Compartmental Flow Model or Decision Matrix method, which estimates changes in live and dead root biomass and losses from dead roots due to decomposition. The third approach was introduced by Persson [54] where all positive differences in root biomass between each sequence of sampling dates were summed up. If the intervals between the root sampling are too long, the intervening variation can be lost [55]. Vogt et al. [51] suggested that since a mean fine root biomass value is obtained by integrating all sampling intervals during the year, the error is less in this method compared to other methods of measuring production.

Ingrowth cores: The ingrowth core technique involves the replacement of a mesh bag filled with root-free soil into a cored or augured hole, and after a period of time when new roots grow into the core, the whole mesh bag is removed from the hole by complete excavation. The ingrowth core method has been used alone or in association with the sequential core method to estimate fine root production [55]. An over estimation of root productivity due to high proliferation of new root growth into the competition-free spaces is the major disadvantage

of ingrowth core method. The artificial repacking of the soil may alter bulk density. However, it allows the direct calculation of fine root production and is thus especially suitable for comparison of fine root production between sites and treatments.

Minirhizotrons: The minirhizotron uses a clear transparent tube with a miniature camera, which is inserted into the ground. The camera fitted inside the tube can capture photographic images of fine root growth at different depths outside of the tube surface. The minirhizotron technique allows spatial sampling by the placement of multiple observation tubes in the ground. Within the last decade, the use of minirhizotrons has become a favorite method of many researchers [56, 57]. The minirhizotron technique can be used to obtain (1) quantitative information on root length, rooting density, root dynamics, lateral root spread and the depth of rooting and separation of roots into structural/functional diameters classes and (2) qualitative information on root color, branching characteristics, patterns of senescence and observations of parasitism and symbiosis [58].

Root mesh method: The root mesh method has been proposed as an alternative technique that overcomes the problems associated with the conventional methods for estimating root production [59]. Using this method, root production is estimated by placing a mesh vertically into forest soil for a specific period of time and then measuring the number and weight of root that grow through the mesh. The procedure that is much easier than other methods requires only simple equipment and causes minimal soil disturbance [59]. Recently, ground penetrating radar (GPR) is becoming popular to estimate root biomass because of less laborious and nondestructive nature of the approach. In this method, 3D images of the root system can be acquired by close range remote sensing techniques. Although a convenient and promising approach, the accuracy of the method is low for estimating entire root system [60, 61].

2.3. Soil microbial biomass and community structure

Soil microorganisms are main players of most of the biogeochemical processes in forest soils such as decomposition, respiration, fixation of nutrient elements and soil formation and can be quantified as soil microbial biomass—a broad index to express the relative amount of microbes in soil. As soil microbes themselves constitute a very active C pool, they are considered as labile C in soil. Typically, microbial biomass comprises about 1–5% of total organic C in soil [62]. The quantity of soil microbial biomass is influenced by the quantity of organic matter and also availability of nutrients from these organic sources. Because microbes are entirely depend on these substrates for their energy requirements. Due to their key roles in cycling and availability of soil nutrients, formation of soil structure and sensitivity to management and land use, microbial biomass is recognized as an indicator of soil quality. On the other hand, soil microorganisms and enzymes are the most important factors for decomposition and subsequent respiration processes and thus directly link to the storage and stability of soil organic C.

Among the microbial community in soil, bacteria and fungi are the key decomposers. They breakdown and mineralize litter and decompose most of the plant biomass produced in the terrestrial ecosystem. Fungi are generally considered to play a dominant role in decay processes, and its degrading mechanisms and enzyme systems have been well documented [63, 64]. In contrast, although recognized as important decomposer, bacteria received less attention

and its role in leaf litter decomposition remains unclear [63]. In general, the mechanism of heterotrophic respiration includes the mineralization of C that is incorporated to soils through plant litter and rhizodeposition and conversion to CO₂ by the soil microbes. Therefore, soil microbial community plays a crucial role in the respiration process. In this process, fungi play the dominant role than bacteria through their higher enzyme capabilities and affect soil C cycling processes efficiently. However, the role of soil microbial community structure on soil respiration in forest ecosystems is still unclear, particularly in tropical regions [65].

2.3.1. *Factors affecting microbial biomass*

Many soil biotic, abiotic and environmental factors can affect the respiration process. Climatic factors, particularly temperature and precipitation, play major roles on distribution of soil microbial community from local to regional scales. As global climate change predictions indicated significant changes in temperature and rainfall patterns, it is uncertain how climate change may reshape the soil microbial community and the functioning. Temperature sensitivity of soil microorganisms can affect their relative abundance and function. It has been shown that in temperate forest increasing temperature by 5°C can change the relative abundance of bacteria and bacterial: fungal ratio [66]. Similarly, soil moisture is also an important determinant of microorganisms and change in precipitation can alter soil microbial biomass through changing structure of microbial community. However, the response of different microbial community to soil moisture may not be similar. For example, Kaisermann et al. [67] reported the shifting of one dominant fungal group to another due to small change in soil moisture availability, while soil bacteria remained constant.

Soil properties such as organic matter content, soil pH and soil texture are strongly correlated with soil microbial biomass and community structure at local level. Soils with higher organic matter content are generally high in soil microbial biomass, most probably because of higher nutrient availability. Decomposable soil organic matter can provide sufficient C and N for growth and activities of soil microorganisms and consequently higher microbial biomass in soil. Soil pH is one of the most influential factors that affect microbial community in soil. In fact soil pH regulates multiple soil parameters that are closely related to microorganisms, such as C and nutrients availability, solubility of metals, crop growth, etc. Rousk et al. [68] reported higher fungal growth and lower bacterial growth at low pH (~4.5) and below pH 4.5 inhibited all microbial growth due to release of free aluminum. Clay minerals in soil can influence the distribution of soil microbial biomass through absorbing organic compounds and influencing substrate availability. A positive correlation between clay content and soil microbial biomass C in soil was reported by some investigators [69]. Tree species could influence the composition and function of soil microbial community structure by changing forest microclimates, quality and quantity of above and belowground litter production, production of root exudates and symbiotic association with mycorrhiza and other fungi [70]. Thus, in general, it is presumed that tree species can influence soil microbial biomass C and N. However, Liu et al. [71] reported that the influence of individual species identity on microbial communities of soil and rhizosphere could be pronounced when the trees were grown in monoculture. For example, the concentration of total phenols and condensed tannin in leaf litter can suppress soil microbial biomass depending on the concentration of these compounds. Qu and Wang

[72] found that low concentration of phenolic enhance soil microbial biomass by providing energy source for microbes; however, the allelopathic effects of high concentration phenolic can suppress soil microbial biomass C.

2.3.2. Methodological aspects

Microbial biomass pool size in soil can be measured by various direct and indirect approaches. The basic principal of these methods is based on the estimation of the quantity of C present in the biomass of soil microbes. The direct methods include straight microscopic counting and counting of density-based most probable number (MPN) of microbes in soil dilution series. However, MPN method is suitable for bacterial cell and fungal spores [73]. The indirect methods include fumigation and extraction method, extraction of phospholipid fatty acids (PLFAs) and substrate-induced respiration (SIR) methods. The classical method of measuring soil microbial biomass includes the extractions of C in soil samples with and without chloroform fumigation. Fumigation process lyses the microbes in soil producing higher CO₂ than nonfumigated soils, and C in microbial biomass can be calculated from the difference between chloroform treated and untreated samples. The method yields a good estimation of soil microbial biomass although some microbes may be resistant to chloroform fumigation. Another common indirect approach is extraction of phospholipid fatty acids (PLFAs), which is the integral component of microbe's cell membrane and accurately reflects the amount of microbial biomass in soil. An important advantage of this method is the analysis of soil microbial biomass according to different taxonomic groups. Recently, DNA- and RNA-based analyses are receiving more attention, because the genetic materials are powerful tools to discriminate various microbes more accurately. DNA can be extracted and analyzed following polymer chain reactions (PCR). To analyze soil microbial diversity, 16 s ribosomal RNA (rRNA) sequencing technologies are also considered very useful approach [74]. Although there are some limitations with analyzing soil samples, the genetic approaches are seemed to be promising for the studies of soil microbial ecology in future.

2.4. Dissolved organic C in forest soil

Dissolved organic C (DOC) is a heterogeneous mixture of various organic compounds in soil solution, derived from both biotic and abiotic origins and recognized as a bioavailable and mobile C pool in soil. DOC consists of a wide range of substances ranging from low molecular weight compounds such as aliphatic carboxylic acids to large polymers of fulvic and humic acids. The major part of the DOC comprises macromolecules of fulvic and humic acids and the dominant low molecular weight compound is monocarboxylic acid [75]. Other constituents of DOC include sugars, organic acids, dissolved nutrients (C, N, P, and S) and low molecular phenolic [76].

2.4.1. Ecological significance

DOC plays important roles in many processes of C cycles in lithosphere and hydrosphere including C flux to deep mineral soil layers and aquatic bodies. Tree biomass C is transferred to soil systems through litter fall, throughfall and subsequent decay processes. Release of

DOC from vegetation and soil organic matter is recognized as an important pathway of C flux during these processes. Studies on DOC production and flux are indispensable for evaluating the impacts of environmental changes on C cycles in terrestrial ecosystems. In deep mineral soil, most of the DOC is subjected to adsorb on mineral surfaces or formation of particulate organic materials (POM), which are highly resistant to decomposition and thus potential for long-term C storage [77]. The movement of DOC from the litter layer to lower mineral soil plays an important role in the activities of belowground autotrophic and heterotrophic soil microorganisms and leaching loss of C and N. DOC is the major form of C that can be sequestered by clay particles in the deep soil layers or hydrologically transported from the forest floor to underground and surface water resulting eutrophication and thus can damage water quality. The negative impact of DOC on C storage was also reported by some investigators [78]. DOC in dissolved organic matter provides readily available C as a source of energy for soil microbes to stimulate the degradation of old organic matter and thus can have negative impacts on soil C storage. Recently, Jones et al. [79] proposed to use DOC as soil quality indicator in large-scale soil and land use survey, because DOC contains different chemical compounds that are specific to particular functional soil and plant types.

2.4.2. *Production*

In forest soil, dissolved C compounds are released from both fresh and decomposed organic materials. Other sources of DOC are throughfall, microbial biomass and roots exudates [76]. Between these two primary sources, humus has been recognized as the more dominant sources of DOC than the recent fresh litter. In forest floor, incompletely decomposed litter by fungi might be the most important source of dissolved organic materials, and the microbial metabolites contribute significantly to the amount of DOC released during the degradation processes. It is obvious that DOC production is closely related to litter decomposition on forest floor and a positive correlation between carbon decomposition rate and DOC leaching in forest ecosystems has been reported by some investigators [80]. McClaugherty [81] reported that 33% of the soluble compounds in sugar maple litter gradually leached to DOC pools.

2.4.3. *Factors controlling DOC production*

Both field and laboratory experiments showed that the production rate of DOC was controlled largely by substrate (litter and soil organic matter) quality, activities of soil microorganisms and temperature [82]. At the field level in northern Germany, annual carbon transport from litter layers of alder and beech forest was estimated as 0.8–1.4% of annual gross carbon production [83]. In temperate forest ecosystems, it has been estimated that annual DOC flux from forest floor to mineral subsoil horizons was 115 to 500 kg C ha⁻¹ [84]. But below the mineral soil layers, the concentration of DOC is very low, most probably because of fixation of organic molecules on the mineral particles or mineralization of organic substances to CO₂. The quantity of annual DOC production depends on numerous biotic and abiotic factors. In forest ecosystems, tree species identity can influence the production of DOC, because of species-specific quality and quantity of litter which is primary source of DOC. In general, coniferous trees accumulate higher amount of organic C in the forest floor than the deciduous broadleaved

species and consequently affect quantity of DOC in soils. However, in a study with coniferous (*Abies grandis* and *Picea abies*) and broadleaved species (*Fagus sylvatica* and *Quercus robur*), Strobel et al. [85] found that although quantity differs significantly between tree species, the composition, chemical properties and reactivity of DOC were not influenced by tree species identity. Abiotic factors such as temperature and soil pH found to have impact on the amount of DOC accumulation in forest floor and peat soils [82].

2.4.4. Measurement

Determination of dissolved organic nutrients in soil received less attention than in fresh water and marine ecosystems. In general, dissolved organic compounds in soil can be extracted directly from soil solution by centrifugation except when soils are in dry condition [86]. A more suitable approach is chemical extraction with various extracting solvents. The most common method consists of extraction with potassium sulfate (0.5 M) at 20°C, shaking and centrifuging. The concentration of DOC in the extract is measured by total organic C (TOC) analyzer. Shaking time, temperature and the ratio between soil weight and volume of extraction solution (w/v) are the most critical factors during the analysis. Overall, the efficiency of DOC recovery depends on the sample preparation and extraction procedures [86].

3. Stability of storage C in soil

Soil organic C stock is sensitive to climatic, ecological and management changes, and thus, the stability of soil C is one of the major sources of uncertainty to forecast the impacts of forest ecosystems on future climate change. In general, the stability is thought to be an inherent property of organic matter and mainly depends on the quality, decomposability and turn over time of organic substances. However, some researchers argued that stability is not a molecular property of soil organic matter and therefore it cannot be intrinsically stable, rather the surrounding environment that developed by soil physicochemical and microbial properties is the main determinant of soil C stability [7]. For example, although lignin and lipids have long molecular structure and recognized as recalcitrant in nature, the isotopic analysis revealed that under appropriate conditions these compounds can be decomposed faster than the other organic compounds [7]. As the components of soil organic matter are complex and heterogeneous in terms of origin, chemical structure and biodegradability, the existing time of these components in soil varies widely and eventually affects the long-term storage in soil. Therefore, simply estimating soil carbon content is not sufficient to study soil carbon storage in relation to ecosystem carbon balance. It is necessary to characterize the quality of soil organic C in relation to biodegradability and subsequent residence time in soil. In the following section, we will discuss the basic concepts of C fractionation in relation to stability along with two contrasting mechanisms related to soil C stability and finally how these processes influence the deep soil C stock. A summarized description of various soil organic C stability processes and their mechanistic interpretations are presented in **Table 2**.

3.1. Fractionation of C in soil

The dynamic nature of SOM causes release of C and other elements through the decomposition processes. But the decomposition rate and turnover time of different organic compounds vary considerably. Although a wide range of physicochemical to biogeochemical and environmental factor affects the process, the chemical nature (quality) of organic compounds is the first regulator of decomposition dynamics [87]. The chemical properties of soil organic substances that reflect the ability of microbial decay referred as biochemical quality [88]. Soil organic matter is the heterogeneous mixture of substances with variety of biochemical quality. Therefore, fractionation of soil organic carbon refers to repartition of SOM into several discrete pools on the basis biodegradability. This concept of fractionation is simple and suitable for ecological research. Other approaches of carbon fraction include the physical fractionation to quantify free and physically protected organic fractions and the chemical fractionation of humus into fulvic acid, humic acid and humin [89]. Carbon in SOM has been divided into several pools on the basis of decomposition rate and turnover time. The most common approach is the two pools system, in which the C fractions having rapid turnover time is termed as labile and the slow one as recalcitrant. The labile pool is further divided into two types, labile-I and labile-II, based on the chemical composition of organic compounds [87, 90].

3.1.1. Labile C pool in soils

Labile soil carbon refers to the organic C fraction having a turnover time of hours to less than a few years in contrast with recalcitrant C having turn over time of several thousand years [91]. Chemically labile C is largely composed of carbohydrate, polysaccharides of plants (hemicellulose, starch residues) and microbial origin (chitin) and cellulose. Polysaccharides of both plant and microbial origin (hemicellulose and starch) termed as labile-I, which is hydrolysable with acids of medium concentration. On the other hand, labile-II fraction is largely cellulose and rather resistant to decomposition. This fraction is hydrolysable with very high concentration of acid [87]. However, transformation of labile-II to labile-I can be occurred during decomposition of litter. For example, cellulose can be quickly cleaved by exoenzymes into simple sugars, which are readily metabolized by soil microorganisms. Labile C compounds are generally easily biodegradable; however, some labile C cannot be subjected to microbial attack due to protection by clay particle or coated by recalcitrant materials, hence labile C must be chemically degradable and physically accessible to microbes [92].

3.1.2. The recalcitrant C pool in soils

The recalcitrant C pool consists of more stable (chemically humified and physically protected) C compounds in soil organic matter with a slow turnover time. It includes humic substances, lignin and related compounds along with fats, waxes, resins and suberins [93]. These compounds consist of large polymers which cannot pass through cell membrane; in addition, the irregular chemical structure and complex bonding cause these substances to be resistant to enzymatic attack. Using an acid hydrolysis technique, Collins et al. [94] isolated recalcitrant C and found it comprised 30–50% of total soil organic carbon in US Corn Belt soils and estimated the mean residence time (MRS) of 2600 years for this fraction.

Process	Major causes	Long staying C compounds	Residence time	Mechanisms of stability
Recalcitrance/ selective preservation	Aromatic polymer structure	Lignin, phenolics, tannin, cutin, suberin, chitin, melanin, phospholipids, ceratin	Years	Polymethylenic structure, hydrophobicity, recalcitrant C-C bonding and aromatic ring prevent initial decomposition and progressive alteration of residues leads to relatively resistant substances
	Atomic bonding	n-Alkanes, alkanoic acid	Decade	
	Complex macromolecules/poly aromatic	Humic polymers	Decade	The residues of decaying lignin mix up with fats, waxes, etc. resulting complex humus which are resistant to common microbes
	Fused aromatic structure	Black C	Century	Exact mechanism is unknown. Complex and highly condensed aromatic chemicals might prevent microbial decay.
Physical protection by aggregates	Inaccessibility of microbes, enzyme and oxygen	OC (organic C) in macro and micro aggregates (>20µm & 20–250µm)	Years-Decade	Cell secretions, root exudates and mucus act as cementing agents along with fungal hyphae to form aggregates. Pore size distribution control the accessibility (pore size limit for bacteria is < 2µm).
		OC in clay microstructure including intercalated phyllosilicates	Century	
		Trapped inside organic macro-molecules	Century	
Organo-mineral associations	Microbes unable to utilize organic molecules sorbed on the mineral surfaces	OC on the layer silicates, sesquioxides and amorphous clays	Century	Strong bonding with OH ⁻ on the edges and sorption sites of phyllosilicates clays, strong Fe-O-C bonds by ligand exchange and cation bridge are the major mechanisms
Organo-metal complex	Direct interaction with Fe ³⁺ , Al ³⁺ and Ca ³⁺ ions and through microbes	OC in podzols, metal-rich soils and in dissolved organic matter (DOM)	Century	Al toxicity inhibits functions of microbes and extracellular enzymes, alters the size of organic molecules and thus reduces microbial decay. Precipitation of dissolved organic C with metal ions enhances the stability of C compounds
Suboptimal biogeochemical environment	Unknown. Probable causes: scarcity of decomposer, nutrient and energy	OC in deep soil layers	Millennium	Exact mechanism is unknown

Data sources: von Lutzow et al. [120] and Schmidt et al. [7].

Table 2. Various processes of C stability in soil organic matter: residence time and stability mechanisms.

3.1.3. Ecological significance of soil carbon fractionation

The dynamics of soil organic matter influences different types of ecosystem services such as release and sequestration of C, energy and nutrients, affect structure and functions of soil the microbial community etc. SOM comprises heterogeneous mixture of organic compounds with different degradability depending mainly on the susceptibility to microbial attack, which influence overall residence time of organic C in soils. Therefore, the fractionation of SOM into discrete degradable pools provides information about the following ecosystem processes.

Release and sequestration of C: Increasing emissions of carbon dioxide from soil is related to rapid biological decomposition of soil organic matter and thus enhance global warming [95]. The labile fraction of soil organic matter plays a dominant role in the CO₂ efflux process due to its rapid turnover rate. Typically, the turnover rate of labile C in organic compounds such as soluble sugars, starch and carbohydrates is very rapid, as fast as a few days to a few years. In contrast, the contribution of recalcitrant C pool in long-term C storage is enormous. Lignin and some physically protected labile SOM can stay in soils for several thousand years [95]. Therefore, C fractionation provides information about both short- and long-term soil C responses to changes in the soil environment.

Provide nutrients and energy to plants and microbes: The labile C pool has potential to provide nutrients to other primary users and thus is associated with ecosystem productivity in the short term [96]. During initial stage of SOM decomposition, readily degradable C components, especially carbohydrates, are the major source of energy for microorganisms to synthesize new cells [96]. Plant nutrient elements such as nitrogen, phosphorus, potassium, etc. are released from labile portion of SOM within a short time and become readily available to other plants. As forest soils are generally deficient in plant nutrients due to high demands of major nutrients, the labile fraction of SOM plays a vital role in plant nutrient supply.

Structure and functions of microbial community: Fractionation of C into labile and recalcitrant pools is based on microbial degradability of the SOM. These two broad pools further consist of different organic compounds, and many microorganisms are involved in the degradation of these compounds. Soil microbial biomass itself is a component of labile SOC pool because of its availability to other decomposers within a short period [96]. Other labile compounds of SOM are generally decomposed by rapidly growing opportunistic microorganisms [63]. Specific groups of fungi and bacteria are involved in enzymatic degradation of more recalcitrant parts of SOM. Cellulose is degraded by hydrolytic and cellulolytic organisms that produce enzymes to breakdown polymers, and degradation of lignin is dominated by different types of fungi, especially white rot, soft rot and brown rot [63]. Labile and recalcitrant C pools in soil thus influence the size, composition and function of soil microbial community engaged in decomposition of a particular pool.

3.2. Organo-mineral complexes and physical protection to soil C

The association between soil organic matter and mineral particles is recognized as a fundamental mechanism for long-term storage of C in soil ecosystems by preventing immediate microbial attack. The process depends on the physical and chemical and morphological/structural

properties of the two components, involved in the interaction, i.e. organic materials and mineral particles [92]. Different types of aluminosilicates, primary minerals such as quartz and feldspars, Fe and Al oxides and hydroxides can interact with various forms of organic C such as aromatic C, polysaccharide and carboxyl C; however, metal oxides are more active than aluminosilicates in forming association, because of large-specific surface area with high density of surface charges [97]. A simple approach to estimate the organic C fixation capacity of a soil is to study the correlation between soil organic C and specific surface area of clay particles in soil [98]. However, an approach combining mineralogical, chemical and microbial research approaches could be more effective to explain the complex associations. Soil microorganisms especially Gram staining bacteria can accumulate the adhesive substances like extracellular polysaccharides, proteins and other polymeric substances on the surface of minerals, and thus the variability in microbial community composition can affect organo-mineral associations [99].

3.2.1. Mechanistic considerations

Different types of soil minerals showed mechanistic variations in fixing organic molecules on their surface area. In phyllosilicate clays, organic C generally adsorbed as oxidized C compounds. The hydroxyl group at the edges of the clay particles forms a strong bonding with carboxyl and phenolics groups of organic matter [100]. Some expanding minerals such as smectites can hold oxidized organic matter through weak H-bonding [101]. In addition, polyvalent cation bridges between dislocated charges on the surface of phyllosilicates and negatively charged organic functional groups have been proposed as a potential mechanism for organo-mineral associations [101]. Primary minerals such as quartz and feldspars also play important role in storing soil organic C, although these minerals generally low in specific surface area and reactive sites. Jones et al. [79] reported the aliphatic C and protonated N as dominant forms of organic compounds on the surface of these minerals. Similarly, significantly higher proportion mineral-associated aliphatic C was found in soil with high sand content by some investigators [102], implying that the H-bonding of non-ionic lipids, polysaccharides and waxes might be played a major role in bonding between organic matter and quartz and feldspars. Among different types of minerals, Fe and Al oxides and hydroxides play the dominant role in sorption of soil organic compounds. Both crystalline and amorphous minerals of Fe and Al can bound organic C; however, amorphous metal oxides are more efficient in stabilizing this soil organic C [103]. Metal oxides carry a net positive charge promoting a strong exchange reaction with negatively charged organic domains such as carboxylic acid and phenolics [79].

3.2.2. Role of soil aggregates

Soil aggregates provide protection of soil organic C against microbial decay, which is attributed by inaccessibility of decomposers and enzymes due to mechanical barrier provided by aggregates. During the formation of soil aggregates, soil organic matter mainly decomposed plant debris, bacterial and fungal biomass acts as a cementing agent between mineral particles and forms microaggregates (<250 μm). These microaggregates are further combine together to form a larger aggregate, termed as macroaggregate (> 250 μm) using fine roots and fungal hyphae as binding agents [104]. However, roots and hyphae can decomposed rapidly; therefore, the macroaggregates are less stable. Some mycorrhizal hyphae contain glycoprotein, glomalin, which can form more stable macroaggregates in soil [105]. Soil textural and mineralogical composition

particularly clay particles affect the formation of aggregates and hence the protection for soil C [106]. The size and distribution of intra-aggregate pore space play an important role in effective protection to organic C, because the larger the pore space the greater the oxygen and air supply resulting a faster decomposition and release of CO_2 . The quality of protected C can affect the stability of aggregates depending on the pore size. If the protected C is the non-particulate labile, the microbial decomposer can have easy access to the labile C through the pore space, causing the instability of C.

3.2.3. *Role of clay minerals*

Isotopic and elemental analysis indicated that interactions between organic C and amorphous clays of Fe and Al oxides are the dominant mechanisms to protect soil C from the decomposers and enzymes [107]. Kögel Knabner et al. [101] reported that the stabilization through the formation of organo-mineral complexes, particularly sorption of organic molecules on Fe oxides and aluminosilicate clay minerals, is more common in deep soil than the surface. Selective dissolution extractions provide useful information about the types of stabilization present in these soils, both qualitative and quantitative. Fe and Al hydroxides and poorly crystalline phases are involved in the stabilization of organic matter. Changes in the relative amounts of these substances across the chronosequence may have important implications for the potential stability of SOM. Close interaction of the surface of fine roots to the surface of soil minerals can enhance the stability of root-derived exudates, which are generally readily decomposable, by formation of organo-clay complexes. The process may be particularly important in forest ecosystems where the absence of tillage or other mechanical operations prevents the admixture of aboveground litter with the mineral soil. Therefore, physical protection of soluble organic matter by soil mineral may be more likely in case of root exudates.

3.2.4. *Methods of evaluation*

Various physical, chemical and mineralogical techniques are generally applied to study the quality, quantity and turnover of organic matter adsorbed on the mineral matrix by isolating the organic and mineral parts. The physical separation of organic and mineral compositions can be accomplished by combination of ultrasonic disruption, particle size and density fractionation [108]. In the first step of physical approach, soil aggregates are disrupted by sonification and agitation in water, and secondly, fractionation of mineral particles is based on their sizes by sedimentation or dry and wet sieving methods. Density fractionation includes separation of light and heavy organic fractions by floating and ultrasonic techniques. In chemical methods, adsorbed organic substances can be extracted using hydrolyzing, oxidizing and desorbing reagents. Chemical fractionation of C in soil organic matter could be performed following acid hydrolysis methods [88]. Oxidation of unprotected organic matter by oxidative reagents is a common to isolate the labile C, leaving behind the residual C on the clay surfaces [108]. Despite the development of numerous separation techniques, the direct investigations of organo-mineral association for explicit information regarding link between mineralogy and organic compounds are still lacking. Recent studies focused on spatial distribution of organic molecules on clay surfaces with structural features of the association by scanning transmission X-ray microscopy (STXM) and near edge X-ray absorption fine structure (NEXAFS) [97, 109]. These techniques might be a powerful technique to study the organo-mineral assemblies at nanoscale [106].

3.3. Priming: a potential mechanism of destabilizing soil C

In studies of soil organic C turnover, priming effect can be defined as an extra decomposition of organic C after addition of easily decomposable organic substances to the soil [110]. This process has received much attention as a potential mechanism of degradation soil organic matter [107, 111] and thus important for modeling the fate of ecosystem C dynamics under future climate change impacts. The concern over the huge impacts of elevated atmospheric CO₂ on earth's climate is leading many management efforts to enhance C storage and stability in soil; however, the protection of already stored soil C is equally important. Priming of soil organic C is a potential threat to relatively stable soil C that could be considered as a valuable ecosystem resource. Some authors argued that the higher plant productivity under elevated CO₂ supplies a large amount of labile organic C to soil continuously and thus can compensate for the loss of C by priming [111]. However, the recalcitrant and protected C (from microbial attack) that lost by priming are generally buried under top soil and obviously more stable than the fresh C [7]. Although considerable research activities are being carried out globally, our mechanistic understanding regarding the priming process is still poor.

3.3.1. Mechanisms

The mechanism of priming effect can be illustrated by 'Co-metabolism' theory [112]: addition of labile organic substance provides energy for microbes promoting the synthesis of enzymes that are capable of degrading recalcitrant C in soil and thus facilitating SOM mineralization. Labile organic substances are leached out from the fresh substrates and transported as dissolved organic C (DOC). The sources of labile C could be the root and root exudates, decomposed litter and applied fertilizers. As a part of ecosystem processes, plant litter in forest provides soil microbes with different organic compounds containing essential sources of energy and nutrients. These include readily available sugars and amino acids and easily degradable cellulose and protein, which can stimulate different groups of microbial decomposer to growth and degrade complex organic substances [107]. These mechanisms are particularly destructive for recalcitrant soil organic matter pools, which were so far protected from microbial attack due to energy and N limitation [113]. Negative priming was reported by some authors when fresh labile C suppresses soil organic matter decomposition in the presences inhibitory substances, resulting no loss of C due to the presence of labile substrates [114].

3.3.2. Factors influencing the priming process

As priming is a biogeochemical phenomenon, many biotic and abiotic variables can influence the magnitude of the process. Supply of dissolved organic C (DOC) from fresh sources is an important factor at initial stage of priming process. Release of low molecular weight compounds such as sugar, amino acids, other organic acids, etc. through hydrolysis and leaching processes from fresh organic matter is the first step of priming process. In this connection, soil hydraulic properties, especially drainage conditions and hydraulic conductivity of soil, might be important factors for DOC transportation. Favorable conditions for water movement lead to easy DOC redistributed throughout the soil profile to facilitate priming effects in buried soil organic C [113]. Secondly, soil microbial community composition and structure play a vital role in priming by promoting the growth of new microbes, producing necessary enzymes

and attacking the old organic substrates. The dynamics of microbial biomass particularly the role of microbial necromass in priming mechanisms is still unknown. Future climate change projection indicated increase in temperature and atmospheric CO₂ concentration resulting increase in NPP and supply of fresh litter in forest ecosystems. Therefore, the priming effects will likely be more intensive; however, it depends on the responses of the associated factors like quality and quantity of DOC, precipitation, etc. Significant impacts of climate change on vegetation dynamics have been predicted in climate models which could alter not only DOC quality but also the community composition of soil microorganisms and thus can directly affect the priming process.

3.4. Protected C in deep soil

The major part of soil C occurs at the surface layer of soil profile because of accumulation of organic matter from above and belowground plant litter and also due to maximum soil microbial and root activities. But due to natural and anthropogenic soil, organic matter can be distributed deeper soil horizon as well. Although top 30 cm sampling depth has been recommended by IPCC for soil C inventories [115], the typical sampling depth is 1 meter to estimate soil C stocks. Most of the previous studies on soil C were limited to the upper 15 to 30 cm of soil because of the difficulties associated with sampling. However, recent studies confirm that considerable amounts of C can accumulate in subsoil layers (below 40 cm), and in some ecosystems, more than half of stabilized C is below 30 cm [116]. The deeper the soil profile the older the C and less susceptible to decay processes. The origin, nature and properties and most importantly the dynamics of deep soil C (below 1 m depth) under changing global environment are largely unknown. Fontaine et al. [107] estimated mean residence time of soil organic matter 2000–2010,000 years at subsoil layers below 20 cm. Although microbial activity is the primary active agent for soil organic matter stabilization and mineralization, the mechanisms underlying the processes at deep soil layers are still unclear. It is hypothesized that the restricted biotic activities due to oxygen limitation could be the major cause of slow C turnover in deep soil layers. In addition, subsoil C is considered more resistant to microbial degradation due to physical protection and chemical recalcitrance of substrates.

3.4.1. Controlling factors

Vertical distribution of SOC storage is controlled by many biogeochemical and climatic factors, yet at identical soil and climatic conditions, vegetation and soil texture are likely to be more active factors [26]. In forest ecosystems, plant-induced processes such as litter input and root activities might be the dominant factors in regulating the vertical C distribution. Physical processes regarding landscape formation such as erosion, landslides and flood may cause burial surface soil resulting accumulation of C in deep soil layers. One of the major sources of deep soil C stock is the root systems including the production of root necromass, release of exudates and turnover of the mycorrhizal hyphae network [117]. The contribution of these processes to SOC storage is uncertain except the contribution of root necromass because of rapid turnover of labile C in these substrates. However, C release from root exudates and mycorrhizal turnover may be potential route to soil C storage through the formation of soil micro aggregates or clay coatings [43]. Another important process leading to the distribution

of C storage at deep soils is bioturbation by earthworms some of which can reach to 1–2 m depth [116] and transport of fresh SOM into the burrows and mixed with mineral soils.

3.4.2. Dynamics of deep soil C

The dynamics of deep soil is difficult to evaluate. In general, the mineralization of C in soil organic materials is largely mediated by extracellular enzymes produced by soil microorganisms. The processes vary significantly depending on the quality and quantity of substrate, available nutrients and soil properties [118]. These factors differ greatly between top soil and deep soil in forest ecosystems [116]. Little is known about catalytic properties of soil enzymes and their functional link to the microbial community structure in deep soil horizons, where abiotic environmental conditions are quite different compared with top soils. Microbial priming has been recognized as a major process that involve in mineralization of recalcitrant deep soil C [107]. Two possible situations may occur in case of microbial degradation of organic C in this condition. First, the abiotic environment at deep soil, particularly scarcity of oxygen, can create adverse conditions for microbial functioning; secondly, microbes cannot acquire sufficient energy from recalcitrant compounds to sustain their activities, resulting the slow-down of microbial decay. The exact mechanisms are not well understood; therefore, more research efforts are needed for explicit understanding of deep soil C dynamics and hence to protect this valuable ecosystem resource.

4. Conclusions

Organic C sequestration in forest is considered as a potential mitigation option for climate change by storing atmospheric CO₂ in the tree biomass and soil organic matter. Ecosystem C inventory is essential for C accounting, control of greenhouse gas emission, forest conservation and land development programs. In addition, due to establishment of the Kyoto Protocol, the interest of scientists and policy makers has been increased dramatically about the studies of C storage and its stability in soil. Among different C pools in forest ecosystems, aboveground tree biomass is the first sink of atmospheric C and plays a crucial role in ecosystem C balance. Tree roots provide many ecosystem services, of which resource acquisition from the soil and contribution to C sequestration are the most crucial. Fine roots are recognized as the most dynamic part of the root systems and regulate belowground C flux and net primary production. The typical methods of biomass estimation are extremely laborious and time consuming. Recently, remote sensing, GIS data and 3D canopy structure images are used for estimation of aboveground biomass, and software-based image analysis is receiving much attention in root studying. In spite of these methodological advances, a robust method for estimating tree biomass is still far reaching. Soil microbial biomass and community structure are extremely crucial for regulating dynamics of soil organic C and subsequent emission and storage in soil. Dissolved organic C is also important active C pool in soil that stimulates microbial activities and thus might have link with soil respiration.

Stability of soil organic C is coupled with various biogeochemical processes in the soil and therefore regulated by multiple biotic and abiotic factors. Thus, the link between different

pools and processes are crucial for understanding the soil C storage and stability. Soil organic matter in the deep soil layers is potentially stable due to long residence time and surrounding soil properties. The accumulation of these highly processed C is influenced by the translocation of dissolved organic carbon (DOC) through the soil profile. Plant biomass can also be a major determinant of the vertical distribution of C in soil, through above and belowground C allocation patterns. Similarly, root activities such as incorporation of structural coarse roots, mycorrhizal fine roots and hyphal mycelium can influence the vertical distribution of organic C. The effect of clay content on soil C stability is well established, particularly in deeper layers with higher proportion of protected organic molecules. Although a large portion of fine root C returned to atmosphere through root and rhizomicrobial respiration, root residues can stay in soils for long time compared to aboveground litter and thus contributing significantly to the SOC stock. Priming process can impact soil C stock negatively. Fresh litter and root may also stimulate the microbial activities that leading to rapid decomposition of old C in soil, creating an antagonistic effect on the storage of soil organic C. Advanced analytical techniques can be instrumental for explicit understanding of these complex interactions at ecosystem level. Overall, the interdependency of various soil C pools and processes is a fundamental determinant of storage and stability of forest soil C that need to be addressed by applying advanced technologies, such as molecular, isotopic and genomic analytical tools.

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