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Review

Unveiling the Role of Edaphic Microalgae in Soil Carbon Sequestration: Potential for Agricultural Inoculants in Climate Change Mitigation

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Abstract: Agricultural soil has great potential to address climate change issues, particularly the rise in atmospheric CO_2 levels. It offers effective remedies, such as increasing soil carbon content while lowering atmospheric carbon levels. The growing interest in inoculating soil with live microorganisms aims to enhance agricultural land carbon storage and sequestration capacity, modify degraded soil ecosystems, and sustain yields with fewer synthetic inputs. Agriculture has the potential to use soil microalgae as inoculants. However, the significance of these microorganisms in soil carbon sequestration and soil carbon stabilization under field conditions has yet to be fully understood. Large-scale commercial agriculture has focused on the development and use of inoculation products that promote plant growth, with a particular emphasis on enhancing yield attributes. Gaining more profound insights into soil microalgae's role in soil carbon cycling is necessary to develop products that effectively support soil carbon sequestration and retention. This review comprehensively explores the direct and indirect mechanisms through which soil microalgae contribute to soil carbon sequestration, highlighting their potential as microbial inoculants in agricultural settings. This study underlines the need for more research to be conducted on microalgae inoculation into agricultural soil systems aimed at mitigating carbon emissions in the near future.

Keywords: biochar-based inoculants; biological soil carbon sequestration; cyanobacteria; green algae; microbial inoculants; soil carbon dioxide emissions

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Citation: De Silva, A.G.S.D.; Hashim, Z.K.; Solomon, W.; Zhao, J.-B.; Kovács, G.; Kulmány, I.M.; Molnár, Z. Unveiling the Role of Edaphic Microalgae in Soil Carbon Sequestration: Potential for Agricultural Inoculants in Climate Change Mitigation. *Agriculture* **2024**, *14*, 2065. https://doi.org/10.3390/agriculture14112065

Received: 1 October 2024
Revised: 11 November 2024
Accepted: 12 November 2024
Published: 16 November 2024

1. Introduction

The increase in greenhouse gasses and their potential effects on global climate change is a growing concern worldwide [1]. Emissions of methane (CH_4), nitrogen oxide (NOx), carbon dioxide (CO_2), and carbon monoxide (CO), which are gasses that could contribute to global warming, are generated by different agricultural and livestock management practices [2]. Land use conversion and agricultural practices generate about 30% of the total anthropogenic emissions, both directly and indirectly through hidden carbon costs [3]. Moreover, the terrestrial carbon pool is depleted through conversion from natural to managed ecosystems, extractive farming practices based on low external input, and soil-degrading land use [4]. For instance, tillage practices increase the decomposition rates of soil organic carbon (SOC) by exposing physically protected SOC in aggregate fractions [4], resulting in CO_2 emissions from the soil. Thus, inappropriate soil management techniques and land use changes cause direct emissions of CO_2 through increases in the decomposition rate of SOM [5].

Agricultural land covers roughly 38% of the earth's land surface, covering approximately five billion hectares [6], but its soils have significantly lower SOC levels than undisturbed or natural ecosystems, ranging from 25% to 75% less [5,7]. Therefore, degraded soils on arable lands have significant potential to sequester carbon and help offset anthropogenic emissions [5]. Hansen, Sato [8] reported soil carbon sequestration as a feasible strategy to store 50–100 petagrams of carbon by 2100–2150, significantly reducing atmospheric CO_2 levels. Therefore, reducing soil carbon depletion and increasing soil carbon content in intensive-land-management and immense-degraded-land areas is paramount. This can be achieved by adopting various sustainable agricultural practices, which not only enhance environmental regeneration and increase agricultural productivity but also play a crucial role in mitigating climate change, and strengthening the resilience of food production systems [9].

The agricultural "green shift" involves transitioning to sustainable food and fiber production methods, focusing on natural processes to diminish human inputs and improve productivity while minimizing environmental impact [10]. For example, ecological intensification involves harnessing soil microorganisms to reduce the need for synthetic inputs, a practice embraced by regenerative agriculture movements [11]. These movements actively restore natural systems and processes to increase productivity and abate deleterious agricultural practices [12]. To make this vision a reality, further technologies are necessary to facilitate the shift from a resource-intensive to a resource-regenerative food production model. Furthermore, it is essential to better understand how these technologies may be used address climate change, one of the most significant biophysical hurdles for life on Earth [13].

Microalgae are a diverse group of microorganisms that perform photosynthesis; this group includes cyanobacteria and eukaryotic organisms like green algae, euglenoids, and diatoms, found in aquatic, terrestrial, and sub-aerial surfaces, including soil [14]. Among other soil microorganisms, microalgae represent 27% of the total biomass of agricultural land [15] and soil algae in croplands have the highest net primary productivity among the biomes, accounting for 6% of terrestrial vegetation's net primary production, estimated at 157 g C m^{-2} $years^{-1}$. The average number of soil algae per gram is $5.5 \pm 3.4 \times 10^6$, and soil algae capture around 3.6 Pg carbon each year globally [16]. Microalgae can capture and store CO_2, which means they can potentially impact the carbon flux in soil. Consequently, the availability of quantitative data on soil algal carbon fixation is limited, and such data primarily focus on drylands [17] and are not easily accessible globally. Therefore, it is crucial to understand how soil algae influence soil carbon dynamics, including their contributions to carbon intake and the stabilization and sequestration of carbon in the soil [18]. Microalgae, when incorporated into the soil, act as a source of organic carbon [19] and offer a potential solution to the problem of SOC depletion, which is a significant type of degradation in croplands that leads to reduced soil quality and fertility [20]. Microalgae's contributions to soil carbon sequestration remain virtually unknown; however, they play a crucial role in global soil carbon uptake, and hence their role should be considered in the terrestrial carbon model [16]. Therefore, soil inoculation with living microalgae is a viable solution to tackle the issues of SOC depletion and CO_2 emissions from agricultural soil.

This review aims to synthesize the direct and indirect pathways of microalgae's contribution to soil carbon sequestration. It also explores their potential use as inoculants and suggests microalga-derived products with biochar in agriculture as a viable solution to address soil carbon depletion. Furthermore, the review emphasizes the need to utilize genetic engineering techniques and/or screening as one feasible method of overexpressing genes involved in photosynthesis to increase the efficiency of microalgae's photosynthesis capabilities under field conditions. The review also emphasizes the need for future research to elucidate the precise interactions among soil algae, environmental conditions, and soil carbon dynamics to optimize their use in sustainable agricultural practices.

2. Soil Carbon

The soil carbon pool is essential for sustaining the global carbon cycle. Moreover, soil carbon is the fuel and driving force of ecosystem functions [21]. Soils represent the largest terrestrial carbon reservoir and are essential for understanding the changing global carbon cycle [22]. SOC reserves are around 1550 Pg, or approximately 62% of the total soil carbon pool [23]. Two main pools of SOC exist in the soil system: labile organic carbon, which has a high turnover rate and is short-lived, and recalcitrant organic carbon, which is stable, long-lived, and not sensitive to environmental conditions. Labile organic carbon consists mainly of coarse fraction material (>0.4 mm), known as particulate organic matter (POM). POM is a recently decomposed or decaying soil input, such as plant leaves, animal excrement, and root exudates, including readily oxidizable organic carbon, dissolved organic carbon and MBC (microbial biomass carbon), and other organic wastes [24]. Particulate organic carbon (POC) refers to the carbon component of POM, constituting approximately 50% of the total POM. POC refers specifically to the carbon component of POM, which also encompasses the mass of other elements, such as nitrogen (N), hydrogen (H), and oxygen (O). Recalcitrant organic carbon pools consist of a fine fraction (<0.4 mm) of persistently stabilized carbon, such as mineral-associated organic matter (MAOM), which includes relatively low-molecular-weight compounds consisting of polysaccharides, lipids, and heavily decomposed plant and microbial products [25]. These pools also contain aggregated carbon (AggC), formed through various microbial and plant-mediated mechanisms. For carbon to be stored in soil, it needs to be chemically protected in organo–mineral complexes, adsorbed on the inner surface of clays, or protected from degradation by microbes within stable microaggregates (<250 μm) [26].

3. Soil Carbon Sequestration

Carbon sequestration refers to the conversion of atmospheric CO_2 into other long-lived global pools, such as oceanic, pedologic, biotic, and geological pools, to mitigate the net rise in atmospheric CO_2 levels [27]. Plants, plant debris, and the other organic materials maintained as components of SOM characterize sequestering atmospheric CO_2 as the soil of a land unit [28]. Carbon sequestration is becoming increasingly popular as a multipurpose approach to address climate change, protect the environment, increase biodiversity, rehabilitate degraded soils, and enhance agricultural productivity [29]. The CO_2 sequestration approach, also known as capture and storage, occurs through bio-concentration during photosynthesis [30]. The process of microbial carbon fixation is essential for those who aim to stop the rise in CO_2 emissions and achieve carbon neutrality. As a result, the possibility of storing carbon in marine and terrestrial carbon sinks has attracted significant attention in recent years. The present investigation emphasizes the significance of microbial carbon sequestration as an essential pathway [31]. Advancements in future research on carbon sequestration may mean that microbial carbon sequestration can be used to attain peak CO_2 emissions and carbon neutrality objectives [32]. However, recent findings indicate that microalgae have better carbon-capturing and sequestration potential than terrestrial plants. According to Bhola, Swalaha [33], microalgae capture and sequester carbon 10 to 50 times more efficiently than terrestrial plants. As a result, using microalgae for carbon sequestration may offer substantial advantages over other sequestration technologies [34].

4. Microbial Inoculation

Soils serve as a globally significant reservoir of biodiversity, supporting at least a quarter of all living species on Earth [35]. They are primarily composed of microbes, among the planet's most diverse and ubiquitous organisms [36]. Soil microbial communities are crucial to the operation of agricultural ecosystems [37]. They are essential for the health of plants and soil at the field scale since they enhance ecosystem functionality and biogeochemical cycling, notably via carbon sequestration and N_2 fixation [13] and controlling the fluxes in critical greenhouse gasses, such as CO_2, CH_4, and N_2O [38]. Managing and enhancing soil and plant microorganisms can promote ecological intensification in production systems while lowering atmospheric CO_2 levels through increased soil carbon sequestration and stabilization [39] and increasing the plants' productivity and resilience.

Microbial inoculation is a cost-effective and eco-friendly formulated microbial inoculant for soil and seeds, which provides renewable plant nutrients (microbes as renewable bio-fertilizers) as a substitute for conventional chemical pesticides and fertilizers [40]. This environmentally friendly approach significantly contributes to sustainable agriculture by serving as a natural bio-pesticide and bio-fertilizer, thereby reducing the adverse effects of mineral fertilizers and chemical pesticides on agricultural land and crops, which could have environmental and health consequences [41]. Biofertilizers offer numerous advantages over chemical fertilizers, including the establishment of symbiotic bonds between plant roots and soil microorganisms, the N_2 fixation ability of individual strains, the solubilization of phosphorous, the production of a hormone that promotes plant growth, the ability to mitigate greenhouse gas emissions and sequester CO_2 through the addition of organic carbon into the soil, and the progressive nutrient release for plant uptake [42]. Microbial inoculants (microbial biopesticides) offer a cost-effective and sustainable alternative to chemical pesticides to control plant pathogens and pests. While chemical pesticides can provide immediate solutions to pest problems, they often lead to long-term economic challenges, such as the development of resistance in pests and soil and water contamination [43,44]. Chemical pesticides pose considerable risks to human health, including potential carcinogenic effects and long-term exposure risks for farm workers and consumers [45]. Unlike chemical pesticides, which can harm beneficial insects and microorganisms [46], microbial inoculants enhance soil quality [41]. Moreover, microbial biopesticides can be cost-effective, exhibit minimal or no toxicity to humans or non-target organisms, and demonstrate non-persistence in agricultural products [47]. Thus, microbial inoculants reduce dependency on chemical inputs and reduce risks to human health. Furthermore, their potential to reduce the long-term costs associated with chemical pesticide use, which can lead to pest resistance and increased environmental cleanup expenses, underscores the economic viability of microbial inoculants.

The inoculation procedure introduces several viable, effective microorganisms at high densities into the host rhizosphere. This temporarily disrupts the balance of microbial communities in the soil; however, modifications in the microbial community structure (bacteria) resulting from inoculation could be buffered by the ecosystem's resilience, which is influenced by the level of diversity and interactions within the plant–soil biota [48]. Humans have employed microbial products for centuries [49], during which soil inoculation has significantly improved plant growth and resilience, increasing productivity. Microbial inoculants are significant to agricultural systems because they have numerous advantages, such as promoting plant growth [50], making heavy metals less harmful [51], making plants more resistant to drought [52], alleviating plant growth stresses [53], protecting against various pathogens [54], enhancing nutrient uptake through improving the bioavailability of nutrients in crops [55], which is associated with organic acid production (the solubilization of complexed nutrients) and N_2 fixation [56], reducing the requirement for chemical fertilizer and pesticides [57], reducing the impact of synthetic fertilizers and agrochemicals on agricultural lands and crop production, enhancing the soil's organic matter to improve soil fertility, and synthesizing bioactive compounds such as plant hormones and enzymes [58], as well as advantages in terms of mitigating the effects of climate change [59]. Furthermore, researchers have identified microbial inoculants as the most important determinant of soil quality [60]. Thus, microbial inoculants are a highly effective option for restoring agricultural fields and alleviating the effects of adverse soil conditions that hinder crop productivity [59].

5. Soil Carbon Sequestration Pathways: Direct and Indirect Mechanisms

There are two main primary pathways of carbon input into soil systems: (1) aboveground plant inputs, plant litter, and associated leachates (e.g., dissolved organic carbon), and (2) below-ground plant inputs (or rhizodeposition), root litter, and exudates. The most crucial element in maintaining adequate organic matter in agricultural fields is enhancing carbon storage by increasing carbon intake and decreasing carbon release [59]. Plant biomass production and the formation and decomposition of SOC regulate the balance between carbon inputs and outputs in the system, which determines the accumulation of organic carbon in soil [9]. Various agricultural management techniques can enhance organic matter and increase soil carbon input. These techniques include incorporating crop residues, using livestock manure, applying compost made from wastewater or raw sewage, reducing runoff and soil erosion, and promoting the rotation of crops that contribute a large amount of biomass to the soils [61]. Another possible way to increase SOC is by sequestering CO_2 from the atmosphere [59]. Therefore, applying the photosynthesis capability of microalgae inoculants is another viable option to increase SOC in agricultural fields.

Soil microorganisms are essential for both the cycling and retention of carbon in soil [62]. Most carbon produced by plants is assimilated by soil microbes, which use it to generate either energy (leading to CO_2 emissions) or biomass. Thus, it is possible to use soil microorganisms as microbial inoculants for carbon sequestration [59]. Mason, Salomon [13] suggested two primary mechanisms, direct and indirect, through which soil microorganisms participate in various ways to cycle and retain soil C through soil carbon sequestration. Although prior studies have explored the carbon storage capabilities of fungi and bacteria [13,41], it is essential to recognize that microalgae also hold the potential for reducing CO_2 levels. Therefore, they could contribute to carbon sequestration and CO_2 emission mitigation through various direct and indirect mechanisms (Figure 1).

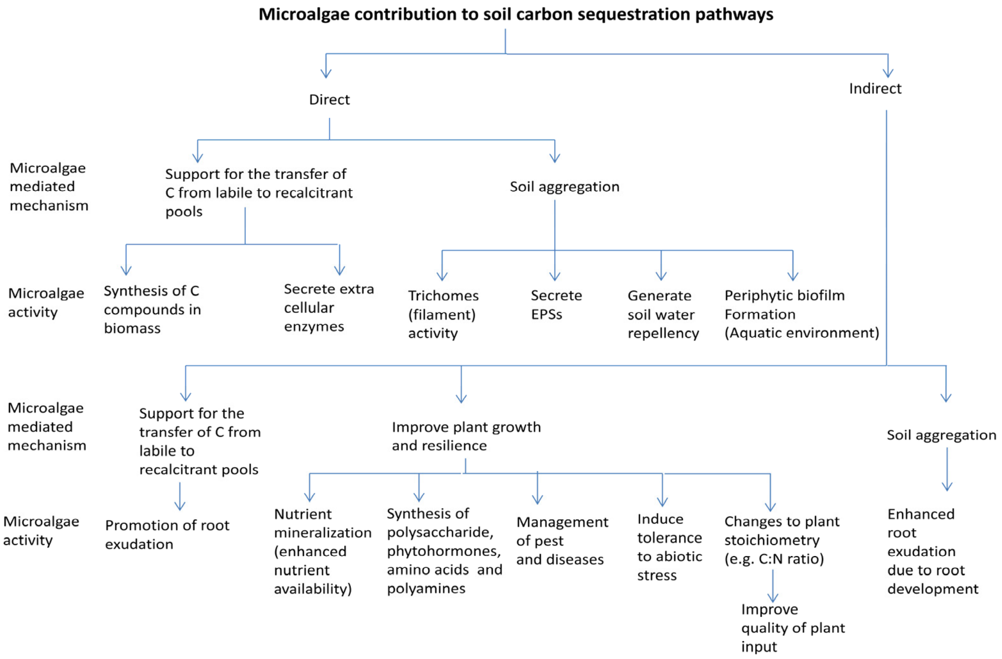

Figure 1. Microalgae contribute to soil carbon sequestration and retention through direct and indirect mechanisms that can affect soil carbon levels. These mechanisms link to microbial activities that can influence and enhance soil carbon stocks.

6. Direct Mechanisms

Mason, Salomon [13] define direct mechanisms as mechanisms facilitated by microorganisms that directly provide carbon to the soil and/or aid in stabilizing soil carbon. Of these, the process of the synthesis and accumulation of plant-derived carbon materials in the biomass of microbes (known as microbial biomass; this term encompasses soil organisms with a volume of less than 5×10^3 μm^3, excluding living plant tissue) and their resulting residue (necromass) are important factors, comprising around 50 to 80% of stable SOC [63]. Moreover, Ahmed and McKay [59] reported that soil microbes can sequester carbon via various mechanisms, including biochemical processes that capture atmospheric CO_2, carbonate's sedimentation capability, the formation of recalcitrant tissues and components, and a tendency to create stable structures such as aggregates that preserve total organic components. Microbes significantly influence the physicochemical composition of soil in their active, dormant, and deceased forms. Here, we define all the activities mentioned above as direct mechanisms.

6.1. Synthesis of Various Carbon Compounds in the Biomass and Secretion of Carbon Compounds

Soil carbon-fixing microorganisms, primarily autotrophic, fix carbon from CO_2 and CH_4 in the soil, playing a vital role in the process of the fixation of carbon in soil [64]. Algae are essential for carbon fixation and are found in various environments, like water bodies and soil. Algae are present in several forms, including macroalgae and microalgae [65]. Microalgae, typically classified as autophototrophs, are the principal microorganisms responsible for oxygen generation through photosynthesis on Earth. They effectively absorb CO_2 and convert it into organic compounds [66]. Through their biological sequestration, soil microalgae can enhance soil's carbon content and stability by engaging in various activities. For instance, microalgae can secrete extracellular polysaccharides (EPSs), which can supply nutrients to soil microbes, enhance SOC, and thus influence soil characteristics [67] (Figure 2). Some microalgae species secrete extracellular enzymes that help decompose organic residues in soil. For instance, the extracellular enzymes produced by cyanobacteria, such as *Nostoc muscorum* and *Tolypothrix tenuis*, decompose organic residues. In addition, they are employed as inoculants to enhance the polysaccharide concentration and microbial activity in soil [68,69]. Additionally, following the lysis of microalgae cells, the produced residues and metabolites can persistently accumulate and interact with minerals, leading to the formation of organic–mineral complexes that become part of the SOC (Figure 2). When microalgae are added to the soil, they become a source of organic carbon [19]. They may help solve the problem of SOC depletion, a significant type of soil degradation in croplands that causes soil quality and fertility to drop [20]. Kumar, Singh [70] reported that *Spirulina* spp. cells consist of approximately 86% organic substances. Moreover, microalgae's total glucose and starch compositions are around 20% and 10% of the dry weight, respectively [71,72]. Cyanobacteria species contain significant glucose content, reaching up to 60% of the total dry weight [72]. Microalga plant-growth-promoting substances are components of organic materials that enhance biochemical reactions and serve as a carbon supply [73]. The study by de Mulé, de Caire [74] reported that cyanobacteria not only enhanced the yield of paddy crops but also exhibited the most significant increase in oxidizable carbon and soluble C in the soil post-harvest compared to pre-harvest. The lysis of algal cells releases exopolysaccharides. These exopolysaccharides increase the production of oxidizable carbon, which increases the amount of organic matter in the soil [75] (Figure 2). Certain microalgae species grow, leading to a significant increase in their intracellular and extracellular polysaccharide content, which enhances carbon fixation in the soil, thereby increasing levels of dissolved organic carbon and total carbon [76]. In most environments, cyanobacterial genera such as *Anabaena* spp. represent the dominant species that sequester carbon, highlighting their potential for competitiveness and adaptability [77,78]. Thus, microalgae harness sunlight to transform CO_2 into organic matter through photosynthesis. This ability enables them to sequester carbon and promote sustainable agriculture by reducing greenhouse gas emissions [42].

The CO_2-concentrating mechanism (CCM) in algae relies on carbonic anhydrase to provide CO_2 for Rubisco's carbon fixation process. According to estimates, 1 kg of microalgae can sequester 1.83 kg of CO_2 through the Calvin–Benson–Bassham cycle. The inherent capacity of CO_2 sequestration and effectiveness in many microalgal species is low. However, active bicarbonate pumps in microalgae allow for more effective carbon uptake during photosynthesis than higher plants. These pumps can increase internal CO_2 concentrations and prevent photorespiration [79]. Active bicarbonate pumps in microalgae are generally associated with aquatic environments, where microalgae need to efficiently capture and concentrate inorganic carbon, primarily in the form of bicarbonate (HCO_3^-), for photosynthesis. One key factor that sets the soil environment apart from aquatic environments regarding carbon availability is the role of microbial respiration and decomposition processes. These processes play a significant role in increasing CO_2 levels in the soil. Therefore, the need for CCMs (like active bicarbonate pumps) might be less pronounced in soil compared to in aquatic environments. The presence and role of these pumps in soil environments are less straightforward and depend on the specific conditions and types of microalgae present. For instance, microalgae may benefit from having active bicarbonate pumps in specific soil microenvironments, such as the rhizosphere (the zone around the plant roots), where roots or other organisms might rapidly take up CO_2. This would ensure a sufficient supply of inorganic carbon for photosynthesis.

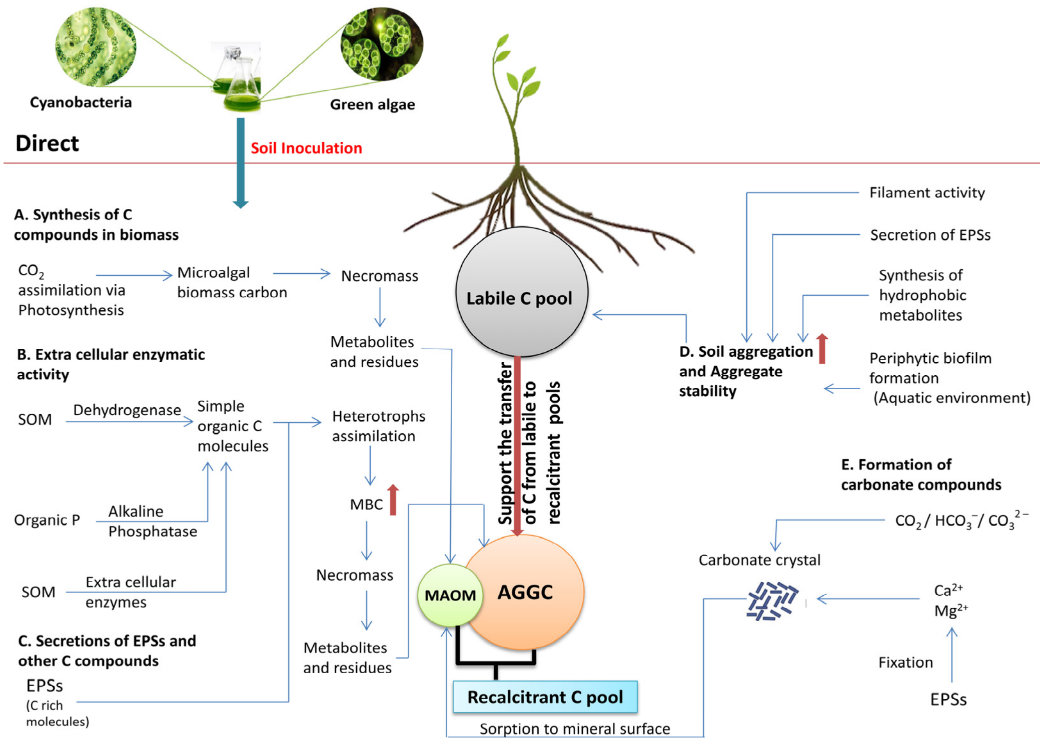

Figure 2. Overview of the direct pathways though which microalgae contribute to soil carbon sequestration and the key activities involved in this direct mechanism. The arrow (⬆) indicates the increase in micro-algal activity or their mediated mechanism.

Some microalgal strains can grow heterotrophically or mixotrophically, allowing them to assimilate organic carbon. This metabolic behavior overcomes the limitations of light, enabling faster growth, a higher biomass content, an increase in lipids and protein productivity, and the simplification of operations [80]. This metabolism was observed in waste waters; no evidence of its presence is recorded in soil. Further, heterotrophs fix CO_2 content in soil, which is referred to as the "dark fixation of microorganisms" [81]. Nevertheless, we hypothesize that scientists have yet to discover some species of soil microalgae that may exhibit an obligatory heterotrophic or mixotrophic metabolism when light is a limiting factor. In the soil, there are specific microorganisms, like picocyanobacteria, that are capable of producing carbonate crystals (calcite nucleus) by facilitating the conversion of CO_2 or dissolved inorganic carbon (such as HCO_3^- and CO_3^{2-}) [82]. Cyanobacteria induce significant levels of carbonate precipitation [83,84]. Photosynthesis facilitates the precipitation of carbonate by exchanging HCO_3^- and OH^- across the cellular membrane. This exchange raises the pH of the cell's microenvironment, creating favorable conditions for carbonate precipitation [81]. Conversely, cyanobacteria secrete EPSs composed of numerous acidic residues and sugars. These substances can trap significant quantities of divalent cations, such as Ca^{2+} and Mg^{2+}, promoting the formation of carbonate precipitation [85] (Figure 2). However, inorganic carbonates, like calcium carbonate, indirectly influence SOC stability and cycling by interacting with SOM, providing surfaces for adsorption and forming organo–mineral complexes [86], which are more resistant to breakdown and contribute to the recalcitrant organic matter pool. They also alter soil pH and cation exchange capacity, affecting decomposition rates and overall organic carbon dynamics. Despite not directly adding organic carbon content, inorganic carbonates significantly influence soil persistence and turnover.

6.2. Microalga Biomass and Necromass' Contribution to Soil Carbon Sequestration

Soil microbial biomass and microbial activity (including soil enzymes) are key microbiological indicators of soil quality [87,88]. Microbial biomass acts as both a source and a sink of nutrients (e.g., the mineralization of organic C, N, and P) and plays a key role in the transformation and cycling of SOM [89]. The MBC content in the soil accounts for about 10–30% of the total SOC [90,91]. Kallenbach and Grandy [92] and Li, Brouwer [93] have reported that microbial biomass is a sensitive indicator of the initial soil condition and any changes due to management practices. Additionally, microbial necromass plays a significant role in SOC accumulation [94] and can persist in the soil for extended durations, ranging from decades to thousands of years. The availability of soil carbon, specifically SOM, significantly impacts this. Most research assesses the impact of cyanobacterial biofertilizers, namely live inoculants, on MBC. However, fewer studies include eukaryotic microalgae in their experimental treatments [95]. Therefore, microalgal biomass and necromass may facilitate SOC formation and stabilization. Table 1 represents the majority of the available studies on microalgae-based inoculants in soil MBC.

A commonly employed method to study microbial physiology is the measurement of microbial carbon use efficiency (CUE), which quantifies the effectiveness of microorganisms in converting organic carbon into growth [96,97]. Soil microbes consume plant carbon inputs through microbial decomposition. They use this carbon to grow (anabolism), then release it as extracellular products and CO_2 (catabolism). CUE balances these metabolic reactions, determining the amount of carbon that enters and remains in the system [98,99]. Microorganisms with a higher CUE and growth rate may benefit carbon sequestration and stability in the soil. These organisms can transfer more carbon from labial to more recalcitrant pools through more efficient biomass synthesis [100]. Carbon that assimilates into the microbial biomass can become part of the SOM pool and persist in soils for extended periods of time [101]. After the microorganism's death, its remains, such as its necromass, can undergo two processes: either the microorganism breaks down and serves as a substrate for new microbial growth or it transforms into stable carbon (recalcitrant C) pools (e.g., cytosolic acids and glucosamine from microorganisms) [102]. This transformation occurs either through micro-aggregation, which results in aggregated carbon (AggC), or absorption onto soil minerals' surfaces, forming mineral-associated organic matter (MAOM) (Figure 2). Therefore, preserving and improving microbial biomass and necromass can help to stabilize soil carbon pools [103]. The photosynthetic capability of soil algae is comparable to that of plants when calculating the amount of chlorophyll per unit area. Additionally, calculating the small amount of carbon in the live-standing biomass of soil algae could lead to underestimations of the carbon that is processed through this pathway, as microbial growth and turnover occur at higher rates than in plants. As a result, most of the carbon taken up by soil algae is quickly released through respiration and decomposition after the algae die, limiting its effect on soil carbon storage [79]. Recent research has revealed that carbon in the soil algal biomass [104] and microbial necromass [103] can contribute considerably to SOC. It has been suggested that soil algae contribute to long-term soil carbon sequestration [16]. Microalgal cells and their specific biomolecules have a vital role in the sequestration of SOM due to the presence of recalcitrant algaenans in their cell walls [105]. These biomolecules, which are highly aliphatic and difficult to decompose, protect algal cell walls, particularly at the soil surface [73]. However, many environmental factors, such as the formation and mean residence time of the organic compounds generated by soil algae, likely determine how much this contributes to soil carbon storage [106].

Table 1. Examples of the effect of individual cyanobacteria strains, a different mixture of bacteria and cyanobacteria combinations, or different plant-beneficial microorganisms (plant-growth-promoting bacteria and/or fungi, cyanobacteria and/or eukaryotic microalgae, and/or different combinations and/or a combination of biofilms) on enhanced soil MBC using different crops and experimental setups. Since the cyanobacterial strains were N_2 fixers, some studies used the inoculants to partially substitute the necessary N dosage while maintaining the whole dosage of phosphorus and potassium (+PK). Bacterial strains are denoted by PW1, PW5, PW7, and cyanobacterial isolates are denoted by CW1, CW2, and CW3. The consortium of CW1 + PW5 represents the microbial cultures of *Azotobacter* sp., *Anabaena* sp.—*Providencia* sp.; the consortium of CR1 + PR3 denotes *Anabaena* sp.—*Providencia* sp.; and the An-Az biofilm denotes *Anabaena* sp.—*Azotobacter* sp. biofilm. The treatment is denoted by the letter "T", with treatment numbers "1, 2, 3, 4, . . ., 33".

Inoculant	**Crop**	**Results**	**Reference**
Individual cyanobacterial strains: *Anabaena* sp., *Calothrix* sp., and *Anabaena* sp.	Wheat	Significant increase in MBC mid-crop stage and harvest stage compared to control.	[107]
Individual cyanobacterial strains: *Calothrix Ghosei* (K1) + *Hapalosiphon intricatus* (K2) + *Nostoc* sp. (K3).	Wheat	Highest MBC found mid-crop growth stage in T_{10} (1/3 N + PK + K1K2K3). Lowest MBC—T_3 (1/3 N + PK, uninoculated).	[108]
Individual cyanobacterial strains with *Trichoderma viride and Mesorhizobium ciceri biofilm-based formulation* *T. viride*—*M. ciceri* biofilm-based formulation; *T. viride*—*Bacillus subtilis* biofilm-based formulation; *Anabaena torulosa*—*M. ciceri* biofilm-based formulation; *Anabaena laxa*-based formulation.	Chickpea	Significant increase in MBC in the inoculated treatments compared to control, with the application of *Anabaena laxa* alone—373.05 (µg C/g soil) of MBC; control 163.34 (µg C/g soil) of MBC.	[109]
Different mixtures of bacteria and cyanobacteria combinations: BF1 *Anabaena torulosa*; BF2 *Nostoc carneum*; BF3 N. piscinale; BF4 *A. doliolum*; CR3 *Anabaena oscillaroides*; and bacterial strains *Brevundimonas diminuta* PR7, *Ochrobactrum anthropi* PR10, *Pseudomonas fluorescens* PF1, and *Rhizobium* sp. (*Mesorhizobium ciceri*; IC4059).	rice	The highest MBC values were recorded for biofilmed inoculants—T_8 (50% N + full recommended dose of fertilizers (FD) PK + *Anabaena* –*Pseudomonas* biofilmed formulation) and T_5 (50% N + FD PK + *Anabaena torulosa* + *Nostoc carneum* + *N. piscinale* + *A. doliolum*).	[110]
Different mixtures of bacteria and cyanobacteria combinations: Three bacterial (PW1, PW5, and PW7) and three cyanobacterial isolates (CW1, CW2, and CW3).	Wheat	The highest MBC values were recorded for T_{28} (PW1 + PW5 + CW2) and T_{15} (CW1 + CW3).	[111]
Different plant-beneficial microorganisms: cyanobacteria, *Anabaena*-based biofilms, cyanobacterium bacterium consortia, and bacterial strains.	Cotton	The highest MBC values were recorded in T_2 (*Calothrix* sp.-based formulation), followed by T_4 (*Anabaena*—*B. subtilis* biofilm-based formulation).	[112]
Different plant-beneficial microorganisms: Microbial cultures of *Azotobacter* sp., *Anabaena* sp.—*Providencia* sp. (CW1 +PW5) consortium; *Anabaena* sp.—*Azotobacter* sp. biofilm (An-Az biofilm), *Anabaena* sp.—*Providencia* sp. (CR1 + PR3) consortium, and *Calothrix* sp.	Okra	Highest MBC was recorded in T5 (CR1 + PR3), followed by T_6 (*Calothrix* sp.) and T_4 (CW1 + PW5), during the mid-crop growth stage. Four–five-fold higher values in harvest stage of T_2 (*Azotobacter* sp.), followed by T_3 (An-Az biofilm) and T_4 (CW1 + PW5), as compared to mid-crop values.	[113]

Table 1. *Cont.*

Inoculant	Crop	Results	Reference
Different plant-beneficial microorganisms: microbial biofilm inoculants (*Anabaena–Azotobacter, Anabaena-Trichoderma* and *Trichoderma—Azotobacter*).	Chrysanthemum (varieties: White Star, Thai Chen and Zembla)	Highest MBC values recorded in the *Anabaena–Azotobacter* inoculant in varieties Thai Chen Queen and Zembla.	[114]
Different plant-beneficial microorganisms: Bacterial strains (*Providencia* sp., *Brevundimonas* sp., *Ochrobacterium* sp.) and cyanobacterial strains (*Anabaena* sp., *Calothrix* sp., *Anabaena* sp.).	Rice	Highest values recorded in T_{33} (*Providencia* sp., *Ochrobacterium* sp., *Anabaena* sp.) and T_{34} (*Providencia* sp., *Ochrobacterium* sp., *Calothrix* sp.)	[78]

Dehydrogenase is an enzyme that signals overall microbial activity in the soil [87], representing the oxidative metabolic activity of living, intact cells and often correlating with microbial biomass [87] (Figure 2). Moreover, the increased dehydrogenase activities facilitate the more significant mineralization of SOM and nutrients. The increase in MBC often serves as a crucial carbon reservoir for heterotrophic microorganisms, including bacteria and fungi [114]. Cyanobacteria biofertilization (live inoculants) increased dehydrogenase enzyme activity in soil following plant growth. Some examples of this include the following: (1) *Tolypothrix tenuis*, *Microchaete tenera* in corn [115]; (2) *Anabaena torulosa*, *A. doliolum*, *Nostoc carneum*, and *N. piscinale* in rice [110]; (3) *Anabaena laxa*, *A. azollae*, *A. oscillarioides*, *Calothrix crustacea*, and other bacterial co-inoculants in rice and wheat [116]; (4) co-cultures of cyanobacteria and bacteria in wheat [111]; (5) *Anabaena* sp., *Calothrix* sp., and *Providencia* sp. bacteria consortia in okra [113]; (6) *Anabaena laxa*, *Anabaena* sp., *A. oscillarioides*, *Providencia* sp. (bacteria), *Brevundimonas diminuta* (bacteria), and *Ochrobactrum anthropi* (bacteria) in rice [78]. Alkaline phosphatase is also another critical enzyme related to SOM content and is highly correlated with microbial biomass [111,117] (Figure 2). Cyanobacteria biofertilization (live inoculants) also increased alkaline phosphatase enzyme activity in soil during plant growth. Some examples of this include the following: (1) microbial cultures of *Azotobacter* sp., *Anabaena* sp.—*Providencia* sp. consortium, *Anabaena* sp.—*Azotobacter* sp. biofilm (An-Az biofilm), *Anabaena* sp.—*Providencia* sp. consortium, and *Calothrix* sp. okra [113]; (2) bacterial strains (*Providencia* sp., *Brevundimonas* sp., *Ochrobacterium* sp.) and cyanobacterial strains (*Anabaena* sp., *Calothrix* sp., *Anabaena* sp.) in rice [78]; (3) bacterial isolates of PW1, PW5, and PW7 and cyanobacterial isolates of CW1, CW2, and CW3 in wheat [111].

6.3. Microalga's Contributions to Soil Aggregation, Aggregate Stability, and Carbon Sequestration

Microalgae play a significant role in soil aggregation through several vital actions. Soil aggregation is another critical, direct, microbial-driven mechanism of soil carbon sequestration [13]. Soil aggregation determines soil structure and serves as an indicator of soil fertility and crop productivity [118]. Aggregation is the central unit of the soil structure and a fundamental to the retention of organic carbon [119]. It is critical for protecting soils from water and wind erosion. It also contributes to several other soil functions, including moisture and nutrient retention, improved soil structure and aeration, gas exchange, water infiltration, and soil carbon sequestration [120]. Soil aggregates prevent SOC from breaking down by making it easier for carbon compounds to move from labile carbon pools to recalcitrant carbon pools [13] (Figure 2). Diverse abiotic and biotic mechanisms produce soil aggregates at varying strengths [121].

Bhattacharyya, Ros [122] examined the interaction between soil microbial communities and SOM, emphasizing several mechanisms through which soil microbial communities influence soil carbon storage, including the contribution of soil microbial communities to soil aggregation. Clays, silica, metal oxides, and aluminosilicates are mineral particles and cation complexes that stick together to make small microaggregates (<0.05 mm). Organic matter and exopolymeric substances in the soil, released by microorganisms or plants, biochemically stick to and join these microaggregates into larger microaggregates (0.05–0.25 mm) [123]. Microbes may adhere to aggregates more easily when exopolysaccharides are present. Microorganisms, mainly fungi and bacteria, play a central role in the creation of micro- (20–250 μm in diameter) and macro- (>250 μm in diameter) aggregates [124], and their significance to soil aggregates' stability has been thoroughly demonstrated in agricultural soils [125,126]. Researchers have discovered that green algae and cyanobacteria influence soil aggregation, forming a biological soil crust in arid, semi-arid or coastal dune ecosystems [127,128]. These photosynthetic microbiotic soil crusts can fix N_2 and CO_2 [129,130]. Moreover, several studies have investigated the role of green algae or cyanobacteria in promoting soil aggregation using external strain inoculation procedures [131,132] (Figure 2). Nevertheless, there has been limited research on the role of indigenous edaphic green algae and cyanobacteria in promoting topsoil aggregation in temperate agricultural soils [133]. Similarly, researchers have not extensively studied the communities and functions of soil green algae and the cyanobacteria of mesic agricultural croplands [132,134] located in regions with temperate oceanic or mesic continental climates [135].

Cyanobacteria are usually primary producers of the organic matrix. Specifically, cyanobacteria that form sheaths and excrete polysaccharide-dominant organisms in dryland biological soil crusts [136,137]. This review will not explore the application of cyanobacteria in the restoration of drylands' biological soil crusts, as its primary focus is on agricultural soils. Cyanobacteria and certain types of green algae can bind and cement soil aggregates through biophysical means, such as entangling with cyanobacterial trichomes, as well as biochemical means, such as adhering to secreted EPSs [127,138]. A remarkable feature of cyanobacterial trichomes is their mucilaginous sheaths, which allow them to firmly adhere to soil aggregates and one another, forming a gluing mesh [139,140] (Figure 1). Cyanobacteria and other non-filamentous microalgae secrete large quantities of EPSs, such as many exopolysaccharides, into the nearby soil [141]. The adhesive properties of EPSs, stemming from their slimy texture and ionic charges, are of significant scientific interest. EPSs can serve as a glue, adhering to clay and ions and binding solid particles together [142]. These substances create a mechanical structure-covering aggregation that strengthens biophysical cohesion [136] (Figure 1). Cyanobacteria species produce EPSs that are high-molecular-weight carbon-rich molecules consisting of different proportions of polysaccharides (often 40–95%), proteins (up to 60%), nucleic acids, lipids, and humic compounds, exhibiting diverse chemical properties and structures [143,144], which can promote the microbiota present in the rhizosphere by supplying organic carbon for microbial growth (Figure 2). Additionally, they can enhance soil aggregation and expand the soil's root exploration capacity, indirectly stimulating root development (Figure 3). Osman, El-Sheekh [145] assessed the impact of *Oscillatoria angustissima* and *Nostoc entophytum* on pea plant growth and found that soil inoculation with these species significantly increased the plants' root length. Several compounds found in cyanobacteria may help pea seedlings grow longer roots. These compounds include auxins [146], cytokinins [147], and gibberellins [146]. The development of roots may enhance root exudation [148,149], which indirectly contributes to soil aggregation and plant growth (the promotion of root exudation contributes to soil binding) [13] (Figures 1 and 3). Therefore, this leads to soil carbon sequestration and contributes to soil carbon cycling. Experiments conducted on arable soils demonstrate enhanced soil aggregation and stability. In a pot experiment with maize, adding EPS-producing *Nostoc* sp. to low-organic-carbon soils increased aggregate size and water stability. However, the extent of this impact varied depending on the strain of *Nostoc* sp. used and the presence of plants [150,151]. Additional instances include the enhanced water stability of soil aggregates seen in addition to cyanobacterial strains, including *Nostoc muscorum* [152], *Tolypothrix tenuis* [74], and a mixture of *Aulosira fertilissima*, *Tolypothrix tenuis*, *Anabaena*, *Nostoc*, and *Plectonema* [153]. Furthermore, the hydrophobic substances produced by the soil algae are crucial in generating water repellence [154]. Hydrophobic algal metabolite derivatives are used to stabilize water aggregation, aggregate mineral particles, and reduce the breakdown of soil [155] (Figure 2). In temperate agricultural soils, the presence of eukaryotic microalgae *Chlamydomonas mexicana* and *C. sajao* resulted in an improvement in aggregate stability [156,157]. Malam Issa, Défarge [140] investigated the effects of inoculating native cyanobacteria strains (*Nostoc*) on the physical properties of poorly aggregated tropical soils from Guquka (Eastern Cape, South Africa). Six weeks after inoculation, their data show that aggregate stability increased to two to four times higher than that of uninoculated samples. The inoculation of cyanobacteria into the soil for six weeks revealed that organic soil aggregates are primarily composed of algal filaments and EPSs (Figures 1 and 2). Mixing acidic soils with acid-tolerant microalgae, such as *Desmodesmus* sp. MAS1 and *Heterochlorella* sp. MAS3, led to the formation of an algal crust on the soil surface, as demonstrated by Shanthakumar, Abinandan [158]. The release of exopolysaccharides helped to stabilize soil aggregates and raise the pH of the soil (Figures 1 and 2).

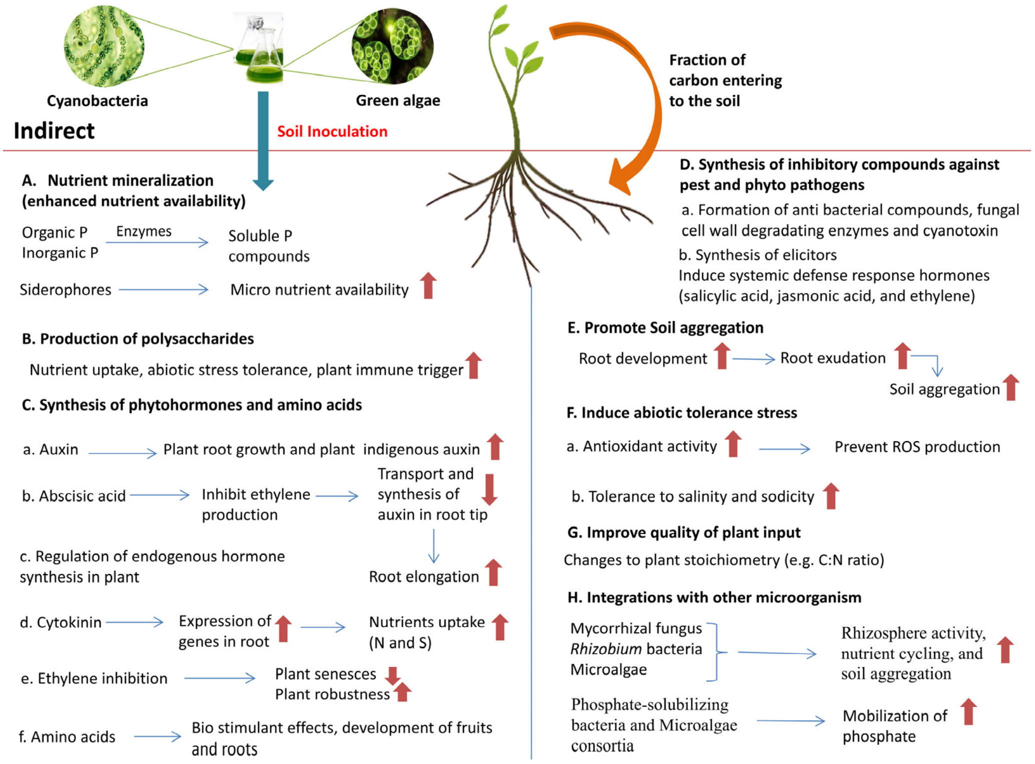

Figure 3. Overview of the indirect pathways through which microalgae contribute to soil carbon sequestration and the key activities involved in the indirect mechanisms. The arrows (↑↓) indicate the increase or decrease in microalgal activity or their mediated mechanism.

Crouzet, Consentino [133] examined the impact of indigenous soil algae and cyanobacteria on the stability of topsoil aggregates in cereal cropping systems. The findings showed that the growth of soil microalgae under both light treatments, light alone and "light + IPU" (a commercial form of isoproturon herbicide), made the aggregate more stable than it was under dark treatment. The primary process involves creating large, water-stable aggregates. As a result, the larger aggregates (>2 mm) increased in percentage due to the increased cohesiveness among the smaller macroaggregates (ranging from 0.25 to 2 mm), which correspondingly reduced. The study found that the presence or absence of algae may account for the variations in the biochemical composition of bound EPSs (as reflected in the MIR spectra) in aggregates subjected to light treatment compared to those undergoing dark treatment. These discrepancies may influence the stability of the aggregates. Moreover, their study suggested that the soil microalgae, via biochemical processes, function through the formation of exopolymeric matrices that surround soil aggregates (bound exopolysaccharides: 0.39–0.45 mg C g^{-1} soil) and biophysical mechanisms, whereby filamentous live microorganisms entangle with soil aggregates (Figure 1). In microcosms with silt loam, sandy loam, loamy sand, and sandy soil, Chamizo, Mugnai [159] added two types of cyanobacteria: *Phormidium ambiguum*, which does not fix N_2, and *Scytonema javanicum*, which is capable of N_2 fixation. After 90 days, cyanobacteria's introduction led to the development of biocrusts. *P. ambiguum* formed biocrusts with thin filaments covering the soil particles, while *S. javanicum* formed biocrusts with thicker filaments clustering between the soil particles. Remarkably, the presence of *P. ambiguum* led to an increase in both the overall exopolysaccharide concentration and the resistance to soil penetration. The cyanobacterial filaments and exopolysaccharides act as binding agents, bringing soil particles together and increasing soil aggregate development (Figure 1). The mechanism involved in soil aggregation is cyanobacteria physically binding soil particles together using multicellular filaments or organic materials, such as sand, silt, or clay, that can chemically adhere to their mucilaginous cellular sheaths or exopolysaccharides [160]. Cyanobacteria can synthesize EPSs that bind to soil metallic ions, forming a gel that maintains soil aggregate stability [161]. In addition, chelators form organo–mineral complexes by binding metals, including calcium, iron, zinc, and alumino–silicate clay minerals, promoting aggregation [162] (Figure 2). *Chlamydomonas* sp. can colonize abiotic surfaces like sand particles through adhesion to their flagella and electrostatic interactions, facilitating soil aggregation [163]. Applying microalgae to sandy loam and silty or clay loam increased soil aggregation by 85%, 130%, and 160%, respectively [164]. Microalgae assimilate organic carbon into their biomass via photosynthesis, and several strains secrete EPSs, which serve as both a source and a sink for carbon and enhance soil aggregation and stabilization [165,166] (Figure 2). Therefore, microalgae's ability to form soil aggregates helps protect SOC from degradation. This increases residence time by making it easier for carbon compounds to move from pools of labile to pools of recalcitrance (Figure 2). Moreover, microbial and plant exudation may facilitate soil particle attachment and the transfer of soil carbon to more recalcitrant pools (MOAM) located deeper within the soil complex [13].

Periphytic biofilm (PB) is a ubiquitous microbial aggregation that forms on the surface of soil or sediment in aquatic environments, especially rice paddy soil; PB comprises up 7–97% of the primary production in aquatic environments [167,168]. Microalgae is a dominant biophase in these biofilms; other phases include fungi, bacteria, protozoa and metazoan, along with a minor abiotic phase composed of EPSs, minerals (iron, Fe, aluminum, and calcium) and nutrients (N and P) [169,170]. Mixed-species groups in PB generate EPSs in paddy soil that block the pores and interfere with the soil–water contact [171]. This encourages carbon's interaction with minerals and competing ions in the matrix while limiting its transport to the atmosphere [172]. The study by Wang, Sun [172] showed that algae increased CO_2 fixation in PB, accounting for 7.2%–12.7% of the overall CO_2 sink. This is due to autotrophs present in PB that enhance CO_2 fixation. After applying fertilizer and flooding, PB quickly colonizes the soil surface due to the optimal light and nutritional conditions [169,173]. Moreover, microbiomes in the PB secrete various organic substances, including complex organic acids and monosaccharides, into the extracellular environment [174,175]. Biopolymers, such as cellulose, are likely depolymerized into sugar monomers and lipids within the debris of the PB. These lipids are then transformed into glycerol and long-chain fatty acids [176,177], as evidenced by the higher concentrations of lipids, organic acids, and other organic molecules in soil with PB [172]. The presence of microbial aggregates on the surface layer of soil in tropical, subtropical, and temperate rice fields was linked to the processes of CO_2 fixation and carbon release, and the subsequent rise in labile SOC availability (Figure 2). Overall, microbial aggregates on the soil surface have a critical impact on rice paddies' carbon biogeochemistry. This confirms that they need to be considered while developing and improving prediction models of global carbon fluxes [172].

7. Indirect Mechanisms

Mason, Salomon [13] define indirect processes of soil carbon sequestration as those that contribute to the accumulation of carbon in the soil by promoting plant growth and resilience and releasing organic compounds of plants (exudation) into the soil. This leads to an enhancement in the amount of plant biomass material entering the soil, a portion of which is subsequently converted into recalcitrant carbon pools that are resistant to decomposition. Researchers have extensively studied the potential of specific microbial groups to promote plant development, primarily due to their advantages in plant yield and agricultural productivity [178,179]. Among them, two major categories are mycorrhizal fungi and plant-growth-promoting bacteria. However, microalgae also promote the plant's growth and resilience in numerous ways.

Microalgae play a crucial role in plant and soil systems, directly contributing to plant growth and resilience. Increasing evidence suggests that cyanobacteria and eukaryotic microalgae are highly effective in promoting plant growth [95]. The potential of cyanobacteria biofertilizers and their colonization of agricultural plants have been thoroughly examined [180]. According to evolving definitions, microalgae may serve as biofertilizers, which are microbial inoculants that enhance the growth of plants when applied to soil, seeds, or the plant surface by increasing the supply or accessibility of nutrients to the plant via the actions of living microorganisms [181,182]. These activities include N_2 fixation, solubilizing, and/or mobilizing P [181,182], K, and micronutrients (e.g., Fe, Cu, Zn, and Mn, etc.) [95], as well as plant-growth-promoting activity [79]. Generally, microalgal biomass is considered an organic amendment or organic fertilizer that provides nutrients when used as a soil amendment [183,184]. It can also serve as a source of plant biostimulants [185], mixtures, or microorganisms that enhance plant growth, improve nutrient use efficiency, increase tolerance to abiotic stress, form root associations, enhance quality traits, and make nutrients confined to the soil or rhizosphere more widely available [186,187]. Additionally, they protect plants against phytopathogens [112,188] and act as phytostimulators by producing phytohormones such as cytokinin, ethylene, abscisic acid, and gibberellins, as well as other bioactive compounds that directly promote plant growth and resilience through directly binding to plant roots [189,190].

7.1. Availability of Nutrients and Nutrient Use Efficiency in Soil

Microalgae can enhance the availability of nutrients in the soil or rhizosphere, which can work in addition to fertilizers to optimize their effectiveness and reduce the amount of nutrients applied [187]. Active microalgal-derived biofertilizers can enhance the soil's microbial community, promote plant growth, increase nutrient use efficiency, and reduce reliance on chemical fertilizers [73,191]. The production of phosphatase enzymes, the exudation of organic acids that lower soil pH and solubilize phosphate, and the synthesis of biomolecules that chelate calcium and release phosphate from calcium phosphates all contribute to phosphorous solubilization [192]. Plants readily absorb the polyphosphates that soil microalgae convert from inorganic phosphate [193]. Cyanobacteria can secrete enzymes that break down inorganic phosphate in the soil, enhancing its bioavailability for plants [194]. Recent findings suggest that inoculating soil with cyanobacteria can significantly increase alkaline phosphatase activity near the roots, leading to beneficial outcomes in phosphorus mobilization [113]. Microalgae may not only solubilize insoluble inorganic P but also contribute to the release of inorganic P from organic P compounds in the soil [95]. Microalgae and cyanobacteria utilize organic phosphoesters for growth, either directly or with enzymes like alkaline phosphatase, phosphodiesterases, and $5'$-nucleotidases [195,196] (Figure 3). Moreover, *Nostoc* sp. can colonize plant root systems and facilitate the transfer of nutrients and metabolites by forming a close association with hormogonia [197]. Although the exact mechanisms by which soil microalgal inoculations boost plant micronutrients remain unclear, cyanobacteria's synthesis of siderophores is one proposed mechanism [107]. Siderophores boost iron concentrations in the root zone (a strong affinity for Fe^{3+}, which contributes to Fe solubilization) and facilitate the uptake and translocation of iron, and potentially other metals, within the plant [107,198,199] (Figure 3). Additionally, chelation binds negatively charged nutrients like phosphates, nitrates, and sulfates in a form that allows for their exchange with the chelated cations present on microalgal sheaths, increasing the accessibility of micronutrients like Fe, Cu, Mo, Zn, Co, and Mn [200]. The application of cyanobacteria-based formulations to soil has resulted in higher levels of Fe, Zn, Mn, and Cu in the soil [113], as well as higher concentrations of micronutrients in various plant components. For instance, maize leaves have an increased Zn content [201], while wheat grains show increased Fe, Zn, Mn, and Cu levels [107]. Researchers have proposed cyanobacterial inoculation as a technique for bio fortifying staple crops [107,202]. The addition of *Anabaena* sp. and *Calothrix* sp. to wheat seeds increased seed protein content by 13% and improved micronutrient concentration (Zn and Cu) compared to the application of chemical fertilizer alone, indicating that N's nutritional condition positively influences the translocation of nutrients from roots to shoots and the movement of micronutrients from vegetative tissues back into seeds [107,203]. As a result, cyanobacteria's ability to improve nutrient utilization efficiency has the potential to ultimately improve the nutritional content of grains [185] and biofortified crops, providing a viable alternative for regions with inadequate nutrition.

7.2. Synthesis of Polysaccharides, Phytohormones, Amino Acids, and Polyamines

Microalgae polysaccharides are usually heteropolymers of different amounts of glucose, galactose, and xylose linked by glycosidic bonds. However, *Gyrodinium impudicum* and *Chlorella vulgaris* also synthesize homopolymer polysaccharides, which consist solely of galactose and β-(1, 3)-glucan. Microalgal polysaccharides, along with sugars like rhamnose, fucose, fructose, and methyl sugars, can act as bio-stimulants to enhance the nutrient uptake, growth performance, physiological status, and abiotic stress (drought or salts) tolerance of crop plants. They achieve this by promoting root growth, chelating metals in soils, and improving reactive oxygen species (ROS) scavenging [186]. Moreover, the root system expands, resulting in a larger root surface area, which immediately enhances the uptake of nutrients and water from the soil, promoting plant growth and vigor [204]. The phytohormones help plants prevent abiotic stress and maintain growth [205]. Cyanobacteria and microalgae, in a symbiotic relationship with plants, produce hormones like auxins, cytokinin, abscisic acid, gibberellins, and ethylene, which have been found to enhance plant growth [206,207]. Phytohormones, particularly auxins, which act on root growth by improving the formation of lateral roots and increasing the overall volume of the root system, are responsible for the observed effects [208,209] (Figure 3). It has been reported that higher concentrations of abscisic acid inhibit ethylene production, which subsequently decreases the transport and production of auxin in the root tip, thus promoting root elongation [210] (Figure 3). The accumulation of cytokinins in plant roots can increase the expression of genes that encode root nitrate and sulfur transporters [211,212], thereby enhancing the uptake of nutrients by plants (Figure 3). Recent findings reveal that cyanobacteria's potential to improve plant development is linked to their hormone content and their influence on the induction of endogenous hormone synthesis in treated plants [213] (Figure 3). The endogenous auxin level in wheat inoculated with cyanobacteria has been proven to be highly associated with exogenous auxin synthesis via cyanobacterial strains. Furthermore, in the presence of plants, cyanobacteria exhibit an increase in the production of both endogenous and exogenous auxins (Figure 3). This observation implies that plants may release signals that regulate the increased production of auxins [189]. The use of algae or algal solutions also has an impact on plant senescence (anti-aging agents that delay senescence and enhance plant robustness) due to their inhibitory effect on the ethylene signaling or biosynthesis pathway in plants [214] (Figure 3). Notably, the use of spraying and irrigation on the *C. vulgaris* culture resulted in a prolonged period of freshness for strawberries, lettuce, beets, and kale [215]. The specific mechanism through which *Chlorella* exhibits anti-aging properties in plants remains mostly unidentified [214]. High levels of amino acids in the microalgal biomass have beneficial effects on the plants. Amino acids function as biostimulants, providing significant benefits to plants even at low concentrations by vigorously promoting the development of fruits and roots [216]. As a result, the amino acids produced by microalgae in the soil encourage plant growth.

7.3. Management of Pest and Diseases

Microalgae may release a wide range of active compounds, including proteins, free volatile fatty acids, carotenoids, EPSs, vitamins, and antibiotics, in addition to phytohormones. The chemical groups of fatty acids, phenols, indoles, acetogenins, terpenes, and volatile hydrogenated hydrocarbons include microalgal metabolites that have antibacterial, antiviral, and anti-protozoal properties [79] (Figure 3). Zhou, Bao [217] assessed the biocontrol ability of nine N_2-fixing cyanobacterial strains against rice sheath blight induced by the fungus *Rhizoctonia solani*. *Nostoc piscinale* and *Anabaena variabilis* (SCAU04 and SCAU26) were found to be the best N_2-fixing cyanobacteria for the biocontrol of *Rhizoctonia solani*. The primary mechanisms by which N_2-fixing cyanobacterial strains assist rice plants in combating *Rhizoctonia solani* include the synthesis of antagonistic compounds, the secretion of phytohormones (which enhance growth and induce disease resistance), and the enhancement of soil nutrient levels (which facilitate growth). In addition, cyanobacteria generate bioactive substances that inhibit fungi, nematodes, and numerous diseases by inactivating key enzymes, disrupting cytoplasmic membranes, and inhibiting protein synthesis. As an illustration, cyanobacteria produce enzymes like chitosanase, β-1,4-glucanase, β-1,3-glucanase, and benzoic acid, which can degrade fungal cell walls, inhibiting the growth of *Fusarium*, *Penicillium*, and *Candida* sp. [218,219] (Figure 3). Furthermore, cyanobacteria can synthesize pesticidal and nematocidal secondary metabolites known as cyanotoxins [220]. The nematicidal properties result from the release of neurotoxins, including anatoxin-A, microcystin, and nodularins, which inhibit the proliferation of nematode pests. Anatoxin-A mimics the neurotransmitter acetylcholine and permanently attaches to acetylcholine receptors, resulting in persistent muscular contraction in nematode pests, causing immobilization [221]. It has been demonstrated that the root treatment of tomatoes with cyanobacteria such as *Microcoleus vaginatus* reduced gall formation caused by the nematode pest of *Meloidogyne incognita* [222].

Plants have a complex defense mechanism to protect themselves from biotic stress, which has sparked scientific interest in finding new compounds for agricultural sustainability. When pests or pathogens attack plants, they need to detect chemical signals related to biotic stress, such as herbivore-associated molecular patterns (HAMPs), pathogen-associated molecular patterns (PAMPs), or damage-associated molecular patterns (DAMPs), from the harm caused to initiate specific, targeted defense responses. Plant receptors recognize chemical structures called elicitors, which activate pattern-triggered immunity (PTI). Plants' PTI activates both local and systemic defense responses against biotic stresses. Hormones like salicylic acid, jasmonic acid, and ethylene play a significant role in the systemic defense response [223,224]. Both chemical derivatives and the structural components of microalgae can serve as elicitors of plant defenses in agriculture (Figure 3). The application of microalgae to crop roots entails the systemic activation of plant defenses, involving a reciprocal relationship between microalgae and plants. Studies have shown priming-type reactions in many crops, but the specific microalgae molecule involved remains unknown [225]. *Chlorella vulgaris* (Chlorophyta) inoculation of the roots of broccoli and guar plants resulted in systemic increases in ascorbate peroxidase, catalase, superoxide dismutase, and glutathione reductase activities, as well as enhanced tissue accumulation of flavonoid and phenolic compounds [226,227]. The priming-type defense responses enable plants to prepare for invasion by different pathogens. Plants recognize the ability of microalgae to synthesize various chemical compounds and molecules as elicitors (Figure 3). Lactic acid is a chiral organic acid known to be synthesized by some types of green microalgae [228]. The cellular receptors of *A. thaliana* can identify the D-lactic acid isoform generated by *C. fusca*, which stimulates the systemic expression of salicylic acid- and jasmonic acid-related genes and reduces the effects of the disease caused by *P. syringae* pv. tomato [229]. Thus, microalgae-induced plant immune responses closely correlate with the activation of defense-related hormone signals.

7.4. Induced Tolerance to Abiotic Stresses

Abiotic stressors like drought, salt, and extreme temperatures significantly limit agricultural productivity globally, reducing crop yield and production quality [230]. In stressful environments, cyanobacteria can stimulate plant growth and development by synthesizing and releasing a wide range of biologically active compounds that can trigger systemic responses to combat stress in plants [231]. These signaling molecules, referred to as elicitors, can influence the expression of genes in plants and promote the accumulation of various phytochemicals, such as glucosinolates, alkaloids, polyphenols, flavonoids, flavonoid glycosides, saponins, terpenes, and phytoalexins. These phytochemicals protect plants against biotic and abiotic stresses [231,232]. Singh, Prabha [233] found that potted rice plants cultivated with different cyanobacterial strains exhibited a uniform buildup of phenolic acids, flavonoids, phytohormones, proteins, and chlorophyll in their leaves. Elevated levels of phytochemicals serve as a reliable signal of increased gene expression in plants caused by elicitor molecules. Inoculated plants directly link this increase to a higher germination rate, shoot length, root length, and biomass [231]. Various abiotic conditions, such as drought, salt, and severe temperatures, induce osmotic stressors in plants, resulting in the accumulation of ROS that cause damage to DNA, lipids, carbohydrates, and proteins and disrupt standard cell signal processing [234]. Researchers have shown that inoculating soil with cyanobacteria enhances the antioxidant activity of treated plants, thereby reducing the effects of stress-induced free radicals through direct scavenging and preventing ROS production (Figure 3). Singh, Prabha [233] found that inoculating soil with *Oscillatoria acuta* and *Plectonema boryanum* increased the enzymatic activity of peroxidase and phenylalanine ammonia lyase in rice leaves, leading to systemic tolerance against stress. Additionally, the total phenolic content reached its highest levels after inoculation with *Anabaena oryzae*.

The detrimental effects of salt on plant development are attributed to plant metabolism, nutritional deficiencies, osmotic stress, specific ion toxicities, or a combination of these factors. Upon reaching plant cells, salts can induce ionic stressors, predominantly through Na (and Cl), which inhibit vital functions such as protein synthesis, photosynthesis, and energy and lipid metabolism [70]. Microalgae use the following mechanisms to tolerate salinity and sodicity in the soil: producing EPSs to buffer salts (EPSs contain negatively charged groups, like uric acid), releasing calcium and forming carbonic acid, utilizing chelators to bind and immobilize calcium and sodium, maintaining low internal sodium by either restricting uptake or efflux through algal biomolecules or the consortia of microalgae's activities with other rhizosphere microorganisms, releasing organic acids through the microbial decomposition of organic matter to react with calcium carbonate, synthesizing and accumulating osmoregulatory compounds such as sugars and quaternary amines to impart high osmotic tension to plant roots for the absorption of water and nutrients, improving permeability, aeration, and water movement through soil aggregation, substituting calcium or potassium ions for sodium ions in clay complexes, and expressing of a set of salt-stress-responsive proteins [70,192]. Therefore, microalgae are promising organisms for the remediation of saline–alkaline soil (Figure 3). They exhibit unique characteristics such as varying degrees of salt tolerance, high tolerance to extreme conditions, rapid growth rates, and efficient nutrient cycling capabilities [235]. A microalgal eco-farm on salt-affected soil was proposed by Pei and Yu [236]. It achieved both in situ soil improvements, including making it possible to increase SOM content from carbon fixation through the cultivation of these microalgae, CO_2 reductions, and the harvesting of microalgal biomass and agriculture production [235,236]. Therefore, microalgae also potential have diverse roles in enhancing plant growth through enhancing nutrient acquisition and availability and improving resilience by supporting plant defenses against pathogens and other environmental stressors. This increase in plant biomass, both above and below ground, facilitates the entry of carbon into soil systems.

7.5. Plant Stoichiometry, Integration with Other Microorganism, and Microbial Community Composition

The fate of organic amendments to soil is also dependent upon the characteristics of the substrate used, including its stoichiometry, usefulness, and quality [237]. The cycling of soil nutrients and release of plant-available nutrients from organic substrates relies on microbial biomass activity [88,89]. Microalgae, including cyanobacteria, may mediate the plant's uptake of nutrients such as N and P, thus altering plant and soil stoichiometry. The chemical composition of plant material, particularly the N:P and C:N ratios, influences the decomposition rate and the correlating CUE of the involved microorganisms. When a high C: N ratio (>30:1) is present, low-quality organic matter can take longer to break down due to the microbes' need for more N than C. This causes N immobilization, preventing plants from using N until the bacteria's biomass is altered [13]. However, introducing N_2-fixing cyanobacteria inoculants may overcome this issue due to their ability to fix atmospheric N_2 and provide the N requirements of heterotrophic microbes, especially bacteria and fungi, allowing for organic matter with a high C:N ratio to be decomposed or providing N to available plants (Figure 1). Harper and Belnap [160] showed that *Nostoc* fixes approximately 5% to 88% of the N_2, which leaks into the adjacent substrate and converts 11–16% of the total N being mineralized [160]. This is because protein complex nitrogenase facilitates the conversion of atmospheric N_2 into ammonia, forming various nitrogenous compounds, including amino acids, polypeptides, auxin, and vitamins-like substances. These compounds can be released either through microbial secretion or through degradation after cell death [238]. Therefore, algalization, also known as cyanobacterization, is a very important step in the addition live N_2-fixing cyanobacteria to soil via inoculation in order to raise the soil's N pool. This positive N balance is good for soil fertility [239,240].

On the other hand, the low C:N ratio (C:N ratio of 20–25:1) found in higher-quality organic material may decompose more quickly, leaving enough N for the available to plants. Microorganisms increase their CUE when they consume high-quality organic matter, converting more carbon substrates into new biomass materials than the carbon they absorb. As a result, the amount of CO_2 released into the atmosphere decreases while the residual microbial biomass simultaneously increases [241]. The addition of N may enhance the CUE of microorganisms in low-quality plant litter or may be directly used by microorganisms during the decomposition process. This could help to correct imbalances in soil stoichiometry and facilitate the conversion of litter into SOC [242] (Figure 1). At the laboratory scale, several successful artificial associations have formed between free-living [243,244] and symbiotic cyanobacteria for the non-natural host [245,246] crop plants. Researchers have studied artificially induced relationships between crop plants and N_2-fixing cyanobacteria to promote N-independent cereals or reduce the need for chemical N-fertilizers despite the absence of natural symbioses in agriculturally significant plants [247,248]. One advantage is that cyanobacteria can transfer the fixed N and other metabolites to the plant and other soil organisms during their growth, as opposed to after death and decay [244]. Additionally, cyanobacteria can fix N_2 in oxygenic environments, unlike other microbial technologies like rhizobia [249,250]. Microalgae and cyanobacteria form beneficial relationships with plant roots by secreting extracellular enzymes that decompose soil organic matter, releasing essential nutrients like N and P. Consequently, plant roots release exudates (e.g., simple sugars, amino acids, organic acids, and other chemical substances) that serve as a nutrient source for microbes. These microbes can subsequently establish colonies around the plant roots, forming a biofilm that aids in safeguarding the roots from pathogens and other stressors [251]. Algae and plants exhibit a symbiotic relationship, as seen in the colonization of monocots like wheat and rice by *Nostoc* genus species [247,252]. The co-inoculation of wheat seeds with 2,4-D and *Nostoc* sp. strain 2S9B may enhance shoot development without additional N [250,253]. Gantar, Kerby [247] isolated various heterocystous N_2-fixing cyanobacteria from plant roots and soil, including *Nostoc*, *Anabaena*, and *Cylindrospermum*. A study of wheat seedling roots identified two distinct association patterns: *Anabaena*, which loosely colonized the root hair, and *Nostoc,* which tightly colonized the root surface within a restricted zone [247]. Researchers attempted to develop nodule-like structures named paranodules and biologically fixed N in non-leguminous plants [254]. Nilsson, Bhattacharya [244] reported that a treatment with 2, 4-D and *Nostoc* spp. could also induce para-nodule formation and N fixation in rice seedlings. Thus, adding N_2-fixing cyanobacteria inoculants to agricultural soil may help to correct the imbalances in soil stoichiometry.

Integrating microalgae with phosphate-solubilizing, N_2-fixing, and/or other plant-growth-promoting microorganisms increases the benefits they offer plants [192]. Combining mycorrhizal fungus, *Rhizobium* bacteria, and microalgae stimulates higher levels of rhizosphere activity, nutrient cycling, and soil aggregation [160] (Figure 3). The phosphate-solubilizing bacteria, namely *Bacillus megaterium*, *Bacillus circulans*, *Bacillus subtilis*, *Bacillus mucilaginous*, and *Pseudomonas striata*, form a consortia with microalgae to facilitate the mobilization of phosphate [255] (Figure 3). A study by Swarnalakshmi, Prasanna [256] examined novel biofilm formulations, utilizing the cyanobacterium *Anabaena torulosa* as a matrix for diazotrophic and phosphate-solubilizing bacteria. The scientists evaluated the fertilization potential of biofilms on wheat crops and documented a substantial increase in available N, even 14 weeks after inoculation. The inoculation of the *A. torulosa—Azotobacter chroococcum* biofilm on leguminous crops led to increases of 80% in available N and 24% in available phosphorus. In the same study, the *A. torulosa*–*Bradyrhizobium* spp. biofilm enhanced N_2 fixation, N mobilization, and soil carbon sequestration [257]. Mutualism is a beneficial relationship between organisms of two distinct species, where each derives advantages from the mutually beneficial exchange of resources and services. A mutualistic consortium of microalgae and bacteria relies on the exchange of metabolites, and the well-documented mechanism through which bacteria enhance microalgal growth involves CO_2 supplementation. Environments with diminished O_2 tension and elevated CO_2 levels enhance the primary metabolism of microalgae, leading to population growth [258]. In return, the microalgae's production of EPSs, such as proteins, amino acids (such as tryptophan), and organic carbon (such as myo-inositol or lactate), can promote the growth of bacteria [259].

Several studies have shown extensive alterations in the microbial community after microalgae inoculations. Ibrahim, Kamel [260] showed an increase in the number of *Azotobacter* spp. and nitrifiers after introducing the *Cyanobacterium Tolypothrix tenuis*. Similarly, Rogers and Burns [152] reported increases in some bacterial groups, actinomycetes, and fungi after soil inoculation with *Nostoc muscorum*. Recent studies have shown that introducing biofilms of *Anabaena torulosa* with either *Trichoderma viride* (fungus) or the bacterium *Azotobacter* sp. enhanced gene counts specific to bacteria and cyanobacteria while reducing the archaea in soil containing Chrysanthemum plants [114]. The composition of the microbial community is complicated by the diverse cyanobacterial species used in inoculations, environmental factors, fertilizer treatments, and other factors. Nevertheless, the patterns of changes in community diversity may primarily indicate significant changes in ecosystem functioning, a potential area of research that can inspire and motivate further studies [95].

Identifying and utilizing specific groups of organisms with the desired characteristics is challenging because these traits (such as a high microbial growth rate and CUE) are strongly associated with environmental factors (such as soil type, temperature, nutrient concentrations, and stoichiometry) rather than any particular microbial group. Environmental factors play a crucial role in carbon cycling within soil systems. Soil texture, nutrient content, and climate are important factors determining a soil's capacity to store and stabilize carbon [261,262]. Similarly, temperature, land use, and nutrient management may significantly influence microbe growth and correlate with soil carbon stabilization rates and decomposition [98,263]. Nevertheless, plant cover, namely leaf area index, and soil parameters, including soil moisture, SOC content, and pH, were as significant as climate. Specifically, the average yearly temperature and rainfall, the amount of vegetation, and the moisture in the soil had significant favorable impacts. However, an increase in pH had a detrimental influence on the overall quantity of soil algae. Moreover, the findings suggest that complex relationships between soil parameters, climate, and vegetation influence the growth efficiency of soil algae. However, the precise processes behind these interactions have yet to be determined [16]. Therefore, it is challenging to compare the effects of different studies on soil algal inoculants' contribution to SOC due to the changes in environmental parameters in other regions, which ultimately determine growth efficiency of soil microalgae. However, further research is needed to explore how the application of different soil algal inoculant species influences carbon sequestration in agricultural crops.

8. Future Perspectives and Recommendation

When establishing ambitious goals for soil carbon sequestration, the primary limitation is the requirement of N to sustain the proper C:N stoichiometry balance in soils. Typically, C:N in agricultural soils is around 10–12. Approximately 100 million tons of N are needed each year to raise the level of CO_2 by 4 billion tons to maintain the soil carbon. Applying any synthetic chemical N fertilizer will enhance nitrous oxide emissions, another potent greenhouse gas released by the soil. Therefore, artificially induced relationships between N_2-fixing cyanobacteria and agricultural crops need to be explored to enhance N-independent crops, particularly cereals, or reduce the need for chemical N fertilizers [247–249]. One benefit of these is that cyanobacteria can supply fixed N_2 and other metabolites to plants and soil organisms during their active growth, rather than only after their death and decay [244]. Additionally, cyanobacteria can fix N_2 in oxygen-rich environments, unlike other N_2-fixing microbes such as rhizobia [249,250]. Evaluations of the best management practices and frontier technologies worldwide aim to improve soil carbon sequestration potential by overcoming the technological and economic barriers. Biological negative-emission strategies are increasingly important for controlling biotic processes and enhancing the long-term soil carbon balance. The ability to reduce atmospheric CO_2 without significantly increasing nitrous oxide emissions from the application of fertilizer is desired in the current setting. Reduced tillage or 'no-till' is considered one of the best management methods for improving soil carbon capture, sequestration, and storage. The effectiveness of this approach depends on factors such as soil texture and type and the prevailing climate. However, some research findings revealed that no-till farming also increased soil CO_2 emissions due to seasonal changes. Furthermore, tillage practices, including short-term tillage, affected the community composition of soil microbes [264,265].

Pyrolyzing agricultural organic waste, including crop residue and other materials produced during production, creates carbon-neutral or carbon-negative amendments. It is necessary to investigate the use of various processes to ensure a reliable carbon input (biochar) to provide plants with additional nutrients and protect soil carbon from decomposition, thereby enhancing the soil's capacity to store carbon [13]. Biochar has various characteristics that are advantageous for carbon sequestration [266,267] and CO_2 emission reductions [268]. In their study, Weng, Van Zwieten [269] examined the methods via which biochar increases the SOC ceiling. They presented direct visual evidence and conducted three-dimensional studies to demonstrate how biochar may safeguard newly added carbon inputs to the soil, including microbial products. The findings indicate that biochar may enhance microbial CUE by lowering the activity of enzymes, leading to a negative priming effect and a decrease in SOC mineralization, namely soil respiration. Biochar has various characteristics that are advantageous for carbon sequestration.

One possible method that could enhance the ability of microbial products to store carbon in the soil is applying soil amendments together with specific groups of microorganisms. Understanding the need to maintain productivity and respect the inherent capacity of a particular soil to retain carbon (storage potential) is crucial when considering large-scale commercial agriculture. CO_2 fertilization techniques, such as soil- and algae-based methods, can positively impact croplands. These methods not only stimulate plant growth but also enhance the absorption of carbon by terrestrial ecosystems [79]. The most frequently suggested microalgae-based techniques are directly burying fresh algal biomass, burying algal lipids, and soil amendments with algal biochar. Algal biochar can capture around 50% of the carbon in a biomass [270]. Nevertheless, the agriculture industry is not currently focusing on the use of microalgae as a soil inoculant to improve soil carbon sequestration. Thus, it is necessary to explore further research on the biochar + microbial (specifically microalgae inoculants) system to increase soil carbon sequestration. The experimental studies suggest that biochars' various chemical and physicochemical properties may positively impact microorganisms' habitat conditions, enhancing the production of innovative bio preparations. Moreover, it is vital that incorporating combination of biochar, organic manure and microalgae is essential for enhancing soil carbon sequestration. Utilizing an organic fertilizer may enhance the process of converting carbon into cell molecules by promoting the formation of intracellular polysaccharides in microalgae. Biochar supports soil carbon sequestration in two distinct ways: 1) Biochar binds soil organic matter to its surface, which helps protect it from microbial decomposition, 2) Biochar can modify microalgae's carbon metabolism pathway by altering the production of intracellular saccharides and the amount and type of extracellular saccharides [271]. Most soil microorganisms are heterotrophic, and the interaction between heterotrophic and autotrophic microbes enhances the microbial community's potential to fix CO_2 [272]. Biochar captures CO_2 released through soil respiration, creating a microenvironment enriched with inorganic carbon forms such as CO_2, HCO_3^-, and CO_3^{2-} [273,274]. This environment could provide sufficient carbon for microalgae's autotrophic metabolism [272]. Therefore, further research experiments are necessary to identify the effects of different biochar, organic manure and microalgae mixtures for enhancing soil carbon sequestration. Applying a nanobiochar with a microalgae inoculant is another viable potential method that may enhance soil carbon sequestration. Biochars can enhance their characteristics for particles smaller than 100 nm by decreasing their particle size to the nanoscale. This is due to the increased surface-to-volume ratio, which improves surface energy and thus promotes biological efficacy [275,276]. Therefore, nanobiochar may facilitate a better microhabitat for microorganisms than biochar, which may be more effective at sequestering soil carbon. Moreover, amending soil with nanoalgal biochar is another possible option to improve soil carbon storage. However, the method through which nanoalgal biochar is prepared may destroy the properties of the microalgae. Therefore, we recommend further studies to test the effectiveness of the nanobiochar at the field scale, as well as its contribution to soil carbon sequestration. Several parameters, including temperature, feedstock type, pyrolysis atmosphere, and resident time, can influence biochar quality. These factors work together to control the pyrolysis process and determine the desired qualities of the biochar [277]. Therefore, developing an optimal biochar modification strategy is key to increasing carbon sequestration in soil and reducing CO_2 emissions from agricultural soils into the atmosphere. Applying CO_2 fertilization techniques, such as soil- and algae-based methods, can positively affect croplands. These methods not only stimulate plant growth but also enhance the absorption of carbon by terrestrial ecosystems [79]. Therefore, the environmental benefits of CO_2 sequestration by microalgae must be considered for commercial production.

One key area that requires immediate attention is the identification of potential microalgal strains and strain combinations. These could include biofilms and microalgae-based consortia, which synergistically affect soil carbon sequestration. Conducting laboratory and field tests on various soil types and crop types, and in various agroclimatic regions, is essential to assess microalgal establishment and agronomic efficiency in soils with varying native flora. Utilizing the high-performance algae strains acquired through screening and/or genetic engineering may optimize CO_2 fixation efficiency [278]. Identifying strains that are suitable for a specific application is critical to optimizing carbon sequestration's effectiveness. The first step in utilizing microalgae for carbon sequestration is identifying appropriate strains. Bioprospecting microalgae from local habitats systematically isolate strains that are more likely to adapt effectively to applications with similar environmental conditions to their original isolation sites [279]. Bioprospecting starts with collecting wild strains from local ecosystems, followed by their isolation and screening [280]. High-throughput screening techniques are effective in identifying desirable strains from extensive collections of microalgae in natural environments and algal banks. The M96SS strain screening method effectively overcomes the challenges in miniature culture systems, such as intra-well mixing and sample evaporation, allowing for the simultaneous processing of up to 768 algal samples [281]. The genetic engineering of microalgae is a highly efficient approach to enhancing traits. Experimental studies conducted in recent decades demonstrated that *Chlamydomonas* is a significant eukaryotic algal model for genetic modification. Furthermore, the engineered *Anabaena* sp. 7120 demonstrated a significantly higher efficiency in fixing CO_2. Kang, Shi [282] found that adding two genes encoding fructose-1,6-bisphosphate aldolase and triose phosphate isomerase to Anabaena sp. 7120 significantly increased the expression of these two enzymes compared to the wild-type enzymes under all test conditions. Previous studies proved that increasing the overexpression of critical enzymes strongly linked to the photosynthetic CO_2 fixation pathway could be a very effective way to improve microalgae's ability to fix CO_2 [80].

9. Conclusions

Microalgae, including cyanobacteria and green algae, have the ability to influence soil carbon sequestration. Their role in soil carbon cycling is significant, especially their ability to improve soil carbon storage and ecosystem resilience. We outlined the direct and indirect mechanisms mediated by microalgae and their activities that contribute to soil carbon sequestration and retention. Microalgal activity directly contributes to SOC through carbon fixation, EPS secretion, extracellular enzyme production, and the formation of stable soil aggregates. These activities enhance soil carbon sequestration and promote carbon stability. Microalgae indirectly facilitate soil carbon sequestration through promoting plant growth and resilience, as well as by encouraging the release of organic compounds (exudates) from plants into the soil through nutrient mineralization, the synthesis of polysaccharides, phytohormones, amino acids, and inhibitory compounds against pest and diseases, the promotion of soil aggregation, inducing tolerance to abiotic stress, changes in the quality of the plant inputs, and integration with other beneficial soil microorganisms. This process enhances the accumulation of plant biomass material within the soil, contributing to overall carbon storage. Microalgae have enormous potential for use in agriculture as inoculants to improve soil carbon content and mitigate climate change issues. However, these microorganisms have received less attention in agricultural settings in the context of soil carbon dynamics.

The colonization and establishment of microalgae in the plant root rhizosphere are highly variable. They depend on multiple factors, including climate, soil conditions, plant characteristics, and the interactions among these elements. Therefore, future research should focus on understanding the specific interactions between soil algae, environmental conditions, and soil carbon dynamics to optimize the use of these microorganisms in sustainable agricultural practices. Moreover, further research is necessary to understand the efficiency of strains and identify potential candidates among microalgae species before applying inoculants, in the context of soil carbon sequestration and soil carbon stabilization, under field conditions. We suggest utilizing genetic engineering techniques and/or screening as one feasible method of overexpressing genes involved in photosynthesis in microalgae to increase the efficiency of their photosynthetic capabilities and to enhance biomass production in field conditions, which will help to increase the amount of carbon entering the soil from the atmosphere. The ongoing loss of soil carbon in agricultural soils, caused by various soil management practices and increasing concentrations of atmospheric CO_2 as a greenhouse gas, highlights the need for nature-based solutions in agriculture to conserve and restore soil carbon. Therefore, it is fundamental to develop microalgae inoculant-based fertilization techniques to enhance CO_2 fixation adapted to specific crops and environments in agricultural soils.

Author Contributions: Conceptualizations: A.G.S.D.D.S., I.M.K. and Z.M.; visualization, A.G.S.D.D.S., Z.K.H. and G.K.; writing—original draft, A.G.S.D.D.S.; supervision, W.S., I.M.K., J.-B.Z. and Z.M.; writing—review and editing, all authors. All authors have read and agreed to the published version of the manuscript.

Funding: The research was funded by project no. RRF-2.3.1-21-2022-00001 in the support provided by the Recovery and Resilience Facility (RRF), financed under the National Recovery Fund budget estimate, RRF-2.3.1-21 funding scheme.

Data Availability Statement: Not applicable.

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

Abbreviations

Aggregated carbon	AggC
Bicarbonate	$HCO_3{}^{2-}$
Carbon	C
Carbon dioxide	CO_2
Carbonate Carbon monoxide	$CO_3{}^{2-}CO$
Carbon dioxide concentrating mechanism	CCM
Carbon use efficiency	CUE
Damage-associated molecular patterns	DAMPs
Dinitrogen	N_2
Extracellular polymeric substances	EPSs
Hydrogen	H
Herbivore-associated molecular patterns	HAMPs
Methane	CH_4
Mineral-associated organic matter	MAOM
Microbial biomass carbon	MBC
Microbial carbon pump	MCP
Nitrogen oxides	Nox
Oxygen	O
Particulate organic carbon	POC
Particulate organic matter	POM
Pattern-triggered immunity	PTI
Pathogen-associated molecular patterns	PAMPs
Periphytic biofilm	PB
Phosphorous	P
Potassium	K
Reactive oxygen species	ROS
Soil organic carbon	SOC
Soil organic matter	SOM

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