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Review Article

Root system growth and development responses to elevated CO₂: underlying signalling mechanisms and role in improving plant CO₂ capture and soil C storage

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Carbon storage in soils is one of the most promising strategies for mitigating greenhouse gas emissions and the associated climate change. In this context, how plant root systems respond to the elevation of the atmospheric CO₂ concentration is of crucial importance because these organs are the main source of C input into the soils. It is expected that root growth will be stimulated by elevated CO₂ as a consequence of enhanced photosynthesis, and that this will favour belowground C sequestration. In addition, larger root systems with optimized architecture are also expected to improve water and nutrient acquisition by plants, and to indirectly stimulate photosynthetic CO₂ capture. This review critically examines the evidence supporting these expectations from a molecular physiology perspective. We illustrate the strong but highly variable effects of elevated CO₂ on root system size and architecture, and provide an update on the signalling mechanisms that may trigger these effects. This highlights the lack of knowledge on the physiological and genetic bases of the root growth and development response to elevated CO₂, but shows that candidate genes and genetic resources are largely available to fill this gap.

Introduction

The continuous elevation of the atmospheric CO₂ concentration and its dramatic effects on climate change now urgently call for efficient mitigation solutions. In its sixth assessment report, the IPCC (Intergovernmental Panel on Climate Change) has compared various mitigation options for reducing net greenhouse gases emissions (working group III report, figure SPM.7: <https://www.ipcc.ch/report/ar6/wg3/figures/summary-for-policymakers/figure-spm-7>). It shows that one of the options with the highest potential is carbon sequestration in agriculture, which can lead to a net emission reduction in ~3.5 GtCO₂-eq yr⁻¹ by 2030, therefore almost at the same level as the shift to wind or solar energy. The main compartment into which carbon can be stored in agriculture is the soil. Indeed, at the global level soil C represents ~1500–3000 Gt C, that is two to four times the total C content of the atmosphere, and up to five times that of the Earth vegetation [1,2]. Moreover, the C stored in soil organic matter can be stabilized for much longer periods of time than the C stored in vegetation, thus limiting its re-emission to the atmosphere [3,4]. Considering current C stocks in the soils, it appears that a relevant strategy will be to increase C storage in croplands, because their soils have generally been strongly depleted in organic matter and their potential for additional C storage is consequently much higher than soils of other land types [2,5–7]. Long-term sequestration of C in soils is determined by complex interactions between biotic and abiotic factors of the soil, including among others the amount and the chemical composition of the organic inputs, the activity of micro-organisms

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including those involved in plant symbioses, and the availability of minerals for interaction with the organic matter [3,4,8–11]. Thus, defining efficient approaches for improving C storage in cropland soils definitely requires mobilizing soil sciences, but not only. We also need to think about a new generation of crops that will fulfil a dual role: food and feed production and ecosystemic service associated with enhanced C sequestration in the soil. Because the main origin of soil C is the organic C input from plant roots [4,9,10,12], elaborating crop varieties with improved root system traits appears as a major strategy in this matter [2,7,11]. Increasing the size of the root system is certainly a relevant objective, but modifying its architecture may even be more important. In particular, deeper rooting is often highlighted as a major desirable trait for improving C input and long-term storage into the soil, due to the fact that soil organic matter is generally much less abundant and much more stable in the lower than in the upper soil layers [2,3,10,11].

On the plant side, the overall process ending with C input into the soil includes photosynthetic CO₂ capture in plant shoots, shoot-to-root translocation of the fixed C, incorporation of this C into root structures, and eventually transfer to the soil following root exudation of organic compounds or root decomposition. Because for most crops, improving C allocation to the roots creates a risk of yield loss if it is at the expense of C accumulation into the harvested aboveground organs, a main issue in this context is to enhance all steps of the overall process, including photosynthesis. Accordingly, C balance calculations indicate that increasing net primary production of croplands is required for efficient C sequestration in their soils [6,13]. Until now, little progress has been achieved in increasing the intrinsic efficiency of photosynthesis in crops [14]. Nevertheless, because the current atmospheric CO₂ concentration is not saturating for Rubisco activity in C3 plants, the elevation of this concentration results in a stimulation of photosynthesis (the so-called CO₂ fertilization effect). Indeed, most studies performed with C3 crops grown at elevated CO₂ concentration (eCO₂) indicate that shoot growth and development are stimulated, and that yield is significantly increased as compared with ambient CO₂ (aCO₂), although this can be highly variable between experimental set-ups and species [15–18]. Furthermore, it is now more and more documented that the CO₂ fertilization effect associated with the ~50% increase in the atmospheric CO₂ concentration since the 19th Century actually already resulted in a stimulated net aboveground plant primary production, which constituted a significant terrestrial C sink and thus a negative feedback on global warming [19–22]. In comparison, much less is known about the effects of eCO₂ on root growth and development, in particular at physiological and molecular levels [16,23–26]. This is a strong knowledge gap making unclear if the enhanced aboveground biomass production mediated by the CO₂ fertilization effect actually translates into improved root traits favouring C sequestration in the soil.

Our aim in this article is to provide an overview of the recent literature on the responses of the root system size and architecture to eCO₂, focusing on the signalling mechanisms that are proposed to drive these responses at the root growth and development levels. We also discuss the hypothesis that, in addition to favouring C storage in the soil, stimulated growth and optimized architecture of the root system in response to eCO₂ can have two other positive synergistic effects. First, increased soil exploration with optimized architecture may improve water and nutrient acquisition efficiency [27]. Second, enhanced C allocation to the root system may indirectly stimulate photosynthesis, by preventing the eCO₂-induced down-regulation of photosynthetic capacity (the so-called acclimation of photosynthesis to eCO₂) resulting from sink limitation in the utilization of photosynthates [28]. Most of the literature discussed below concerns C3 plants, because eCO₂ has generally little impact on growth of C4 plants [15,17].

Responses of root system growth and architecture to eCO₂

Many studies have investigated the responses of plant growth and development to eCO₂ on the ecosystem, community, population, physiological and molecular scales [15,16,29,30], but in contrast with the abundance of data available on aboveground tissues, knowledge of the effects of eCO₂ on root system growth, morphology and anatomy is limited [16,31]. As detailed below, the responses of root growth and development to eCO₂ are highly variable, often preventing general conclusions. In addition to the strong methodological difficulties associated with root phenotyping, several factors, such as differences between species, between experimental set-ups and between other environmental parameters contribute to this.

Root growth

The general consensus is that in C3 species, photosynthesis and C allocation to plant roots increase as atmospheric CO₂ rises, which leads to an increase in both above- and belowground biomass [23,24,32,33]. Stimulatory effects of eCO₂ on root biomass have been observed in *Arabidopsis* [34–36], forest trees [37,38],

grasses [39] and many important crops [32,40] among which soybean [41], wheat and sugar beet [42], and tomato [43,44]. Quantitatively, increases in root biomass of 20–40% are frequently reported [23,24,33], which can in specific studies raise to more than 100% [38,41]. However, other studies refuted the generality of these observations, showing no significant effect, or even a negative effect of eCO₂ on root growth in trees [45–47] or crops [42,48,49]. Various hypotheses have been proposed for explaining this lack of root growth stimulation, such as increases in root mortality [47] or down-regulation of root growth resulting from higher water use efficiency [45]. Furthermore, the extent of root growth stimulation may depend on the developmental stage, as shown in barley where the initial increase in root growth was reversed at late vegetation stages to result in a reduced root biomass under eCO₂ as compared with aCO₂ at final harvest [42].

Root/shoot partitioning of biomass

Plant strategically allocate biomass between above- and belowground tissues to optimize growth and functioning in fluctuating environment, and the changes in this allocation are expected to have a major importance on C input into the soil and on the competition with yield. However, observations on the response of root:shoot biomass ratio (R/S) to eCO₂ are contradictory. On the one hand, eCO₂ was shown to have a significant positive effect on R/S at both plant or ecosystem scales [24,34,41,50–53]. This preferential stimulation of root growth has been recorded from direct measurements of total biomass of shoot and root system in controlled environment, or from estimates of root length from minirhizotron experiments, or estimates of root length per unit volume of soil measured from soil cores. Substantial CO₂ research conducted on different forest tree species have revealed an increase in R/S ratio, but more frequently in agricultural crops, particularly root and tuber crops, and grassland [30,39,42,51,54]. Nevertheless, even in these reports, there is no general consensus on the degree of positive response on R/S, as it was shown to markedly depend on species or on interactions with water and nutrient management [23,39,42]. On the other hand, many other reports indicated no effect of eCO₂ on R/S [33,46,48,55,56], or even a negative effect [49]. Of particular interest is a recent large-scale meta-analysis of 630 experiments concerning 460 species, showing a surprisingly stable R/S over a range of 200–1200 ppm CO₂ [56].

Root system architecture

The generally observed increase in root biomass in response to eCO₂ does not obligatory mean a change in root system architecture (RSA). Indeed, an increase in root biomass could also reflect an increase in root diameter and/or root tissue density, accompanied by little change in total root length, root branching or life span [25]. As a matter of fact, thicker roots seems to be a very frequent trait associated with growth under eCO₂ [23,56,57]. Recently, Wang et al. [58] demonstrated that the thicker roots trait under eCO₂ of temperate woody and herbaceous species was primarily driven by the increase in cortical thickness rather than stele radius. However, many studies suggest that eCO₂ has also a strong effect on RSA, by increasing the total root number and total root length. This is especially true for *Arabidopsis*, where plants grown under CO₂ enrichment showed significant increase in total root/lateral root (LR) length and a higher number of these roots [23,34,35,57]. Similar results have been obtained for different crop species, such as cotton [41], tomato [43], and wheat [42]. The meta-analysis study from Nie et al. [24] on the data from 110 published reports showed that the overall eCO₂-induced stimulation of root length (+26%) was much stronger than that of root diameter (+8.4%) and that eCO₂ caused similar increases in root length and total root biomass (+26% vs 28.8%), suggesting that root elongation plays a key role in root biomass accumulation.

Additionally, eCO₂ can influence root branching pattern. Roots can vary significantly in their topology between two extreme branching patterns, dichotomous and herringbone [59]. A herringbone pattern consists in coarser, sparsely branched root systems more efficient at capturing mobile resources over large soil volumes whereas dichotomous structures are highly branched root architectures providing the potential for exploration of local soil volumes. There are only few studies that investigated in detail the root architectural responses to eCO₂, because this requires an experimental access to a more or less entire root system. Most of these studies suggest that plants build more dichotomous root systems with an increased number of laterals in response to eCO₂ [23,25]. In *Arabidopsis*, eCO₂ changed the root branching pattern from herringbone to dichotomous through an increase in LRs density [34,35,57]. Similar responses were reported from Berntson and Woodward with *Senecio vulgaris* L [60]. However, due to the need to access to the root system, these data mainly reflect responses of container-grown herbaceous species and these experiments were often limited to individual juvenile plants physiologically constrained by their environment and root volume. Interestingly, long-term studies (up to 14 years) with loblolly pine grown on soil suggest the opposite response, with a less dichotomous

pattern under eCO₂ [37]. An alternative approach to investigate RSA in more natural or agronomic conditions is to distinguish the respective responses of coarse and fine roots in plants grown in soil. Coarse roots (>2 mm), accounting for up to 40% of total biomass in terrestrial ecosystems, represent a large fraction of the more stable plant C pool and have been predicted to accrue greater biomass under eCO₂ [61]. Fine roots (≤2 mm diameter) are critical in plant water and nutrient absorption and are the main interface between plants and the soil ecosystem. They are also an important component of the global C cycle as their production comprises around one third of global annual net primary productivity (NPP) in terrestrial ecosystems [62]. Fine root production has been shown to be stimulated by eCO₂ in ecosystems ranging from forests [47,54,55,63], grasslands or steppe [64] and croplands [23], or a mixture of these ecosystems [24,65]. However, the direction and magnitude of these responses vary across different study sites and negative or no effects of eCO₂ on fine roots biomass are also reported in long-term studies, depending on other environmental constraints [45,66]. For instance, natural disturbances such as fire and hurricane play a major role in the root growth response of scrub-oak shrubland after 11 years of eCO₂ treatment [51]. Root hairs make also a significant contribution to increasing root surface area, facilitating physical anchorage and providing a large interface for nutrient uptake. Elevated CO₂ not only promoted the initiation of root hairs, but also increased the density and length of root hairs in *Arabidopsis* [67].

Depth patterning

The vertical distribution of roots between the soil layers is a crucial root trait determining both the C sequestration in soils and the efficiency of water and nutrient acquisition by plants [11,27]. As such, it has received significant attention in eCO₂ studies, with very variable conclusions as for many of the above-mentioned aspects of root growth and development. Experimental evidence from a diverse set of forest ecosystems studies indicates that fine root of trees exposed to eCO₂ are distributed more deeply in the soil profile relative to trees grown under aCO₂ [54,68,69]. One hypothesis to explain deeper rooting distribution in forest systems would be limited resources availability in shallower soil profile due to plant competition. For instance, N may become increasingly limiting for long-lived plants and those plants can invest in fine root biomass deeply in the soil to increase the exploration of deeper N resources [70]. In addition, Smith et al. [63] reported that the root biomass response to eCO₂ was greater when tree species were in polyculture compared with 4 years monoculture FACE experiment, suggesting competitive interaction in monoculture which is avoided by root stratification and resources use complementarities in polyculture. Besides trees, a deeper distribution of roots in response to eCO₂ was also reported in other species, including crops [24,64]. In contrast, many other studies rather reported a shallower root system in plants grown at eCO₂ as compared with aCO₂, especially for crops and grasses [16,23,25,49,68].

Signalling mechanisms regulating root growth and development in response to eCO₂

Regulation of sugar transporters

Growth and development of the roots primarily rely on the amount of photosynthates they receive from the shoot through downward phloem transport. In most herbaceous and crops species, export of photosynthates from source leaves involves the loading of sucrose into the phloem via an apoplastic route, which requires the action of dedicated transporter proteins. Sucrose is excreted out of the phloem parenchyma cells into the apoplasm by the SWEET (SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTERS) facilitators, and is subsequently taken up into the phloem companion cells by proton-coupled Suc transporters (called SUT or SUC) [71,72]. In the roots, the same transporters families are involved in the apoplastic unloading of sucrose, although the symplastic pathway (direct cell-to-cell transfer through plasmodesmata) may also be important [71,73]. In addition, SUC/SUT and SWEET transporters contribute to the flux in and out of the root vacuoles [73]. Several members of the SUC/SUT and SWEET families have been shown to be of crucial importance for growth and development of the root system. In *Arabidopsis*, ko mutation of *AtSUC2* leads to an arrest of the primary root elongation following the autotrophy transition of the seedlings [74], and ko mutation of *AtSWEET17* reduces emergence and growth of LRs [75]. Moreover, the expression of *SUCs/SUTs* and *SWEETs* is strongly regulated, and correlations were found in *Arabidopsis* between the transcripts levels of a subset of these genes (*AtSUC2* and *AtSWEET12–13* in leaves, and *AtSUC1–2* and *SWEET11–13* in roots) and the partitioning of carbohydrates between shoots and roots [76]. However, the data on the regulation of *SUCs/SUTs* and

*SWEET*s expression by $e\text{CO}_2$ are scarce, and little is known concerning the role of these transporters in the growth and developmental responses of the roots to $e\text{CO}_2$. In *Arabidopsis* leaves, $e\text{CO}_2$ up-regulates the expression of *AtSWEET12* and that of *AtSUT4(SUC4)*, encoding a minor component of the phloem sucrose loading system, whereas expression of *AtSUC2*, encoding the major component of this system, is unaffected [77]. In rice, the comparison of three cultivars with contrasted yield responses to $e\text{CO}_2$ showed that the expression of *OsSUT1* and *OsSUT2* in the flag leaves is induced by $e\text{CO}_2$ only in the cultivar showing the strongest yield response, and that this induction is associated with the absence of the down-regulation of photosynthetic capacity recorded in the other cultivars [78]. This supports the hypothesis that up-regulation of phloem sucrose transporters may be important to avoid acclimation of photosynthesis to $e\text{CO}_2$ by preventing excessive accumulation of soluble sugars in the source leaves [71]. Unfortunately, neither above studies investigated the putative consequences of the induction of *AtSUT4(SUC4)*, *AtSWEET12*, *OsSUT1* and *OsSUT2* by $e\text{CO}_2$ on root growth and development. However, a recent study unravelled that expression of *AtSUT4(SUC4)* in the roots is induced by exogenous sucrose provision, and that primary root growth in *atsuc4* mutants is partially insensitive to sucrose supply [79]. In addition, *atsuc4* mutants display reduced sucrose accumulation in the roots, and attenuated ABA and IAA responses to sucrose. As *AtSUT4(SUC4)* is localized at the plasma membrane of root cells, this suggests that this transporter may contribute to the uptake of sucrose from the apoplasm into the cells, therefore mediating the responses triggered by sucrose supply.

Sugar signalling

Beside their role as energy substrates and C skeletons, sugars are key signal molecules governing, in interaction with other signals, many if not all growth and developmental processes (see [80–83] for general reviews). It is then often hypothesized that the responses of root system size and architecture to $e\text{CO}_2$ result from the action of sugar signalling mechanisms activated by increased sugar availability [29,84]. Indeed, exogenous sucrose supply to the roots mimics the effects of $e\text{CO}_2$ on primary and LR growth [57], and changes in root elongation in response to various environmental cues correlate with those of local hexose concentrations in the growing zone of the roots [85]. In the section below, we focus on the main sugar-sensing pathways identified in plants [86] that involve HXK (HEXOKINASE), TOR (TARGET OF RAPAMYCIN) and SnRK1 (SUCROSE NON-FERMENTING-RELATED KINASE 1) kinases, or heteromeric G-proteins (Figure 1). We also mention a couple of molecular regulators like PIP5K9 (PHOSPHATIDYL INOSITOL MONOPHOSPHATE 5 KINASE) and WOX7 (WUSCHEL RELATED HOMEODOMAIN 7), that were not related to these main pathways, but are nevertheless involved in the sugar regulation of root growth (Figure 1). Most studies investigating the root responses to sugars indicate that the associated developmental changes result from changes in hormone distribution and signalling triggered by the sugar sensing pathways. These interactions between sugars and hormones will be briefly mentioned in this section but not treated in detail as they have been the matter of recent dedicated reviews [80,83,87].

The HXK glycolytic enzyme has a key dual metabolic/signalling function and acts as a glucose sensor [81,86,88]. In *Arabidopsis*, HXK1-dependent sugar sensing has positive or negative effects on root growth at low or high exogenous glucose supply, respectively. Concerning primary root growth, HXK1 was shown to mediate part of the growth stimulation in response to exogenous glucose supply (up to 3% concentration) because this stimulation was markedly attenuated in the *gin2* (GLUCOSE INSENSITIVE 2) HXK1 mutant as compared with the wild-type [89]. This accelerated root growth by glucose could be explained by an alteration of auxin transport in the root, associated with an increased expression of the PIN1 (PIN-FORMED1) and PIN2 (PIN-FORMED2) auxin efflux transporters at the transcript and protein level, respectively [89]. Interestingly, a similar mechanism may be involved in the opposite effect of HXK1, which represses primary root growth at higher glucose concentrations. Indeed, providing glucose at 3 or 5% concentration led to an inhibition of PIN1 expression in the root meristem, associated with changes in auxin accumulation at the root tip, and a reduction in the apical meristem size and cell number [90]. In addition, HXK1-mediated repression of primary root growth has recently been shown to involve autophagy and production of ROS (REACTIVE OXYGEN SPECIES) upstream of auxin [91]. HXK1 also regulates LR development by stimulating both LR primordia initiation and emergence at low glucose concentrations or high light [92]. The glucose- or high light-induced LR development involves BRI1 (Brassinosteroid Insensitive 1)-dependent brassinosteroid signalling downstream of HXK1, and auxin transport or regulatory genes, including *PIN2*, *AXR3* (*AUXIN RESISTANT 3*) and the *SLR-ARF7/9* (*SOLITARY-ROOT - AUXIN RESPONSE FACTOR 7/9*) module, further downstream of

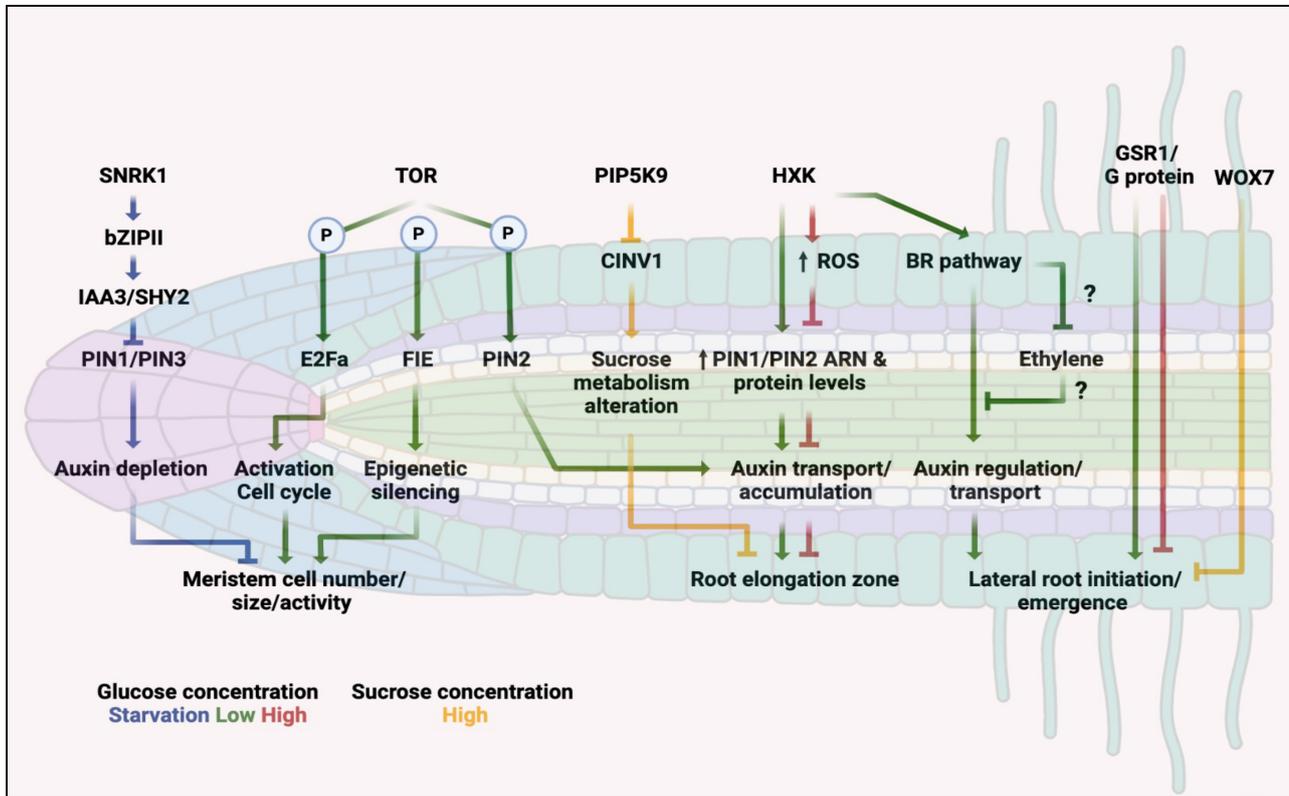


Figure 1. Model of sugar sensing pathways involving Hexokinase (HXK), TOR and SnRK1, or heteromic G-proteins and molecular regulators related to sugar regulation of Arabidopsis root growth.

The different developmental root responses rely on changes in hormone distribution and signalling triggered by the sugar sensing pathways. In response to glucose starvation, SnRK1 regulates meristem activity leading to primary root growth inhibition. TOR also regulates meristem activity but in the opposite direction by phosphorylating specific protein targets involved in cell cycle activation or in key gene regulation. TOR can also act on root elongation by modulating auxin distribution through the phosphorylation of PIN2. The HXK glycolytic enzyme has a dual effect on root growth depending on low or high exogenous glucose supply. These responses rely on change in PIN1/PIN2 expression, altering auxin transport in the root elongation zone. At low glucose concentration, lateral root initiation/emergence is stimulated by HXK1. This involves a BRI1-dependent brassinosteroid signalling, ethylene and auxin signalling pathway. In addition, several genes were identified as regulators of sugar-induced changes in root growth and development such as PIP5K9 or WOX7.

brassinosteroids [92]. In addition, ethylene antagonizes this glucose-brassinosteroid signalling pathway and represses LR emergence by acting downstream of HXK1–BRI1, but upstream of auxin [93].

The TOR and SnRK1 kinases are central regulators integrating nutrient, energy and hormone signals to modulate metabolism and growth [82,86,94]. TOR is generally activated by high energy or nutrient status, whereas SnRK1 is at the opposite active under low energy status. In *Arabidopsis* roots, TOR promotes both cell multiplication in meristems and cell expansion in the elongation zone in response to glucose [95,96]. Glucose-TOR signalling regulates meristem activity through the phosphorylation of the E2Fa transcription factor, which transcriptionally activates cell cycle S-phase genes and therefore accelerates cell division in response to photosynthetic sugar production in the shoot and glycolytic sugar metabolism in the roots [95]. This TOR-E2Fa relay was shown to be independent from HXK1 and auxin/cytokinin signalling pathways. Very recently, TOR was reported to act on meristem activity at an additional level by modulating genome-wide chromatin dynamics [97]. Indeed, FIE (FERTILIZATION-INDEPENDENT ENDOSPERM), a component of PRC2 (POLYCOMB REPRESSIVE COMPLEX 2) that catalyzes repressive histone mark deposition (H3K27me3) is a TOR target. TOR-dependent phosphorylation of FIE promotes its cytoplasm to nucleus translocation, which results in a specific increase in H3K27me3 marks (as compared with other histone marks) and therefore in epigenetic silencing of key regulatory genes [97]. SnRK1 also regulates meristem activity in *Arabidopsis* roots but

in the opposite direction, leading to an inhibition of primary root growth in response to sugar starvation [98]. SnRK1-induced low energy signalling involves bZIP11 (BASIC LEUCINE-ZIPPER 11) and related transcription factors, which activate the *IAA3/SHY2* (*INDOLE-3-ACETIC ACID INDUCIBLE 3*, *SHORT HYPOCOTYL 2*) regulatory module to repress the expression of *PIN1* and *PIN3* in the primary root tip, thereby leading to local auxin depletion and reduced meristem size [98]. Besides meristem activity, TOR triggers the stimulation of root elongation in response to glucose by phosphorylating and stabilizing PIN2, which mediates the transport of auxin out of the root elongation zone [96]. This ensures that the root elongation zone remains a low auxin response zone, which is a requirement for efficient cell expansion and root elongation. Finally, TOR is also involved in the formation of adventitious roots from shoot tissues, through TIR1 (TRANSPORT INHIBITOR RESPONSE1)/AFB (AUXIN-SIGNALLING F-BOX)-dependent auxin signalling [99].

In *Arabidopsis*, the heterotrimeric G-protein complex (GPA1, AGB1 and AGG proteins) is thought to be coupled with the plasma membrane RGS1 (REGULATOR OF G-PROTEIN SIGNALLING 1) receptor-like protein to mediate extracellular glucose sensing [86]. G protein-dependent sugar signalling was shown to play a significant but complex role in regulating LR growth and development. Indeed, while RGS1 acts as a positive regulator of LR density [100], the three G-protein subunits appear to have contrasted functions, with GPA1 promoting, and AGB1/AGG repressing auxin-induced cell division in LR primordia [100,101]. Furthermore, the readout of the G protein-dependent sugar signalling is further complicated by the fact it modulates the glucose-auxin interaction in LR development, which can translate either in synergistic or antagonistic effects of both signals [83,102].

In addition, several genes were identified as regulators of sugar or photosynthesis-induced changes in root growth and development, but were not to date related to the above mentioned main sugar signalling pathways. For instance, PIP5K9, a key enzyme in the phosphatidylinositol signalling pathway, was shown to negatively regulate the activity of the CINV1 (CYTOSOLIC INVERTASE 1) invertase in *Arabidopsis* roots, thereby altering sucrose metabolism and sugar-mediated elongation of the primary root [103]. The *Arabidopsis* *WOX7* transcription factor gene is expressed in LR primordia where it is strongly induced by increasing sucrose concentrations [104]. As compared with the wild-type, a *wox7* mutant and *WOX7*-overexpressing plants display higher and lower LR numbers in glucose-containing media, respectively. This suggested that *WOX7* contributes to the inhibitory effect of high sugar on LR initiation [104].

eCO₂-induced hormonal signalling

Studies that directly investigated the mechanistic bases of the root developmental responses to eCO₂ are scarce. However, most of them point out a role of hormone signalling pathways, but surprisingly rarely in connection with sugar signalling (Figure 2). In *Arabidopsis*, tomato and tall fescue, eCO₂ promotes the development of root hairs and/or LRs [35,67,105,106]. These effects are associated with a higher IAA accumulation and/or sensitivity in the roots, and the induction of auxin biosynthesis genes, such as *YUCCA8* in *Arabidopsis* [35], or *FaYUCCA11* in tall fescue [105]. For root hairs, the growth stimulation in response to eCO₂ is almost totally suppressed in auxin signalling or transport mutants (*axr4-1*, *aux1-7* and *pin1-1*). Moreover, auxin (NAA) and eCO₂ similarly induced gene expression of the positive regulators of root hair development CPC (CAPRICE), TRY (TRIPTYCHON) and ROP2 (RHO-RELATED PROTEIN FROM PLANTS 2), while they repress that of the negative regulator WER (WEREWOLF) [67]. These data suggest a positive role of auxin signalling in the eCO₂-induced stimulation of LRs or root hairs development.

Nevertheless, auxin is certainly not the only player as cytokinins (CKs) were also reported to mediate the stimulation of root growth in response to eCO₂. Indeed, eCO₂ induces the expression of CK biosynthesis genes in the roots, such as *IPT3* (*ISOPENTENYLTRANSFERASE 3*) and *CYP735A2* (*CYTOCHROME P450*) in *Arabidopsis* [107], or *FaIPT8* (*ISOPENTENYLTRANSFERASE 8*) in tall fescue [105]. Although this did not always result in a higher accumulation of active CKs forms in the roots, the positive role of CKs was evidenced by the fact that CK biosynthesis multiple mutants (*ipt3ipt5ipt7* or *cyp735a1cyp735a2*) display a reduced root growth stimulation in response to eCO₂ as compared with the wild-type [35,107]. Moreover, ethylene is probably also involved because the eCO₂-enhanced development of root hairs in tomato is accompanied by a marked stimulation of ethylene production [106]. It has been proposed that the activation of both auxin and ethylene signals in response to eCO₂ leads to an enhanced NO (Nitric Oxide) production in the roots, also contributing to the stimulation of LRs and root hairs formation [108,109].

Despite the abundant literature showing that sugars interact with hormones in controlling root growth (see previous section), whether sugar signalling always explains how eCO₂ triggers auxin, CKs or ethylene synthesis

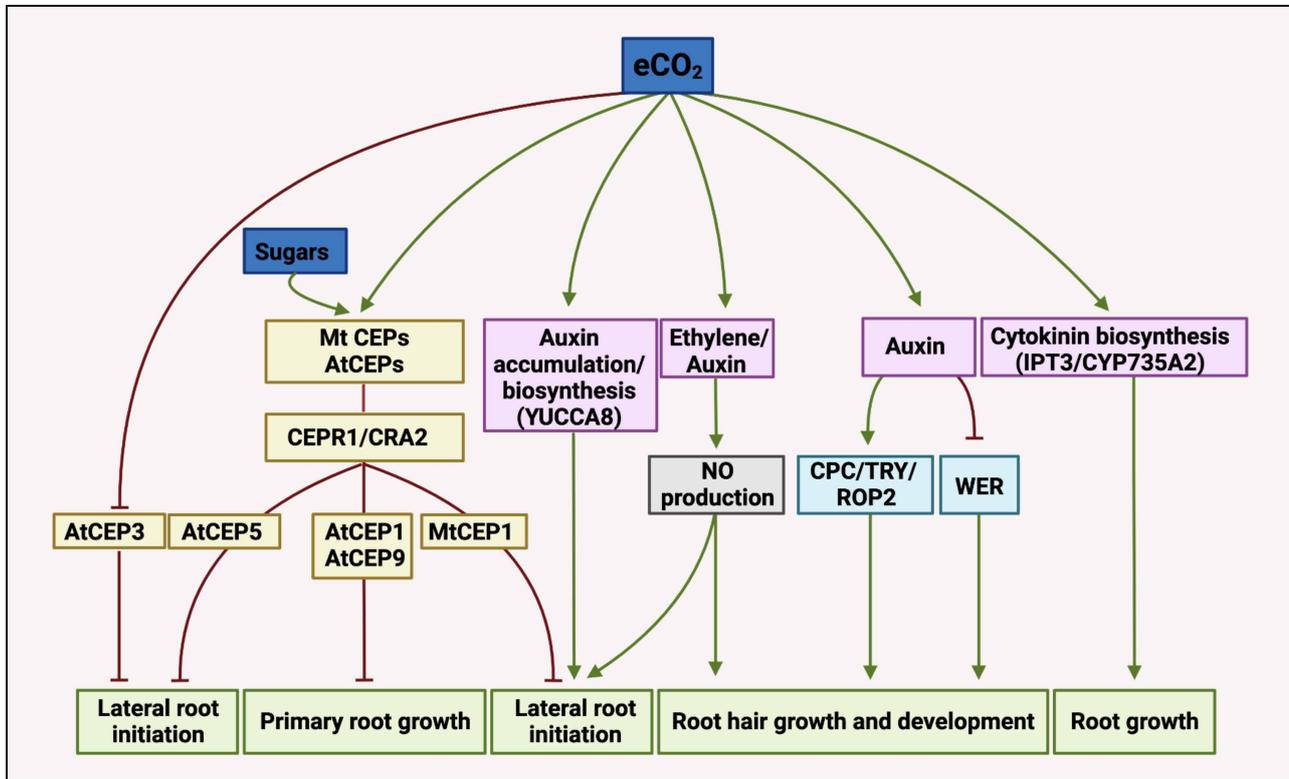


Figure 2. Genetic and hormonal control of root development in response to elevated atmospheric CO₂ concentrations (eCO₂).

Genetic and hormone networks are color-coded. eCO₂ promotes the development of root hairs, lateral roots and/or primary root. These effects are generally associated with hormone biosynthesis, accumulation and sensitivity. The *CEP* gene family encodes short signalling peptides perceived by LRR-RKs receptors (CEPR1/CRA2). CEPs act as negative regulators of root formation in *Arabidopsis* and *Medicago* and many *MtCEP* and *AtCEP* genes are regulated by eCO₂.

in roots remains unclear. As a matter of fact, depending on studies, exogenous sugar supply can mimic the effects of eCO₂-induced hormone signalling on root growth [107], or not [35]. Alternatively, the possibility remains that eCO₂ acts on root growth through changes in long distance transport of hormones between roots and shoots, independently of local sugar signalling in the roots [35,107]. Interestingly, a recent report unravelled that the rice OsGF14b 14-3-3 protein, which activates IAA signalling in shoots [110], acts as a negative regulator of root growth stimulation by eCO₂[111].

Peptide signalling

The *CEP* (*C-TERMINALLY ENCODED PEPTIDE*) gene family encodes short proteins that generate 14 or 15 aa-long signalling peptides (CEPs) after cleavage at the C-terminus [112]. In *Arabidopsis*, CEPs play a key role in systemic N signalling governing root nitrate uptake [113–115]. In addition, CEPs act on root development in both *Arabidopsis* and *Medicago*, in particular by regulating LR and nodule formation [112,116]. Interestingly, many *MtCEP* and *AtCEP* genes are induced in the roots by eCO₂ or sucrose [116,117], with the exception of *AtCEP3*, which is at the contrary strongly repressed by eCO₂ [112]. Functional analysis showed that CEPs act as repressors of root development. Over-expression of *AtCEP1*, 2, 3, 4, 5, 6 and 9 reduces primary root length as compared with the wild-type [112,118,119]. Moreover, combined approaches using over-expressors, null mutants or silenced transformants, and exogenous supply of the putative 15 aa peptide products demonstrated that *MtCEP1,2,5* and 11, and *AtCEP1, 3* and 5 are repressors of LR formation [112,116,118,119]. For *AtCEP3* and 5, the effect is due to a repression of LR primordia initiation, but not of the following steps of LRP development [112,119]. However, CEP5 was also reported to reduce the meristem size in emerged LRs [117].

As for the regulation of root nitrate uptake, the inhibitory effect of CEPs on LR development involves their perception by LRR-RKs receptors (CEPR1 and 2 in *Arabidopsis*) [117,119,120]. Most importantly, the action of CEPs in inhibiting LR growth is dependent on photosynthates availability. Indeed, the *Arabidopsis cepr1* mutant can display reduced LR density and lower LR length as compared with the wild-type, indicating a positive role of CEPR1 in LR development, which is opposite to that of its CEP ligands [117,119,120]. However, this phenotype is totally reversed under high light conditions or exogenous sugar supply, with a markedly stimulated LR development in *cepr1* single or *cepr1cepr2* double mutants as compared with the wild-type [117,120]. As a consequence, these mutants display a strongly amplified stimulation of LR formation in response to sugars. Given the sugar inducibility of most CEP genes, this suggests that CEPs/CEPRs predominantly act as a negative regulatory module to dampen the sugar- or eCO₂-induced stimulation of LR formation. One exception to this may be CEP3, which unlike other CEP genes, was down-regulated by eCO₂ [112]. This may then relieve CEP3-mediated repression of LRP initiation, and at the opposite contribute to the eCO₂-induced stimulation of LR formation.

Unlike for the regulation of root nitrate uptake, the CEP–CEPR module does not only act at the systemic level, but also locally. Indeed, both CEP and CEPR genes are expressed in the roots, and often specifically in or nearby LR primordia or in the basal meristem where LR primordia are initiated [116,118,119]. Furthermore, grafting experiments show that CEPRs function in both roots and shoots to regulate LR development [117,120]. However, a recent study indicated that in both *Arabidopsis* and *Medicago*, the CEP–CEPR signalling also controls the gravitropic set-point angle of LRs, to increase the overall width of the root system [121]. In this case, CEPR1 or CRA2 (COMPACT ROOT ARCHITECTURE 2) (its putative ortholog in *Medicago*) act specifically in the shoot, but not in the root, possibly by lowering rootward transport of auxin.

Interactions with nitrogen and water

N/eCO₂ interactions in the regulation of root growth/architecture

There is a large amount of evidence in many different species showing that root growth and development responses to eCO₂ are strongly affected by other abiotic factors, at the first rank of which N and water [35,37,39,43,50,65], although there may be exceptions [42,64]. As a matter of fact, root system size and architecture are highly plastic in response to changes in N or water availability *per se* [122–125]. Often, stimulation of root growth by eCO₂ is more obvious under moderate N stress [35,65,105], which can be explained by the fact that N limitation favour root over shoot growth, a tendency that is amplified under eCO₂ when photosynthates are even more available in source leaves for preferential allocation to the roots. In addition, at the molecular level N signalling pathways strongly interact in the roots with the above-mentioned hormonal or peptide signalling components participating in the eCO₂ or sugar-induced changes in root growth, e.g. auxin transporters, auxin and cytokinin biosynthesis enzymes or CEPs [113–115,126–129]. However, although some work was done to elucidate how eCO₂ or sugar signalling mechanisms control N acquisition and metabolism [84,130], no attempts have been made yet to investigate how N signalling mechanisms modulate the root developmental responses to eCO₂.

Ideotypes for efficient root acquisition of water and N

A key point that remains under debate is to determine whether the eCO₂-induced changes in root system size and architecture actually lead to improved N or water acquisition efficiency, or not. It is commonly postulated that an increased size of the root system favours the acquisition of water and nutrients, owing to the larger exchange surface between the plants and the soil, and to a more efficient soil exploration by the root system [28,131]. Accordingly, *Arabidopsis* or oil seed rape genotypes with improved root growth actually have a higher N uptake capacity [132,133]. Conversely, mutants impaired in root development can be deficient in N uptake [134]. Furthermore, many reports indicated that an improved biomass production in response to eCO₂ could be attributed to a stimulation of the uptake of water or nutrients, associated with an increase in root system growth [135–141].

However, root system architecture may be more relevant than total size for understanding the relationship between root development and nutrient or water acquisition efficiency [27,142]. Indeed, it has even been proposed that reducing the size of the root system may be advantageous for improving water use efficiency and resistance to drought, provided this is compensated by more optimal architectural or anatomical traits [143]. In maize, genotypes with a low number of LRs or of crown roots performed much better under drought stress

than genotypes with a more branched root system [144,145]. This is in particular explained by the fact that plants with fewer laterals or crown roots display a deeper rooting phenotype, associated with an increased mean root length. This is postulated to allow the roots to grow further down and colonize lower soil domains, where water remains more available than in the topsoil. There have been only few attempts to investigate this hypothesis under eCO₂ conditions, but a series of experiments on wheat and canola plants subjected to contrasted irrigation regimes confirmed that a greater stimulation of root growth in deep soil layers in response to eCO₂ was actually associated with higher water use and yield [138–141]. With the same rationale, deep rooting is also expected to result in an increase in N uptake by the plant and a reduced leaching of nitrate in the soil [27,146–149].

The developmental mechanisms associated with deep rooting phenotypes are still largely obscure. However, a series of recent studies highlighted the importance of the root growth angle as a key architectural trait determining topsoil or subsoil foraging [150], and allowed the identification of underlying molecular regulators (Figure 3). Indeed, steeper angles result in deeper root systems. In rice, the DRO1 (DEEP ROOTING 1) protein of unknown function favours gravitropic downward bending of the root tip growth, resulting in steeper root angles [151]. Increasing *OsDRO1* expression or introducing a favourable allele of *OsDRO1* into a shallow-rooting rice genotype enhanced root colonization of deep soil layers without affecting total root biomass or

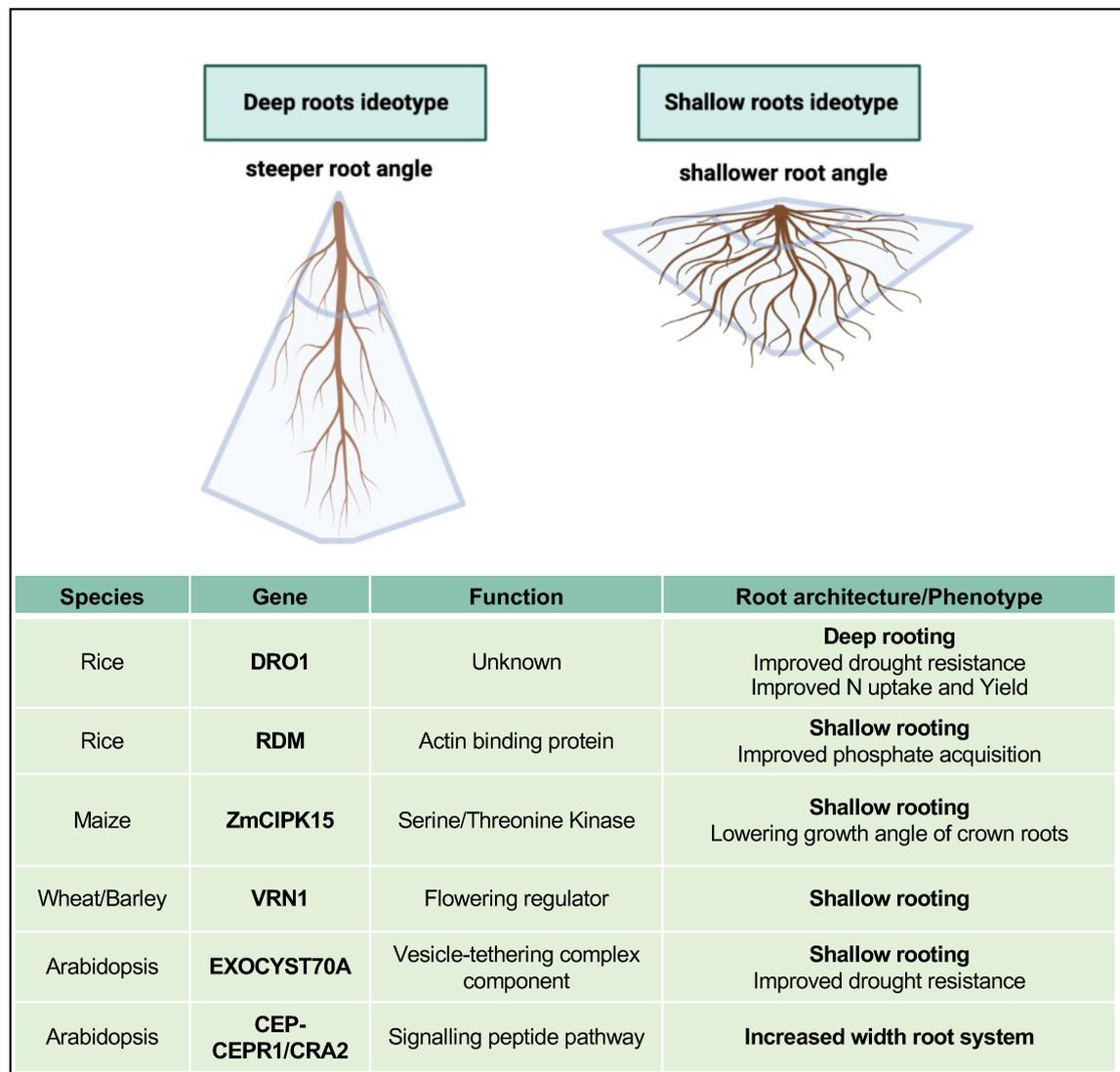


Figure 3. Examples of key genes and functions controlling deep or shallow root system architecture in diverse species.

total root length. This improved both drought resistance, root N uptake and yield [146,151]. At the opposite, the rice actin binding protein RMD (RICE MORPHOLOGY DETERMINANT) inhibits gravitropic downward bending by delaying statolith sedimentation in collumella cells [152]. This results in a shallower crown root angle, leading to a preferential root colonization of the upper zones of the soil and an improved acquisition of phosphate that is predominantly located in the topsoil [152]. In maize, deep rooting also has a positive effect on N acquisition [153,154]. Recently, the ZmCIPK15 (CBL-INTERACTING PROTEIN KINASE 15) serine-threonine protein kinase was identified from a genetic screen for variation in root growth angle and was shown to favour shallow rooting by lowering growth angle of crown roots [149]. Accordingly, a *cipk15* transposon insertional mutant had a steeper root growth phenotype and performed better than the wild-type in field trials, with an 29% increase in shoot N accumulation and an 18% greater shoot biomass production under N limiting conditions [149]. However, no differences were found in shoot biomass between the mutant and the wild-type in response to drought. In wheat and barley, the key regulator of flowering VRN1 was found to also regulate root system architecture. The mutant allele present in spring varieties (which do not require vernalization for flowering) increases the root growth angle, leading to deeper root systems as compared with wild-type winter types [155]. Interestingly, NILs carrying the spring allele have a reduced R/S, confirming that deep rooting is not necessarily associated with a larger size of the root system. In *Arabidopsis*, the *EXOCYST70A3* (*EXOCYST SUBUNIT EXO70 FAMILY PROTEIN A3*) gene, encoding a putative component of vesicle-tethering complex involved in exocytosis, plays an important role in controlling the auxin-dependent gravitropic response, by regulating the level of the PIN4 auxin transporter at the plasma membrane [156]. Surprisingly, the *EXOCYST70A3* alleles that confer a shallow root system were also those associated with an increased resistance to drought. As these alleles are overrepresented in accessions originating from areas with a high variability in weekly precipitation, this may reflect a higher efficiency of shallow root systems for taking advantage of sparse rainfalls [156]. This illustrates the fact that a deep rooting phenotype may not always be beneficial, and that the concept of ideotype markedly depends on the precise environmental scenario that is considered [157]. Interestingly, modelling approaches indicate that in maize, dimorphic root phenotypes with both shallow seminal roots and steep nodal roots perform well in all scenarios considered, and outperform the deep rooting phenotypes [153]. This raises the question of whether an increased C allocation to roots in response to eCO₂ may allow stimulating both horizontal and vertical development of the root system, to avoid problematic trade-offs and combine the respective advantages of shallow and deep rooting. Finally, the CEP–CEPR1/CRA2 regulatory module was found to regulate the gravitropic set-point angle of LRs in *Arabidopsis* and *Medicago*, favouring the horizontal extension of the root system through inhibition of shoot-to-root auxin transport [121]. As a consequence, *cepr1* and *cra2* mutants display a reduced width of the root system, but it is unclear if this also results in a deeper rooting phenotype.

Interactions with photosynthesis

Sink limitation of photosynthesis

One crucial question to address when stimulating C allocation to roots for improving C storage in soil is to know whether this will negatively impact yield, most often determined by C accumulation in reproductive sinks. Such trade-offs between growth of belowground and aboveground organs can explain the negative correlations often found between plant biomass production and C storage in soils in response to eCO₂ [26]. To avoid this, increases in net C input in agrosystems are required, through stimulated photosynthesis [13,26]. However, with regard to the response to eCO₂, one interesting hypothesis is that stimulated photosynthesis may not only be a requirement for, but also a consequence of, increased root growth. Indeed, full stimulation of photosynthetic activity by eCO₂ in C₃ plants is frequently prevented by the so-called acclimation of photosynthesis to eCO₂, which results from a negative feedback exerted by soluble sugars over-accumulating in source leaves [84,158,159]. As a consequence, it is frequently proposed that photosynthesis is sink-limited under eCO₂, due to the inability of sink organs to use all the sugars produced by the eCO₂-induced stimulation of C fixation [28,160,161]. This is supported by eCO₂ experiments where surgical or genetic alterations of the source/sink ratio in the shoots have unravelled a strong positive correlation between photosynthetic activity of the source leaves and sink strength of the other aboveground organs [162–165]. The same rationale could apply for an increased C sink due to a larger root system, suggesting that promoting root growth in response to eCO₂ may be relevant to ‘pull’ the overall C fixation system. However, the effects of an increased sink strength of the root system in response to eCO₂ have received little attention to date. One exception are the legumes, which

are one functional group that responds the best to $e\text{CO}_2$ in terms of biomass production and yield [161,166]. This is often explained by the huge C cost associated with the development and the N_2 -fixing activity of the nodules, which constitute major C sinks preventing over-accumulation of soluble sugars in the leaves [167–169]. Although data are still lacking with non-legumes, this supports the potential importance of root growth in modulating source/sink relationships and avoiding acclimation of photosynthesis to $e\text{CO}_2$.

N limitation of photosynthesis

An alternative hypothesis to the sink limitation for explaining the acclimation of photosynthesis to $e\text{CO}_2$ is the nutrient limitation, which has been mostly evidenced for N [170–172]. Indeed, growth of C3 plants under $e\text{CO}_2$ leads to a general decrease in the tissue N concentrations [130,173], and compelling evidence suggests that at both individual plant and Earth vegetation scales, the CO_2 fertilization effect is often constrained by N limitation [170,171,174–179]. Therefore, enhanced development and optimized architecture of the root system in response to $e\text{CO}_2$ may also be crucial in this context, as it may stimulate root N acquisition and thus significantly contribute to prevent nutrient limitation of photosynthesis. In agreement with this hypothesis, the volume of soil that can be explored by $e\text{CO}_2$ -treated plants is considered as one important factor determining the intensity of the CO_2 fertilization effect, explaining why conclusions from experiments with pots often failed to match those from field experiments [163,180]. Moreover, it was reported that a large and/or a long-lasting CO_2 fertilization effect in ecosystems is associated with increased root system growth and improved N acquisition by the plants [135–137]. However, it is generally not known whether this is directly due to improved N uptake capacity of the plant, or to an indirect positive effect on N availability in soils resulting from modified mineralization of the soil organic matter. In addition, root system size and architecture are not the only factors determining root N uptake efficiency. It is likely that $e\text{CO}_2$ also has direct negative effects on physiological processes of N uptake and assimilation, especially when N is in the form of nitrate, which cannot be fully counteracted by stimulated root growth [130,181]. Interestingly, two recent reports in *Arabidopsis* indicate that the altered expression of nutrient transport systems may be a major determinant of the plant responses to $e\text{CO}_2$. First, genes encoding components of the root high-affinity nitrate uptake system (e.g. *NRT2.1* and *NAR2.1*) were found to be markedly down-regulated by $e\text{CO}_2$ [182]. Accordingly, $e\text{CO}_2$ repressed the positive regulators of these genes, while it induced their negative regulators. This may explain why the CO_2 fertilization effect is often less pronounced at low nitrate availability [175,176], and why legumes generally display higher CO_2 fertilization response and lower N concentration decline, owing to their symbiotic N_2 -fixation capacity [169,183–185]. Second, $e\text{CO}_2$ was found to down-regulate the *PHT4;3* gene, encoding a chloroplastic phosphate transporter [186]. This resulted in a lowered P accumulation in the chloroplast and a reduced production of phytic acid, which in turn stimulated growth in response to $e\text{CO}_2$.

Conclusion

The highly variable response of root system size and architecture to $e\text{CO}_2$ does not help to drive firm conclusions on how the $e\text{CO}_2$ -induced stimulation of C capture by the shoots will translate into developmental changes of the root system that will favour C storage in soil. In addition to the methodological difficulties associated with root phenotyping, this variability can be explained by genotypic differences between plant functional groups, biotic interactions in the rhizosphere or abiotic factors such as nutrient availability. As a matter of fact, nutrients have on their own a dramatic effect on root growth and development that can override any change resulting from enhanced C provision from the shoot [187]. Yet, as compared with the abundant literature addressing the question of the root developmental responses to nutrients, little is known on the mechanisms involved in the responses to $e\text{CO}_2$. It is striking to see that only a very limited part of all candidate genes or genetic resources available for investigating the sugar, hormone or peptide signalling pathways listed in this review has been used in mechanistic studies on the root responses to $e\text{CO}_2$. In addition to the mutants and transformants related to other putative important mechanisms not detailed here, such as trehalose-6-P signalling [188] or redox signalling [189], the use of these genetic resources will certainly help making crucial advances in our understanding of how underground organs behave in a $e\text{CO}_2$ environment.

In this review, we discussed the hypothesis that a larger size and an optimized architecture of the root system in response to $e\text{CO}_2$ may have three synergistic positive effects: (i) to enhance C input into the soil for increased terrestrial C sequestration, (ii) to improve water and nutrient use efficiency for more productive and environmental-friendly crops, and (iii) to prevent photosynthesis acclimation to $e\text{CO}_2$ for stimulating net CO_2 capture from the atmosphere. Evidence is available to support synergism between these effects. For instance, it

is likely that a larger root system with optimized architecture for improved water and nutrient acquisition will help avoiding sink or nutrient limitation of photosynthesis under eCO₂. Furthermore, many studies converge to conclude that deeper root systems in response to eCO₂ will enhance both water and N acquisition by plants, and promote higher and more stable C storage into the soil. However, there are also indications that antagonistic effects may arise. Indeed, increasing the overall size of the root system may not be the most relevant strategy for improving plant resistance to drought. It may also have a detrimental effect on yield if the necessary stimulation of photosynthesis in response to eCO₂ is prevented by other factors (e.g. heat stress). Most importantly, the C/N interactions should deserve specific attention. First, a higher C input into the soil can promote emissions of N₂O, a gas with dramatic greenhouse effect, thereby offsetting the benefit of stimulated net CO₂ capture from the atmosphere [190,191]. Second, it is frequently postulated that N is a crucial factor controlling the unwanted inverse relationship between increased plant biomass production and increased C storage in soil [26,135]. Indeed, improved N uptake by plants leading to higher biomass production in response to eCO₂ has been proposed to result in a decrease in soil organic C associated with low soil N availability. Accordingly, increasing N fertilization suppresses this inverse relationship [26], suggesting that higher N input into agrosystems is required for stimulating both crop yield and C sequestration in soils. Because further increases in N fertilizer input is not a sustainable strategy, this will call for either a wider use of legume crops, or a drastically improved cropland management to prevent N leaching in agrosystems.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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CRedit Author Contribution

Liên Bach: Writing — original draft, Writing — review and editing. **Alain Gojon:** Writing — original draft, Writing — review and editing.

Abbreviations

CEP, C-terminally encoded peptide; CKs, cytokinins; FIE, fertilization-independent endosperm; HXK, Hexokinase; LR, lateral root; RSA, root system architecture; SWEET, sugars will eventually be exported transporters; TOR, target of rapamycin.

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