

Review

Interplay between Plant Functional Traits and Soil Carbon Sequestration under Ambient and Elevated CO₂ Levels

Siddhartha Shankar Bhattacharyya^{1,2,*} , Pedro Mondaca^{3,4} , Oloka Shushupti⁵ and Sharjeel Ashfaq⁶ ¹ Soil and Crop Sciences, Texas A&M University, College Station, TX 77843, USA² Texas A&M AgriLife Research, College Station, TX 77843, USA³ Center of Biotechnology “Dr. Daniel Alcalay Lowitt”, Universidad Técnica Federico Santa María, General Bari 699, Valparaiso 1680, Chile⁴ Molecular Microbiology and Environmental Biotechnology Laboratory, Department of Chemistry, Universidad Técnica Federico Santa María, Avenida España, Valparaiso 1680, Chile⁵ Department of Soil, Water and Environment, Faculty of Biological Sciences, University of Dhaka, Dhaka 1000, Bangladesh⁶ Institute of Soil Research, University of Natural Resources and Life Sciences (BOKU), 1180 Vienna, Austria

* Correspondence: ss_bhattacharyya@tamu.edu or ss.bhattacharyya@ag.tamu.edu

Abstract: Unique plant functional traits (morpho-physio-anatomical) may respond to novel environmental conditions to counterbalance elevated carbon dioxide (eCO₂) concentrations. Utilizing CO₂, plants produce photoassimilates (carbohydrates). A mechanistic understanding of partitioning and translocation of carbon/photoassimilates into different plant parts and soils under ambient and eCO₂ is required. In this study, we examine and present the intrinsic relationship between plant functional traits and eCO₂ and seek answers to (i) how do plant functional traits (morpho-physio-anatomical features) affect C storage and partitioning under ambient and eCO₂ in different plant parts? (ii) How do plant functional traits influence C transfer to the soil and rhizosphere services? Our study suggests that morpho-physio-anatomical features are interlinked, and under eCO₂, plant functional traits influence the quantity of C accumulation inside the plant biomass, its potential translocation to different plant parts, and to the soil. The availability of additional photoassimilates aids in increasing the above- and belowground growth of plants. Moreover, plants may retain a predisposition to build thick leaves due to reduced specific leaf area, thicker palisade tissue, and higher palisade/sponge tissue thickness. eCO₂ and soil-available N can alter root anatomy, the release of metabolites, and root respiration, impacting potential carbon transfer to the soil.

Keywords: elevated CO₂; carbon cycling; carbon emissions; carbon accumulation; rhizosphere



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1. Introduction

Atmospheric carbon dioxide (CO₂), the main source of carbon (C) for plants, has risen in concentration by around 146% since 1750 [1], being now equivalent to or much higher than 8 to 15 million years ago [2,3]. Gayathri et al. [4] quantified an elevated CO₂ concentration (eCO₂) from 250 to 418 ppm (parts per million) during the past 150 years and speculated it may exceed 700 ppm by the end of the 21st century [5]. Fossil fuel combustion, agricultural land use change, and anthropogenic activities are the major causes of eCO₂ [1,4,6]. For example, studies have estimated that 78–133 Pg (Pg = petagram) of CO₂ has been emitted from agricultural soils in the past two decades [1,7,8]. Additionally, Gilfillan and Marland [9] recorded that global CO₂ emission from fossil fuel combustion and anthropogenic activities (e.g., cement manufacturing) was 9.79 Pg.

eCO₂ is responsible for the catastrophic impacts of climate change [10,11], and a 2–8 °C increase in global mean annual surface temperatures is also foretold (global warming) [10,12]. Under such novel environmental contexts, atmospheric CO₂ removal (CDR) technologies are widely implemented to mitigate the hazardous impacts of climate change

and global warming [13,14]. However, most of them are not feasible to implement due to their intrinsic material-intensive and energy-consuming nature [15]. Of these, soil carbon sequestration (SCS) appears as one of the most sustainable options of CDR that intends to reduce atmospheric CO₂ and global warming by transferring and storing CO₂ to soils through plants for a longer period [13,16,17]. Prospects, constraints, and inconsistencies of SCS have been widely reported [18–20]. Yet, reducing uncertainties, as well as strengthening and upgrading SCS potential, are crucial tasks, albeit it is impossible without plants and an enhancement in plant functional traits. Plant functional traits include morpho-physio-phenological traits that determine individual species performance in terms of environmental stimuli, different trophic levels, and other ecosystem properties [21,22], and these traits are responsible for in-plant C sequestration (CS), long-term storage in plant biomass (the bulk of the plant), and later transfer into soils (Figure 1).

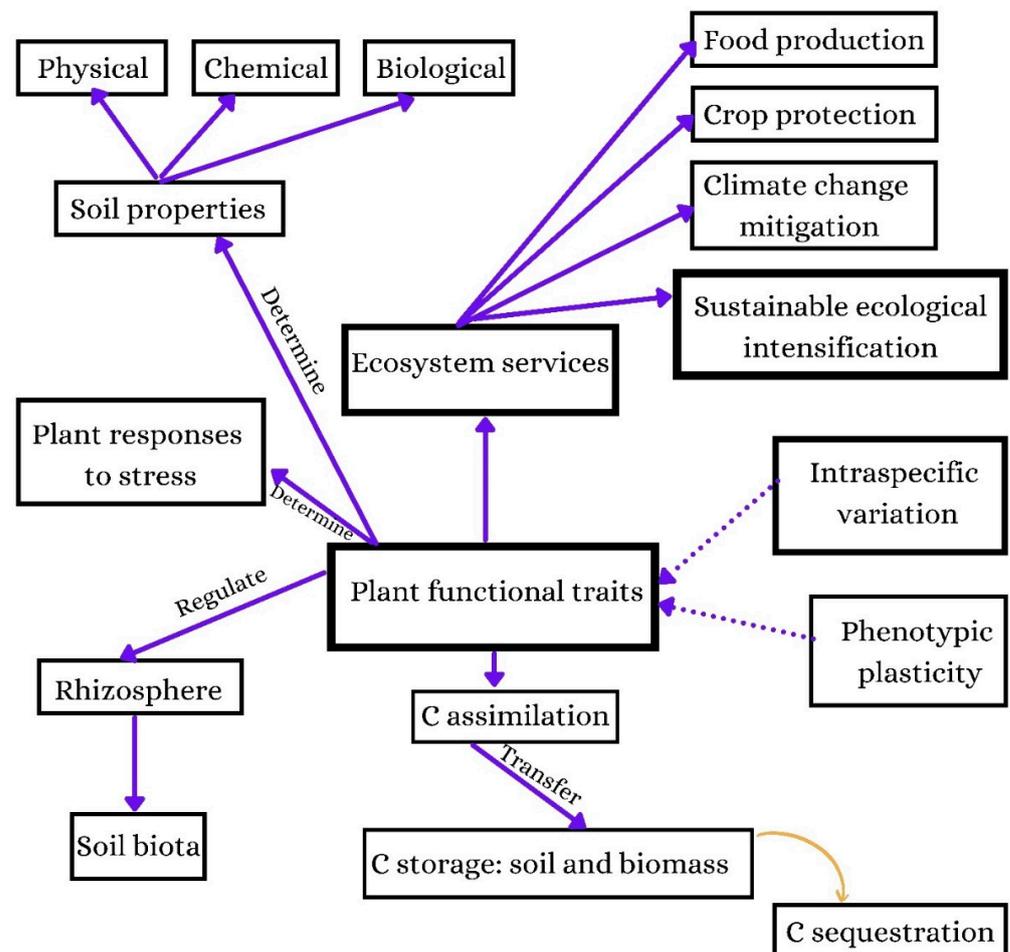


Figure 1. Schematic representation of the role of plant functional traits on soil properties and ecosystem services based on De Deyn et al., 2008, and Faucon et al., 2017 [23,24].

Functionally, plants rely on sunlight for survival and take materials from the soil and the atmosphere. Under the influence of sunlight, leaves reduce CO₂ in the chloroplasts of mesophyll cells, allowing CO₂ to be transformed into carbohydrates (e.g., glucose) [25,26]. The generated photoassimilates are then partitioned, translocated, and stored in different plant parts to meet their energy demands (e.g., in woods). While certain portions become fixed in soils by roots, resulting in SCS, this conversion is fully dependent on plant functional traits. Hence, an in-depth understanding of these traits affecting CS and SCS is required because these traits will also be changing (adjustments) under new normal environmental conditions.

There is now a plethora of literature showing morpho-physio-anatomical characteristics of plants impacted either explicitly or implicitly under eCO₂ [27–34], higher temperatures [35,36], and even under light quality changes [32,37,38]. Studies have shown that eCO₂, in general, may increase the photosynthetic efficiency, transpiration rate, stomatal conductance, water usage efficiency, C content of plant tissues (stem, leaves, and root), shoot and root biomass, stem diameter, wood density, and root growth of plants [39–43]. Increased photosynthesis leads to increased photoassimilate production, and in this context, resource allocation patterns (C partitioning) in plants are critical [44] because C acts as a regulator of many morpho-physio-anatomical characteristics. Additionally, eCO₂ coupled with temperature rise may exhibit the opposite effect, e.g., root growth may be aided by eCO₂, whereas root growth may be hampered by higher temperatures [42]. Such responses of plants to environmental stimuli may be subjected to the responses of plant functional traits [43].

Therefore, our motive for this study is to examine and present the influence of plant functional traits, viz., morphological, physiological, and anatomical, on C sequestration in both biomass/vegetation and soils. We will answer the following questions throughout the study:

1. How do plant functional traits (morpho-physio-anatomical features) affect C storage and partitioning under eCO₂ in different plant parts?
2. How do plant functional traits influence C transfer to the soil and rhizosphere services?

The literature used in this review was collected and synthesized from previous peer-reviewed studies that appeared in peer-reviewed journals. We used “Web of Science”, “Scopus”, and “Google Scholar” for the literature search. Our keywords included (a) plant morphology and elevated carbon dioxide, (b) plant morphological traits change and ambient, elevated carbon dioxide, (c) photosynthesis and eCO₂, (d) respiration and eCO₂/elevated/ambient carbon dioxide, (e) root functional traits and elevated carbon dioxide, and (f) plant anatomical traits and elevated carbon dioxide. We searched for global literature in order to include different plants, vegetation, ecosystems, and the corresponding environmental conditions. Then, we selected the cases deemed most relevant to our study. Our criteria aimed to report a general trend instead of specific cases.

2. Impacts of Morphological Characteristics on Carbon Accumulation in Biomass and Soil

The C storage capabilities of many woody and crop plant species are found to be highest in the trunk, wood stems, branches, and roots [45–47]. The perception of morphological characteristics is crucial in understanding their role in C accumulation (CA). Plant morphology refers to the physical appearance, size, shape, and positioning of external structures of plants and may include shoot length or height, leaf angle, leaf length, leaf width, total leaf area, number of nodes, node density, culm thickness, root diameter, specific root length, number of pod plants⁻¹, 1000 seeds’ weight, fruit shape, etc. [48–51]. Such morphological traits affecting the stages of CA have been considered while exploring the literature. Ideally, soil organic carbon (SOC) is accumulated in two ways: (i) the littering of plant parts that have stored C in them (leaves, wood, stem, branches, etc.) and (ii) the addition of root exudates and dead root biomass to soil. Bhattacharyya et al. [13] simplified the steps involved in SCS as: “atmospheric C capture in shoots by photosynthesis and CA > translocation of C in roots > soils > SOC stock increase > SCS” [52].

Studies have shown that eCO₂ may alter global plant structures [53]. Even though there might be contrasting relationships between eCO₂ and plant structure alterations, changes in plant traits are inevitable due to the competition in natural plant communities [5,54]. For example, an increased rate of photosynthesis under eCO₂ results in increased growth in most plant species [55]. However, this positive response may only persist when a plant grows alone because competition due to increased growth might outweigh the positive effects when grown in a community [55,56]. Competition is more affected by structural characteristics than photosynthetic capacity [53].

eCO₂ generally leads to larger leaf area, size, thickness, increased number of veins, and decreased stomatal density in crop plants. Increased plant height, altered root and shoot branching characteristics, increased ratio of internode length to node number, and increased stem diameter under eCO₂ have also been reported [53,57,58]. Root traits such as root length, root diameter, and other root morphological developments may be enhanced under eCO₂, which implies increased potential for CS [53,59].

Several studies have shown that leaf angle plays an important role in CS. For example, when a single leaf of rice plants is more vertical and has steeper angles with the stem, the total CA may be higher [60]. This indicates that if the leaves are steeper, light can penetrate through both sides of the leaves and also induce photosynthesis in the lower leaves. Moreover, steeper leaf angles can reduce exposure to excess light and radiation during the middle of the day rather than maximize C gain, thereby making it less exhaustive for plants. Hence, woody perennial shrub plant species with shallow-angled leaves can gain higher C because of higher daily light interception than species with steeper leaves. The sun angle, time of day, and seasonality also determine their daily CA [61]. Again, when the leaf elevation angle ranges between 15° and −23°, optimal photosynthesis takes place [62]. Strauss et al. [63] found that a decrease in the angle between leaves and stem causes a decrease in the light capture efficiency and vice versa in the leaves of *Arabidopsis thaliana* and *Cardamine hirsute*, which corroborates with the findings of Falster and Westoby [61] that steeper angles are less efficient. Even though the literature shows contrasting observations for leaf angle, these studies suggest that the main factor contributing to the CA is the light penetration on leaves due to their angles. The angles that favor overall higher light penetration into leaves cause greater CA. This is because different species of plants have different types of leaves. Moreover, leaf shape also influences CA, e.g., longer and narrower leaves have greater light absorption than shorter and wider leaves [62]. Additionally, an increase in internodal length and petiole length can augment the light absorption and photosynthesis of canopies [62,64] because they allow more space for light penetration. However, narrow leaves are conditioned to have higher light-capture efficiencies than petiole leaves when they have comparatively shorter internodal lengths [64]. These studies suggest that the morphological traits, i.e., leaf shape, internodal length, and petiole, can interplay together to affect CA.

Leaf curvature has also been found to impact CA, e.g., drooping leaves reduce CA, whereas erect leaves have a higher CA [60]. Leaf area may affect CA by influencing the photosynthesis rate [65]. For instance, an analysis by Kuronoma and Watanabe [66] among three different green roof plants demonstrated that the plant species with the lowest leaf area ratio per whole plant C content had the maximum CS rate. *Zoysia matrella* (a C4 grass species) had the lowest leaf area ratio per whole plant C content of 0.0094 m²(g-C)^{−1} with a very high CS rate of 2.95 (g-C) pot^{−1}year^{−1} or 670 (g-C) m^{−2}year^{−1}. On the other hand, *Ophiopogon japonicus* and *Sedum mexicanum* had a higher leaf area ratio per whole plant C content of 0.0155 m²(g-C)^{−1} and 0.0277–0.0281 m²(g-C)^{−1}, respectively, with a comparatively lower CS rate of 1.24 (g-C) pot^{−1}year^{−1} and 1.21–1.60 (g-C) pot^{−1}year^{−1}, respectively. However, this study indicates that physiological and morphological traits contribute simultaneously toward CS. Low specific leaf area indicates greater leaf thickness and may give a higher single-leaf net photosynthetic rate [67]. Likewise, a higher specific leaf area can be coupled with low C retention due to its exploitative nature [68]. Overall, both lower leaf area ratio and lower specific leaf area favor higher CA.

Among all types of crops and plants, many species of grasses have a relatively high capacity to store C both in plants and soil [69–72]. This is because grasses have a high growth rate and turnover, which allows for rapid accumulation and turnover of biomass. The average root-to-shoot C stock ratios are highest under grasses and can accumulate up to 45% of their C stocks in the roots [71]. Some grass species (e.g., switchgrass) can be used as bioenergy crops to increase belowground SOC stock, particularly in deeper soil horizons. This can be attributed to their higher root biomass and long-lived root systems [69]. Contrarily, grass species can exhibit lower C storage potential in drought

conditions [73]. In addition, soybeans and legumes can significantly increase SOC stock due to their ability to fix atmospheric N₂ and increase soil organic matter levels. However, crop choices for SCS depend on the regional climate, soil type, and agronomic management practices [71].

Bamboos have a high potential to sequester C, which are giant grasses with woody vascular bundles having a mean CS rate of 6–13 Mg ha⁻¹ year⁻¹ and C storage of 30–121 Mg ha⁻¹ [74–76]. Devi and Singh [77] reported that *Bambusa tulda*, because of its comparatively greater culm diameter, could store C at 27.79 Mg ha⁻¹ year⁻¹ more than *Dendrocalamus longispathus*, even though it had lower aboveground biomass. Likewise, *Moso* bamboos, a fast-growing bamboo species, can accumulate three-fourths of their lifetime C storage (1.58–8.04 kg culm⁻¹) within 40 days (initial growth period) and can preserve it for a long time. Highland bamboo (*Yushania alpina*), when combined with agroforestry systems, can sequester up to 200 tons of C ha⁻¹ over a 30-year rotation period due to its high potential to store C in both biomass and soil [75]. From these studies, it can be concluded that bamboo should be considered superior species for aboveground C storage [76], especially in their culms, which is, however, influenced by the morphological traits of the culms.

Aboveground C inputs only have a conversion factor to SOC of 9%, whereas belowground C inputs have a staggering conversion factor to SOC of 76% [78]. Extensively rooted plants have a high potential to store stable C at a greater depth where dead root biomass is protected from decomposition and microbial activity [73]. Mounting bodies of evidence suggest that plant roots play a significant role in SCS [79–82]. In fact, Rasse et al. [83] acknowledged that the contribution of root-derived C is 2.4 times that of shoot-derived C to SOC, which reinforces the urge to consider root morphology while discussing C accumulation in soil.

eCO₂, in conjunction with higher temperatures, may greatly alter root morphological traits (Table 1). Root diameter and root length are mentionable morphological properties that affect SCS, especially if the root diameter is less than 2 mm [84] because such fine roots have a faster turnover rate and greater specific root length [85–89].

Table 1. Effect of ambient and elevated CO₂; ambient and elevated temperature on some root morphological characters of some selected species [90].

Species	Treatments	RD (mm)	RTD (mg mm ⁻³)	SRL (mm mg ⁻¹)	SRSA (mm ² mg ⁻¹)
<i>Bouteloua gracilis</i>	AC + AT	0.26 (0.01)	0.554 (0.039)	35 (3)	28 (2)
	AC + ET	0.29 (0.01)	0.523 (0.030)	30 (3)	27 (2)
	EC + AT	0.26 (0.01)	0.552 (0.024)	34 (2)	28 (1)
	EC + ET	0.28 (0.01)	0.520 (0.015)	32 (2)	28 (1)
<i>Carex eleocharis</i>	AC + AT	0.23 (0.02)	0.476 (0.032)	56 (8)	39 (4)
	AC + ET	0.22 (0.01)	0.466 (0.013)	57 (6)	39 (2)
	EC + AT	0.24 (0.02)	0.520 (0.019)	44 (6)	32 (3)
	EC + ET	0.22 (0.01)	0.502 (0.032)	56 (5)	37 (3)
<i>Pascopyrum smithii</i>	AC + AT	0.41 (0.04)	0.540 (0.032)	16 (4)	19 (3)
	AC + ET	0.41 (0.04)	0.472 (0.021)	17 (3)	21 (2)
	EC + AT	0.35 (0.03)	0.467 (0.047)	25 (5)	26 (2)
	EC + ET	0.32 (0.05)	0.431 (0.026)	35 (9)	31 (4)
Community	AC + AT	0.23 (0.004)	0.495 (0.015)	50 (3)	36 (2)
	AC + ET	0.25 (0.02)	0.475 (0.022)	44 (4)	34 (1)
	EC + AT	0.22 (0.01)	0.494 (0.024)	55 (4)	37 (2)
	EC + ET	0.20 (0.01)	0.507 (0.048)	65 (7)	40 (3)

Note: AC—ambient CO₂, AT—ambient temperature, EC—elevated CO₂, ET—elevated temperature, RD—root diameter (mm), RTD—root tissue density (mg mm⁻³), SRL—specific root length (mm mg⁻¹), SRSA—specific root surface area (mm² mg⁻¹).

Another root morphological trait, root length, impacts SCS. Studies show that deeper root length (preferably a length extending to 2 m) promotes higher SCS [73,82]. Greater root length, root surface area, and specific root length maintain a positive correlation

with CA because they stipulate increased root surface area per unit root biomass for root exudation [91–96]. They also add to the labile C pool because they are easily decomposable [97,98]. These phenomena also stabilize C in soil by providing substrates for microbial activity [99]. Besides those, for stabilizing SOC, roots form symbiotic relationships with fungi that help in the formation of macroaggregates (>250 μm), whereas root exudates help in the formation of microaggregates [100–104]. Fine roots, root mass density, and root length density positively affect aggregate stability [105]. Higher root length density, such as that of extensive fibrous roots of grasses, can be linked with greater macroaggregates in topsoil than taproots [106–108]. In addition, arbuscular mycorrhizal fungi colonizing forest plant roots can increase aggregation in soils, preventing a loss in C through decomposition [109]. The size and quantity of macroaggregates may increase or decrease through the influence of root diameter [110,111], e.g., roots having <0.2 mm diameter can induce a greater formation of 1000–2000 μm stable macroaggregates, while those of 0.2–1 mm roots promote stable macroaggregates of size > 2000 μm in soils [112,113]. Moreover, macroaggregates influence the development of microaggregates because the formation of microaggregates is enhanced within macroaggregates [83]. Increased root length density can further augment SOC by occlusion within microaggregates [114]. Thus, plant root traits enable them to explore a greater volume of soil and facilitate soil aggregation. The relationship of morphological traits of the associated plant compartments affecting different stages of CS is summarized in Table 2. These studies suggest that smaller root diameters, greater root lengths, and greater root surface area promote higher CA in soil.

Although plant morphological traits can influence the amount of C inputs into the soil through their impacts on CA, it is important to note that understanding plant morphology alone is insufficient for interpreting SCS. SCS is primarily driven by soil processes, e.g., humification, which involves the conversion of organic matter into humic substances. This process incorporates the plant C inputs into the SOC pool, ultimately leading to SCS. However, both are interlinked with each other [115].

Table 2. Summary of impacts of morphological traits on plant and soil CS.

Explored Morphological Traits	Definition	Relationship with Plant CS	Relationship with Soil CS	Deduced Stage of C Accumulation That Is Affected	Refs.
Leaf angle	Angle between stem and leaves	+ / –	n.d	Photoassimilation of atmospheric C	[49,116,117]
Leaf curvature	To the degree leaves are curved	–	n.d	Photoassimilation of atmospheric C	[117]
Leaf shape	Structural outline and appearance of leaf	+ (Length), – (width)	n.d	Photoassimilation of atmospheric C	[118]
Internode length	Distance between leaf nodes	+ / –	n.d	Photoassimilation of atmospheric C	[118,119]
Petiole length	Length of leaf petiole	+	n.d	Photoassimilation of atmospheric C	[119]
Leaf area					
Leaf area ratio per whole plant C	Leaf area to whole plant C ratio	–	n.d	Photoassimilation of atmospheric C and C storage in plant body	[93]
Specific leaf area	Leaf area to leaf drymass ratio and indicates leaf thickness	–	n.d	Photoassimilation of atmospheric C and C storage in plant body	[62]
Crown diameter	Diameter of the span of tree crown	n.k	n.d	Photoassimilation of atmospheric C	[120]
Culm diameter	Diameter of culm (modified stem)	+	n.d	C Storage in plant body	[40]
Root diameter	Diameter of roots	n.d	–	SOC sequestration	[39,52]
Root length and area					
Root length	The depth to which root extends	n.d	+	SOC sequestration	[34,35,63,85,121–124]
Specific root length	Root length to root drymass ratio	n.d	+	SOC sequestration	
Root surface area	Total surface area of root mass	n.d	+	SOC sequestration	
Root length density	Total length of roots per unit soil volume	n.d	+	SOC sequestration	[7,39,125,126]

Table 3. Impact of elevated CO₂ on some selected crop plants' physiological parameters.

Species/Crops	Net Photosynthesis Rate	Leaf Transpiration	Stomatal Conductance	Intercellular CO ₂ Concentration	Reference(s)
Soybean (<i>Glycine max</i>)	+++	---	---	+++	[45]
Basil (<i>Ocimum basilicum</i> L.)	+++	n.d	---	n.d	[115]
Peppermint (<i>Mentha piperita</i> L.)	+++	n.d	---	n.d	[115]
Tea (<i>Longjing changye</i>)	+++	---	---	+++	[129]
Winter wheat (<i>Triticum aestivum</i> L. cv. MV 16)	+++	---	000	000	[96]

Note: +++—increase, ---—decrease, 000—statistically insignificant.

However, these physiological changes termed as “physiological forcing” may lessen “transpiration and associated cooling effect” [134]. eCO₂ usually provides a greater gradient for CO₂ diffusion into the leaves, which increases intercellular CO₂ concentration. Consequently, stomatal closure may decrease transpiration [120]. Stomatal/leaf conductance is important for the plant–water relationship and photosynthetic efficiency (Figure 2) [35,135]. For instance, when water is not limited, eCO₂ may cause a 20% reduction in stomatal conductance and enhance photosynthesis by 24% in a native Eucalypt woodland. However, stomatal behavior and leaf water potential remain unchanged under eCO₂ [127]. Contrarily, Urban et al. [35] observed a 40% increase in stomatal conductance in poplar (*Populus deltoises x nigra*) and loblolly pine (*Pinus taeda*) under rising temperatures. Although higher transpiration, intercellular CO₂ level, and increased xylem and mesophyll hydraulic conductivity were observed, increases in stomatal conductance were not related to these processes. Even these events were not associated with C partitioning and photosynthesis. Such kinds of temperature-dependent openings of stomata can be explained by an increase in xylem and mesophyll hydraulic conductance resulting from lower water viscosity [136]. These findings suggest that our knowledge of plant stomatal conductance in changing environments may be skewed, and it is not reasonable to assume that all plants would respond to environmental stimuli in the same way.

However, a shift in the photosynthetic efficiency of leaves due to biochemical and metabolic alterations derived from long-term exposure to high CO₂ is termed as photosynthetic acclimation [137,138]. Photosynthetic acclimation may cause a reduction in the maximum carboxylation velocity of *Rubisco* and *Rubisco* activase protein contents, as well as a decrease in stomatal conductance [121,125,130]. A *Rubisco* decrease may cause amino acid and total N content reductions [130]. Despite suppressing *Rubisco* activity, elevated CO₂ may promote dark respiration as well as higher photosynthetic C gain and net primary productivity (NPP), known as the “CO₂ fertilization effect” [28,131]. Quick et al. [131] observed that decreasing *Rubisco* activity may cause a decline in photosynthesis, but a three- to four-fold increase in leaf area may compensate for the drop in photosynthesis. Although lower starch and free hexose in leaves may result from reduced photosynthesis, diurnal starch may compensate for this. Moreover, eCO₂ levels can increase or decrease the activities of several enzymes, e.g., 8% and 36% increases in fructose 1,6-bisphosphate and ADP-glucose pyrophosphorylase were observed in maize (*Zea mays* L.) (C4plant) [139]. Additionally, in wheat (*Triticum durum* Desf., cv. Regallo), phosphoglycerate mutase and ATP synthase protein content may increase whereas, ADP-glucose pyrophosphatase may decrease in response to eCO₂ (700 ppm) concentration [130]. Similarly, the *Rubisco* content was considerably decreased under eCO₂ in two forest species, i.e., *Fraxinus rhynchophylla* and *Sorbus alnifolia* [122]. However, photosynthetic acclimation or adjustments are strongly linked with the strength of sink tissues. Adequately strong sink tissues can preserve actual photosynthetic capacity if there is enough N supply [130,140–142]. Sanz-Saez et al. [141] suggested that maintaining C/N balance can prevent this physiological dysfunction in alfalfa (*Medicago sativa* L. cv. Aragon).

Again, C4plants (e.g., maize) may gain the additional capacity to synthesize more sucrose and starch to generate additional energy through respiration under eCO₂ [139]. Such accelerated respiration may act as a source of CO₂, leaving a negative influence

on plant-dominated C balance [11]. Moreover, eCO₂ may inhibit photorespiration [143]. Wujeska-Klaue et al. [143] revealed that decreased nitrate (NO₃⁻) reductase activity led to a 31% decrease in photorespiration under eCO₂ in mature leaves of *Eucalyptus*. Similarly, Asensio et al. [144] showed that eCO₂ inhibits mitochondrial respiration and the conversion of NO₃⁻ to protein. This limits NO₃⁻ translocation in chloroplasts, forcing the plant to rely on shoot NO₃⁻ assimilation throughout both light and dark periods. Contrarily, Bravdo and Canvin [145] showed that, in sunflowers (*Helianthus annuus* L.), photorespiration may trivially reduce, but it is not suppressed under eCO₂. CO₂ rises if it lies between 200 to 800 ppm; then, the rate of dark respiration in plant tissue may frequently decrease [146].

4. Impacts of Plant Anatomical Traits on Carbon Storage in Plant Biomass and Soil

The association between CS and vegetation types (including the corresponding morphological traits) has been well studied (as seen in Section 2). However, less is known at the plant anatomical level. In this section, we show how plant anatomy (both above- and belowground) drives and/or alters potential SCS. Once photosynthetically assimilated, C is partitioned among a wide range of C pools, including respiration, growth, root exudation, chemical or structural defense, and mutual organisms [147]. Thus, these C allocation patterns/partitioning in plants are crucial to the potential SCS and even dependent on vascular cambium (xylem and phloem). Under eCO₂, xylem cells may become larger and cell walls may become thinner [148]. During the cell division of vascular cambium to the secondary growth of the xylem and phloem, they act as the largest C sink in vascular plants. The cambial zone shows all layers of meristematic cells between the xylem and phloem [149]. Most of the C used by vascular plants is transported to different metabolically active areas by phloem, which is a part of the vascular system that moves carbohydrates from storage tissue (sources) to areas of active growth (sinks). Since C transport is influenced by source-to-sink activity, it can integrate changes that occur throughout the plant, potentially influencing everything from growth, respiration, defense, and reproduction [150–152].

Xylem tissues can also transport C [153]. C allocation is affected by protophloem and fine-root turnover rate, which may influence the transport of photosynthates in roots [154]. Seasonal fluctuations may influence the formation of xylem density, and precise quantification of the seasonal dynamics of aboveground woody biomass production is essential [118].

4.1. Aboveground Plant Anatomical Features and Carbon Sequestration

Aboveground plant parts include the leaves, flowers, stems, branches, wood, etc. They may have distinct anatomical features as follows: (a) flower: calyx, corolla, and petals; (b) leaf: epidermis, stomata, and palisade cells; (c) stem: stem structure, vascular tissues, buds, and shoot apex; (d) wood: bark, cork, xylem, phloem, and vascular cambium. Studies have shown that these components may exhibit varied impacts in response to eCO₂ [32,52,155]. For instance, CO₂ may be fixed in the corollas of flowers under both light and dark conditions. The age at which a plant blooms has a significant influence on C fixation, i.e., the C fixation rate in the corollas of parade rose flowers was found to be considerably greater in mature red corollas than in juvenile parrot-green corollas [155].

Leaf attributes, e.g., leaf thickness, spongy parenchyma thickness, and highest adaxial cuticle thickness, respond positively under eCO₂ [52]. Additionally, a 14% decrease in specific leaf area, a 23% increase in palisade tissue thickness, and a 14% increase in the ratio of palisade tissue to spongy tissue thickness were observed [32]. These attributes are also dependent on the light intensity from the sun and can be more prevalent in sun leaves than in shaded leaves, as observed in evergreen oak (*Quercus ilex* L.). Leaf thickness is related to the length of palisade cells, which can enhance photosynthetic capability and is a key factor in C fixation. The increased thickness of leaves occurs due to the higher thickness of palisade parenchyma tissues compared to spongy parenchyma tissues. Leaves grown in strong light have a higher light-saturated rate of photosynthesis per unit leaf area than leaves growing in low light [32,156]. However, at high levels of light, there may be a positive impact on the thickening of leaves, and the advantage of more light is, nevertheless,

limited to specific growth conditions and species, e.g., the leaves of *Arabidopsis thaliana*, but thickening may push away the resources from the area of growth [152]. Stomatal response to CO₂ is crucial since it determines the concentration and assimilation of C through mesophyll cells [157]. Stomatal traits, e.g., stomatal size (μm²) and diameter, respond to environmental changes from minutes to millennia [158].

The stem and branches of trees account for about 50 to 60% of the total biomass and are good sinks of aboveground C [159]. Both stem radial growth and wood density must be included when assessing woody biomass because they store almost half of the plant's aboveground C. However, they differ between species and are considered as genetic characteristics [160,161], as well as reliant on climatic circumstances [160].

The stem plays a significant role in balancing C in the form of non-structural C (NSC) reserves [162]. NSC concentrations may start decreasing in younger sapwood toward the boundary of sapwood–heartwood and become constant along the heartwood to the pith. However, significantly high levels of NSCs have also been observed in the xylem part of broadleaf evergreen trees [123,126]. C fixation within stems and branches occurs through cuticular, wood, or leaf photosynthesis in the stem and branch tissues. Cuticular and wood photosynthesis do not involve stomata; so, these two may have little loss of water and high CO₂ contents in woody tissues, leading to low photorespiration [116,163]. In tree biomass, stems may retain ca. 50% of C. The stem C concentration may increase with an increase in the size and age of the tree [164].

Variations in C contents of heartwood, sapwood, and bark may occur because of the varied chemical and physical characteristics of tissues. The physical variations caused by physiological and chemical alterations in heartwood's activities may occur throughout its production [119]. Sapwood C storage is temporary and is available for respiration when the tree requires it. The heartwood of a tree contains xylem; it is biologically inactive, plays an important role in structural strength, and no longer stores carbohydrates. For instance, C concentration in the heartwood, sapwood, and bark of *Pinus pinaster* and *Pinus sylvestris* may be (87, 156, and 137) and (76, 166, and 166) cg g⁻¹ of dry matter, respectively [119]. However, CO₂ escapes to the atmosphere and another part is fixed by photosynthetic cells in woody tissues and leaves. The woody tissue respiration measures CO₂ fluxes and depicts that the CO₂ flux rate to the atmosphere is poorer than the actual rate of respiration [151].

4.2. In-Depth Overview of Anatomical Features of Belowground Plant Parts in Soil Carbon Sequestration

Plant roots are one of the crucial components of SCS because they control belowground C fluxes (Figure 3) [117]. Roots gain C through photoassimilates produced from photosynthetic organs and the uptake of organic molecules from the soil. Studies have shown that C loss may occur through roots while exporting it to the shoot, or by respiration, rhizodeposition, and symbiosis [165,166]. Under eCO₂, root diameter may increase by 15%, and root tissue density may decline by 14% for absorptive roots, demonstrating the plants' tendency to form greater roots with looser tissue. Additionally, enlarged root cortical thickness and the ratio of cortical thickness to stele radius may imply an upsurge in the potential absorption capacity of roots [32]. However, C compounds (photoassimilates) are transported to numerous plant sinks either *symplastically* via cell connections (plasmodesmata) or *apoplastically* via membrane transporters, which regulate monosaccharide and sucrose fluxes [167]. The amount of C used or transported by roots is known to be high. For example, fine roots represent 33% of global annual net primary productivity (NPP) [168], and 8–52% of the total assimilated C during a day is respired by roots [169].

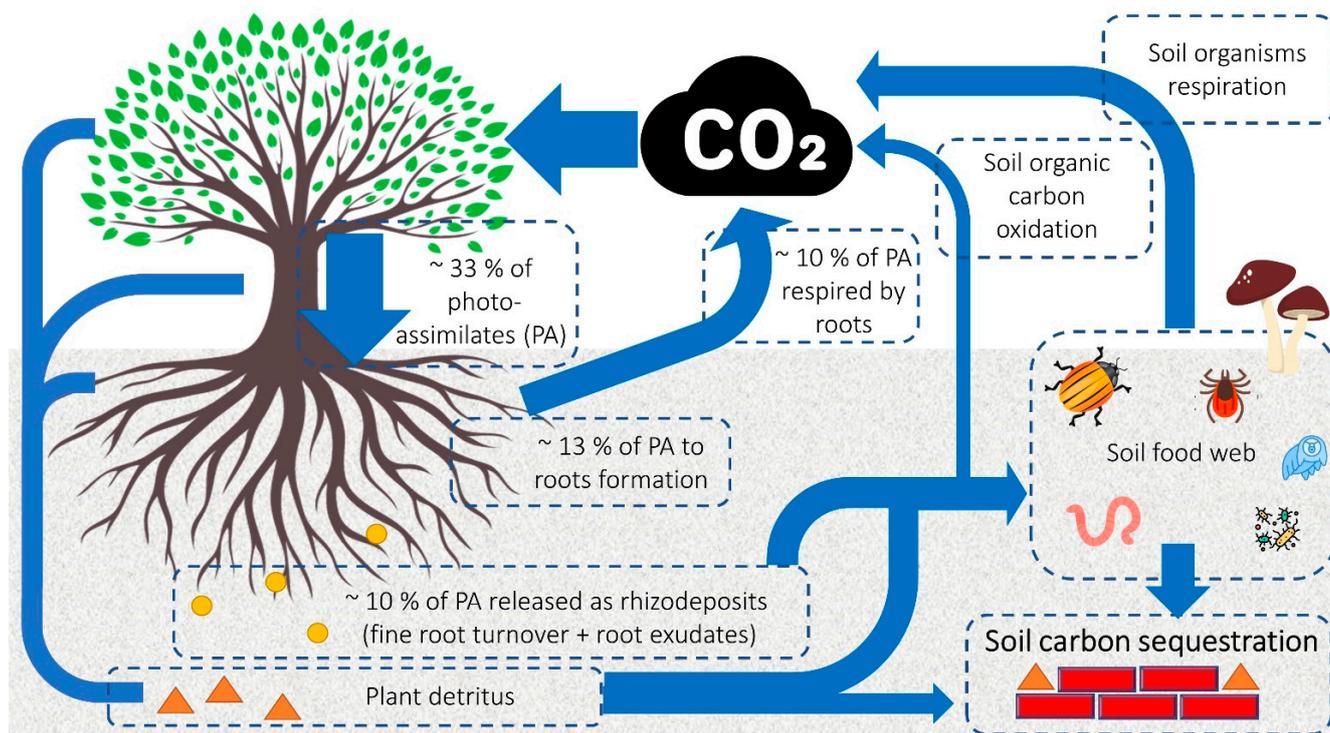


Figure 3. Summary of belowground carbon fluxes (based on [168–172]). Circles: assimilable and fast turnover time carbon compounds; triangles: non-assimilable fast-turnover-time carbon compounds; rectangles: slow-turnover-time carbon compounds.

Primary meristems in the root apices support root primary growth, which allows the plant to seek nutrients and water and absorb them [154]. Secondary meristems (vascular cambium and cork cambium) promote root secondary growth, which increases the girth of roots [173]. Secondary growth tissues are related to several functions, such as structure, allocation, and storage, thereby roots of a higher branch order predominantly consist of secondary tissues, whereas absorption is performed mainly by primary tissues of a few terminal branch orders [154]. The growth pattern of higher branch order roots remains very robust even with external supplies [174]. In contrast, root primary growth in fine roots is highly environment-dependent, e.g., a temperature rise may inhibit fine-root growth and number, while $e\text{CO}_2$ may exhibit a 44% increase in fine-root length and a 39% increase in fine-root numbers, as observed in a Danish grassland [36]. However, such findings are essential to percept rhizospheric chemistry, symbiosis, and even tracking their probable impact on C cycling [175]. Kong et al. [154] distinguished between the stele (the central part of the root), which is specialized in resource transportation, and the tissue outside the stele, which is responsible for resource uptake and facilitates symbiotic interactions in fine roots. The amount of C allocated to these tissues would be determined by a trade-off between maximizing resource acquisition or conservation (root economics spectrum (RES) theory) [124]. Recent findings have shown that this theory may not apply to all plants since C allocation is influenced by more factors than those considered by RES, being especially relevant to symbiotic associations [176–178].

The C allocated in primary growth is tightly related to soil physicochemical parameters. Soil nutrient limitations can promote root primary growth, which increases the allocation of C to roots [179]. This has been well studied under a phosphorus (P) deficit, where C allocation to roots increases with a consequent increase in belowground biomass [180,181]. Low P conditions can also lead to a higher release of *phosphatase*, which favors soil P availability, but it demands higher use of C [182]. Similarly, soil N and water deficiency can also increase C allocation to roots [183]. In response to a deficiency of nutrients, root

secondary growth can be suppressed, which reduces the C cost of producing root length and facilitates soil exploration rather than radial thickening of roots [184]. Root exploration in deep soil layers can also represent a high metabolic cost for plants; however, studies dealing with fine-root dynamics in deep soil layers (depth > 1 m) are still scarce ([185] and references therein).

Light quality changes may cause a variation in secondary metabolism in plants, changing the root structure and the profile of root exudates [37]. High levels of eCO₂ (720 ppm of CO₂) increased tissue thickness but decreased root length and root tissue density, among others, compared to ambient CO₂ concentrations (380 ppm of CO₂) [32]. Similarly, Wu et al. [186] and Gray et al. [187] found that high eCO₂ may alter root anatomy and the release of metabolites. The increase of eCO₂ can also decrease root respiration, although this effect would be dependent on soil-available N (the highest available nitrogen, the most amino acid abundance, and the least abundance of sugars and organic acids) [38,188].

Rhizosphere and materials lost from plant roots (rhizodeposition) may be influenced by eCO₂ (Table 4). Rhizodeposition is crucial for SCS, as a high amount of C, in the form of lysates, root border cells, and exudates, are released into the soil [189]. Root exudates are low-molecular-weight organic compounds released by the rhizosphere as a complex mixture of sugars, amino acids, organic acids, enzymes, and other substances [190]. For instance, root secretion of *Sorghum* known as sorgoleone may act as a C source for some specific soil microflora [191]. Rhizodeposits are rapidly incorporated into soil organic matter (SOM), consumed by microorganisms, and their decomposition may emit CO₂. Therefore, rhizodeposition is rarely quantified and remains the most uncertain part of the soil C fluxes in terrestrial ecosystems [192]. Plants may alter their exudation patterns during their distinct development stages to assist in tuning microbial recruitment to meet greater nutritional needs during periods requiring quicker growth [193]. Once in the soil, the potential SCS would be determined by the C/N ratio of litter or available N in the soil [193,194]. However, a recent meta-analysis claimed that the chemical quality of organic C (categorized as labile, intermediate, or recalcitrant) determines microbial response rather than the C/N ratio [195]. Root exudates influence the general microbial community in the rhizosphere and its biological activities. This effect can be both direct (e.g., by providing C substrates for growth) and indirect (e.g., by altering pH or increasing the bioavailability of nutrients) [135,196].

Table 4. Pearson correlation coefficients among elevated CO₂, root biomass of *Eucalyptus*, and enzymes involved in C cycling (modified from [197]).

Rhizosphere	AG	BG	CBH	XYL
Fine-root biomass	0.333	−0.373	0.561	0.496
Rhizosphere soil mass	0.273	−0.097	0.33	0.69
Coarse-root biomass	0.646	−0.329	0.099	0.389
Total root biomass	0.677	−0.373	0.175	0.449

Note: AG— α -1,4-glucosidase; BG— β -1,4-glucosidase; CBH— β -D-cellobiohydrolase; XYL— β -xylosidase.

Potential SCS involves not only plants but also soil characteristics. Organic C derived from roots is generally more sequestered in the soil than organic C coming from aboveground litter [185]. Estimations indicate that the mean residence time in soils of root-derived C is 2.4 times that of shoot-derived C [83]. Root exudates also allow the creation of micro-environments and ecological niches for diverse microbial species [198,199] and facilitate nutrient acquisition/cycling [182]. For example, carboxylate exudation in the rhizosphere can augment SOM decomposition and N mineralization by destabilizing soil aggregates and other organo-mineral compounds [182]. In addition, although plant mutualist fungi AMF can increase soil aggregation and SOC storage [182], they may stimulate the additional decomposition of SOC, resulting in a net source of CO₂ [200]. These contrasting processes make the role of AMFs in SCS controversial. Details about the SCS by AMFs can be found in Parihar et al. [201]. Additionally, plant root traits explicitly maintain

a continuum between C cycling and microbial functioning, and any deviation from this will result in an anomaly in the environment [52].

5. Conclusions and Perspectives

Our study indicates that eCO₂ levels have a significant impact on plant growth and development and modify the role of plant functional traits in C fixation and storage. CS in both plant biomass and soil is closely linked to plant functional traits, regardless of species. Particularly, under eCO₂, plant functional traits play a key role in determining the amount of C captured and stored within plant biomass and its subsequent transfer to other plant parts and soil. We showed that morpho-physio-anatomical traits, such as leaf area, plant height, stem diameter, and wood density, are substantially altered under eCO₂, which can affect C retention within biomass. While some of these changes may be beneficial for C retention—e.g., an increased shoot-to-root ratio—other changes, e.g., leaf thickness, may weaken the C sink capacity of plants. Additionally, competition within a plant community can also affect CS.

Moreover, the key regulators of plant C metabolism, e.g., photosynthesis and stomatal responses are also significantly altered under eCO₂. Stomatal density regulates light and CO₂ concentration within mature leaves, which, in turn, affects photosynthesis in the developing leaves. The specific leaf area and leaf angle are also crucial factors for CS because they determine the amount of light penetration into the leaves. The availability of additional photoassimilates can aid in increasing the above- and belowground growth of plants.

A thorough understanding of root functional traits and rhizospheric C storage ability is also essential for effective SCS. Future research involving the improvement in root architecture may also prove to be an effective management strategy for coping with changing environmental conditions. Overall, this paper highlights the importance of plant functional traits in CS and provides directions while considering SCS.

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