Effects of elevated CO$_2$ on plant root form and function: a review

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Abstract: Root form and function is key to the productivity of natural and agricultural ecosystems. The growth and development of roots is highly adaptable to the environment. Studies show that species differ in their root system adaptation and function in response to high CO$_2$, which may lead to changes in global species composition in the future. However, knowledge of genetic variation and molecular responses in roots to elevated CO$_2$ is still lacking. This review examines the effects of elevated CO$_2$ on root system and offers perspectives for future research.

Keywords: mineral nutrition, rhizosphere microbes, root exudation, root turnover, water uptake

Abbreviations: APase, acid phosphatase; NO, nitric oxide; PIP, plasma membrane intrinsic protein; R/S ratios, root:shoot ratios

Introduction

Plant root system serves important functions of anchoring the plant and supporting the above-ground shoot growth with water and mineral nutrients. The uptake ability of roots is affected by the availability of water and mineral nutrients in the soil, the size and distribution of roots (e.g., the density of roots within a given volume of soil and the volume of soil explored by roots), and the specific activity of the roots (e.g., rate of uptake per unit of root length) (Gregory 1988, Berntson and Woodward 1992, Barber 1995).

The spatial and temporal distribution of the root system affects both plant and soil processes, including root weathering of soil, input of C to soil, mining soil for resources, and erosion. Roots exude a variety of organic molecules into the soil, modifying its structure and physical properties, affecting availability of soil minerals, and facilitating plants to interact with soil microorganisms. Plant roots are highly adaptable to the environment, and its growth is often described as "plastic". Root growth plasticity responds to the availability of water and minerals, oxygen level, temperature, heavy metals, salinity, and mechanical properties of the soil (Eshel and Beeckman 2013).

The concentration of CO$_2$ in the Earth’s atmosphere was below 300 ppm prior to the Industrial Revolution of the late 18th to 19th centuries. Since then, increased use of fossil fuels has contributed to the present level of CO$_2$ close to 400 ppm, and it is predicted to reach 800 ppm by the end of this century (IPCC 2014). The projected rise in atmospheric CO$_2$ may result in changes in shoot and root structure, higher rate of photosynthesis and increased plant productivity.

In a changing climate with rising CO$_2$ concentration in the air, roots play an important role in the global C cycle, by transferring atmospheric C fixed via photosynthesis into the soil. Coarse roots have been predicted to accrue greater biomass under elevated CO$_2$ and serve as large C storage sites (Norby 1994, Miller et al. 2006). A study shows that scrub oak under continuous CO$_2$ fumigation for over 10 years accumulated more coarse-root biomass under elevated CO$_2$ (700 ppm) than ambient atmospheric CO$_2$ (350 ppm), suggesting more C sequestration in elevated CO$_2$ (Stover et al. 2007).

Fine roots are also an important component of the global C cycle, and as much as one-third of the total global primary productivity is allocated to fine-root construction and maintenance (Jackson et al. 1997). It is believed that the capacity of fine roots to supply sufficient soil resources affects the ability of trees to sustain higher levels of net primary...
production in response to elevated CO$_2$ (Luo et al. 2004). Thus, healthy and functional plant roots are critical to the production of food and many other resources human prosperity depends on, as well as to the health of natural ecosystems and the environment. Alterations in root growth, development, and deployment represent major plant responses to elevated CO$_2$ concentrations, therefore, understanding how plant root system responds and adapts to elevated CO$_2$ is vital for human food security and the environment. The objective of this review is to examine the effects of elevated CO$_2$ (typically between 700 ppm to 800 ppm) on the root system of plants in both natural ecosystem (i.e., trees, grasses) and agricultural field (i.e., crops), covering areas on changes in root growth and architecture, root turnover, uptake of water and mineral nutrients, and root exudation and microbes in the rhizosphere.

**Effect on root system growth and architecture**

Enhanced photosynthesis due to high atmospheric CO$_2$ allows plants to allocate more fixed C belowground, often leading to increased root growth and longer, thicker, and more branched root system. As a result, root-to-shoot mass ratio often increases. High CO$_2$ also stimulates the production of fine roots and root hairs and interacts with other factors such as soil N availability to affect fine root distribution within the soil. The changes in root growth and architecture involve complex interplay of photosynthate, plant hormones such as auxin, ethylene, and cytokinin, as well as nitric oxide (NO), and are dependent on species (Fig. 1).

High CO$_2$ concentration affects root growth positively across most species studied. Under non-limiting water and nutrient conditions, elevated CO$_2$ increased root growth of plant species including trees (Pregitzer et al. 1995, Rogers et al. 1995, Obrist and Arnone 2003). Elevated CO$_2$ increased root growth and root dry weight of many crop plants (Chaudhuri et al. 1990, Rogers et al. 1992a, b, Prior et al. 1994a, b, Wechsung et al. 1995, McMaster et al. 1999, Vanaja et al. 2007) and promoted the formation of lateral roots in Arabidopsis and tomato (*Solanum lycopersicum*), possibly using NO as a signal (Lee-Ho et al. 2007, Yue et al. 2009, Wang et al. 2013). In native, semiarid shortgrass steppe grassland, elevated CO$_2$ resulted in increased root branching, greater root-length, and larger root diameter in the upper soil profile (Milchunas et al. 2005). These changes to the root system may lead to greater soil exploration in both horizontal and vertical directions (Baker et al. 1990, Chaudhuri et al. 1990, Idso and Kimball 1991, Rogers et al. 1992a).

Plants strategically allocate biomass between above- and below-ground tissues to optimize growth in fluctuating environments. Under elevated CO$_2$, root:shoot (R/S) ratios are often altered, suggesting a shift in the functional relationship between these

![Diagram of Elevated CO$_2$ Effects](image)

**Fig. 1.** Elevated CO$_2$ changes root growth and architecture. Changes in certain traits vary among species, e.g., R/S (i.e., root:shoot ratios), fine root distribution.
organs. In crop species, R/S ratios usually increased, sometimes decreased, but rarely remained unchanged. R/S ratio varies among different species due to complex interactions with water and nutrient availability in the soil (Rogers et al. 1995). Increased R/S occurred in several tree species, but more frequently in agricultural crops, particularly root and tuber crops (Biswas and Hileman 1985, Luxmoore et al. 1986, Norby et al. 1986a, b, Norby 1987, Norby et al. 1987, O’Neill et al. 1987a, b, Idso et al. 1988, Norby and O’Neill 1989, Norby et al. 1992). Increased R/S ratio under higher CO$_2$ is more pronounced under abiotic stresses, such as high light and deficiencies of nutrient or water (Bazzaz 1990, Stulen and Den Hertog 1993, Rogers et al. 1995). In agricultural and ecological fields, low pH and lack of N are common stresses. Under high CO$_2$, R/S ratio increased in A. thaliana. This increased R/S ratio occurs via different mechanisms for low pH vs. low N stress. Under low pH/high CO$_2$ conditions, excess C accumulation in shoots may induce biosynthesis of IAA in shoots and its transport into roots, where lateral root growth may be promoted by IAA directly or indirectly via suppression of cytokinin action; under low N/high CO$_2$, however, the high CO$_2$ levels may stimulate plant growth and rapidly deplete N in plants and growth media, leading to preferential root growth (Hachiya et al. 2014).

The distribution of fine root density per unit volume of soil, which determines overall root architecture, increased both vertically and horizontally with increased CO$_2$ (Rogers et al. 1992b, Prior et al. 1994a, Prior et al. 2003). In forested ecosystems, fine roots of trees are distributed deeper in the soil under elevated CO$_2$; in contrast, crops and grasses have shallower rooting distribution under high CO$_2$ (Arnone et al. 2000, Pritchard and Rogers 2000, Iversen 2010). In A. thaliana, elevated CO$_2$ changed the root branching pattern from herringbone to dichotomous. These effects were mimicked by addition of sucrose to the growth media, suggesting that extra C availability may promote root growth and modify root architecture (Lee-Ho et al. 2007). Modifications in rooting patterns (e.g., distributions and the depth of fine root production, branching angles, root diameter) may affect root physiological function, competition among roots, nutrient dynamics, and mycorrhizal infection, leading to altered rates in water and nutrient (e.g., N, P) uptake and root turnover, thus affecting root system competitiveness for soil resources.

Plant growth can benefit greatly from development of root hairs, which are important in increasing root surface area for nutrient acquisition under limited nutrient supply (Peterson and Farquhar 1996, Jungk 2001, Ma et al. 2001). Elevated CO$_2$ promoted root hair initiation and growth in A. thaliana, resulting in increased root hair density due to greater number of trichoblast files and the occurrence of ectopic root hairs, as well as increased root hair length. Elevated CO$_2$ increases the production of carbohydrates, which trigger the auxin or ethylene responsive signal transduction pathways and subsequently the accumulation of intracellular NO. These endogenous signals then modulate the expression of specific gene set and the initiation of the root hairs (Niu et al. 2011).

Changes in root turnover rate

Root turnover, i.e., the replacement of older roots with newly formed roots, affects nutrient and water acquisition, as well as ecosystem nutrient cycling and global C cycle (Madhu and Hatfield 2013). Developing new roots costs a significant amount of energy to the plants (Canadell et al. 1995), however,
production of new roots may be more energetically cost-effective than maintaining old roots under stressful environment (Madhu and Hatfield 2013). Accelerated root growth under higher CO₂ concentration is often accompanied by increased root turnover rate, which can be heightened by increased temperature and reduced soil moisture but lessened by reduced nutrient availability. Under elevated CO₂, the number of actively growing roots of soybean increased significantly (Del Castillo et al. 1989), and root turnover rate was stimulated (Fitter et al. 1999, Allen et al. 2000, Pregitzer et al. 2000, Wan et al. 2004).

The effects of elevated CO₂ on root turnover are complex and system dependent (Fig. 2). Under elevated CO₂, cumulative root birth and death totals were greater in peat and limestone grassland soils, and turnover was faster in the peat soil, with only a small effect in the limestone soil (Fitter et al. 1997). Root turnover rate under high CO₂ may be affected by other factors such as increases in temperature, changes in the pattern of precipitation, and decreased mineral availability in the soil (Rastetter et al. 1997). Decreases in soil moisture or increases in soil temperature may accelerate root mortality (Hayes and Seastedt 1987, Huck et al. 1987, Fitter et al. 1999). However, reduced nutrient availability may decrease root mortality (Eissenstat and Yanai 1997). CO₂ enrichment lowered fine-root turnover in sweetgum (Liquidambar styraciflua) deeper in the soil profile, likely due to lower N availability and cooler temperatures that allowed increased root longevity because of reduced respiration costs (Iversen et al. 2008). The complexity of root turnover suggests that future warmer and elevated CO₂ conditions may generate roots that will differ in function and dynamics.

Changes in root water uptake

Water is a major limiting factor for plant growth and productivity, thus, the effect of elevated CO₂ on plant water uptake and use is an important issue. Under elevated CO₂, water uptake by the root system is affected by both above- and below-ground factors (Fig. 3). Stomata movement affects leaf transpiration rate and regulates the amount of water uptake by roots. Elevated CO₂ can induce stomatal closure directly but can also reduce stomatal conductance by altering the anatomical structure of the hydraulic pathway from the root to the shoot and leaf (Ainsworth and Rogers 2007, Domec et al. 2010). Reduced leaf stomatal conductance and transpiration rate at elevated CO₂ may not necessarily lead to a reduction in water consumption, which may be offset by an increase in canopy leaf transpiring area (Ainsworth and Long 2005, Leuzinger and Körner 2007). For example, cotton plants grown under 640 ppm of CO₂ showed a 41.9% decrease in maximum stomatal conductance and 32.9% reduction in transpiration rate, but a significant 22.5% increase in canopy leaf area (Li et al. 2020a).

Under elevated CO₂, water use efficiency, i.e., C

![Fig. 3. Elevated CO₂ affects root water uptake via effects on canopy growth, as well as root architecture, root anatomy and aquaporin expression patterns. Changes in root hydraulic conductance vary among species, resulting in changes in water uptake.](image-url)
fixed/water transpired, often increases due to lower stomatal conductance and possibly through decreased stomatal density (Kimball and Idso 1983, Rogers et al. 1984, Acocq and Allen 1985, Woodward 1987, Bazzaz 1990). Increased atmospheric CO$_2$ can impact water uptake and transport in roots in a species-specific manner. Huxman et al. (1999) reported that the capacity for water uptake decreased in common sunflower (Helianthus annuus) but was unaltered in creosote bush (Larrea tridentata) under elevated atmospheric CO$_2$. In well-watered peach seedlings, elevated CO$_2$ had no effect on stomatal conductance or total water uptake, but water use efficiency was significantly increased (Centritto et al. 2002).

Root water uptake capacity is greatly affected by its hydraulic conductivity, which is determined by rooting depth, fine-root area and activity, structure, anatomy and the numerous aquaporins present. Root hydraulic conductivity varies among species under elevated CO$_2$; for example, root hydraulic conductance decreased in soybeans, H. annuus, American elm (Ulmus americana) and red oak (Quercus rubra) (Bunce 1996, Huxman et al. 1999, Cheng 2009), remained unchanged in creosote bush, sweetgum and flowering dogwood (Cornus florida) (Huxman et al. 1999, Domec et al. 2010), and increased in loblolly pine (Pinus taeda) and winged elm (Ulmus alata) (Domec et al. 2010). The CO$_2$-induced changes in root hydraulic conductance are related to alterations in root anatomy, architecture, developmental stages, and water stress (Huxman et al. 1999, Domec et al. 2010, Domec et al. 2017, Li et al. 2020b). Elevated CO$_2$ increased root metaxylem area/xylem vessel diameter in tomato that could increase hydraulic conductivity, but the potential adaptive role of development stage-specific widening of xylem vessel diameter awaits further characterization (Cohen et al. 2018, Gray et al. 2020). Interestingly, root xylem development is dependent on N source. Under 800 ppm CO$_2$, tomato plants supplied with nitrate showed greater xylem development compared to those supplied with ammonium (Cohen et al. 2018). Structure and anatomy influence the axial conductance and the distribution of water uptake along the root, while aquaporins in the epidermis and cortex accelerate water movement through membranes and influence the hydraulic conductivity of root cells (Wullschleger et al. 2002, Bramley et al. 2009, Martinez-Ballesta et al. 2009). In cucumber seedlings growing under moderate drought stress and elevated CO$_2$ of 800 ppm, ABA content and the transcript level of aquaporin-related gene CsPIP2-4 decreased, but the transcript level of CsPIP2-7, GA content and root biomass increased; aquaporin-mediated cell-to-cell water transport was maintained, and root hydraulic conductivity was improved (Li et al. 2020b). In soybean roots treated with instantaneous water deficit, exposure to 800 ppm CO$_2$ reverted the expression of water deficit-induced genes related to stress, defense, transport, and nutrient deficiency, indicating that elevated CO$_2$ may mitigate water deficit stress on the soybean roots (Bencke-Malato et al. 2019).

Larger root system produced under elevated CO$_2$ can access sub-soil water better (Uddin et al. 2018), however, the amount of water uptake by a

![Fig. 4. Elevated CO$_2$ can lead to greater demand for mineral nutrients. Uptake of N depends on N forms.](image-url)
greater root volume is determined by the functionality of aquaporins. Elevated CO₂ decreased hydraulic conductance of roots of wild type tomato plants, in which genes encoding five out of eight aquaporins of the plasma membrane intrinsic protein (PIP) in roots were constantly and significantly downregulated, but elevated CO₂ had no effect on hydraulic conductance in roots of an ABA-deficient tomato mutant, in which expression of aquaporin genes was either unaffected or upregulated, suggesting that ABA-mediated regulation of aquaporin gene expression affects root hydraulics in response to increased CO₂ concentrations (Fang et al. 2019).

Changes in root uptake of N, P, and K

CO₂ is an important inorganic substrate required by plants, however, the long-term response of photosynthesis and growth to elevated CO₂ depends on the availability of mineral nutrients and their acquisition by the roots. To understand the response of plant metabolism and growth to elevated CO₂, it is important to consider how mineral nutrients are acquired and used by the plant in a CO₂ enriched environment. Current knowledge on the effects of elevated CO₂ on nutrient acquisition and metabolism is still limited. Elevated CO₂ increases the rate of carboxylation but decreases the rate of oxygenation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) in C3 plants, thereby enhancing plant growth and crop yield (Stitt et al. 1991, Drake et al. 1997). Increased growth rate and biomass accumulation in elevated CO₂ leads to a greater demand for mineral nutrients (Fig. 4). In field grown cotton, elevated CO₂ significantly increased the uptake of N, P, K, Ca, Mg and micronutrients (Cu, Fe, Mn and Zn), which in turn promoted growth and development (Prior et al. 1998). In tomato plants grown in Fe-limited medium, elevated CO₂ enhanced root uptake of Fe that may involve increased NO levels in roots (Jin et al. 2009).

In environments with suboptimal nutrient supply under elevated CO₂, plants need to develop adaptive mechanisms to enhance nutrient acquisition, which may be achieved by modifications of root development and structure; for example, root length was positively correlated with P uptake under both ambient and elevated CO₂, and the longer roots under elevated CO₂ resulted in greater P acquisition (Jin et al. 2012). Changes in root growth and morphology in response to elevated CO₂ would enable roots to explore a greater soil volume and increase the plant’s ability to acquire mineral nutrients, especially immobile nutrient such as phosphate ions (Nie et al. 2013). Other adaptations such as increasing the rate of mineral acquisition and assimilation by the plant, nutrient uptake efficiency (measured by unit of nutrient per unit of root weight or root length), and/or using nutrients more efficiently (i.e., unit of biomass produced per unit of nutrient) are also important. The response mechanisms vary depending on the species involved, the nutrient status of the plant, and the mineral in question (Stitt and Krapp 1999, BassiriRad et al. 2001, Kogawara et al. 2006).

In most temperate ecosystems, N is the primary limiting mineral for plant growth, and different forms of N (i.e., nitrate vs. ammonium) can affect plant nutrient acquisition under elevated CO₂. In tobacco plants grown under elevated CO₂, nitrate reductase activity and uptake of nitrate both increased when supplied with nitrate, whereas those supplied with ammonium exhibited reduced nitrate reductase activity but increased ammonium uptake (Matt et al. 2001). In tree seedlings of Betula alleghaniensis and Pinus strobus grown in ambient and elevated CO₂ (400 ppm vs. 800 ppm) and supplied with either nitrate or ammonium as their sole N source, total root length increased significantly, but root N uptake rates for both nitrate and ammonium were either reduced or unchanged in B. alleghaniensis under elevated CO₂. In P. strobus, however, there was no change in root architecture, but maximal uptake rates increased under elevated CO₂, suggesting species-dependent trade-offs between root physiological and architectural responses to CO₂ (Bauer and Berntson 2001). Recent transcriptomic analyses of Arabidopsis showed that 800 ppm CO₂ induced the expression of genes in roots involved in the transport of nitrate and mineral elements such as Zn, P, and Fe. The resulting accumulation of nitrate in the roots but limited nitrate transport to the shoot suggests different mechanisms for organ-level N assimilation under elevated CO₂ (Jauregui et al. 2016); in contrast, in soybean roots, elevated CO₂ (800 ppm) decreased the transcripts levels of genes involved in Fe uptake and transport, antioxidant activity, secondary metabolism and defense, and stress responses (Bencke-Malato et al. 2019), suggesting species-specific and differential regulation of various ion transporters by elevated CO₂. Wheat plants grown under 700 ppm had increased nitric oxide synthase activity in roots and produced significantly higher level of NO, which was associated with root architectural modifications under elevated CO₂, with lower lateral root proliferation and root surface area under reduced NO. The enhanced NO production under elevated CO₂ and high N levels downregulated the transcript abundance of nitrate reductase and high affinity nitrate transporters in roots, possibly by S-nitrosylation and inhibition of S-nitrosoglutathione.
ammonium under elevated CO\(_2\) with nitrate, but decreased when supplied with... suggest CO\(_2\) increases in root respiration rate, suggesting that CO\(_2\) inhibited root growth. All of this enhanced root uptake of P was accompanied by increased leaf acid phosphatase (APase) activity and chlorophyll content, although there was no change in lateral root respiration rate, suggesting that CO\(_2\) did not affect metabolic changes in the roots during P uptake (Zhong et al. 2018). Consistent with increased demand for P in CO\(_2\) enriched environment, the growth response of *Pinus densiflora* to phosphate reached saturation point at 0.1 mM Pi under 350 ppm CO\(_2\), but did not saturate at twice as much Pi under 700 ppm CO\(_2\) (Kogawara et al. 2006). In Arabidopsis plants grown under P-deficient condition, P absorption per unit weight of root and P concentration in plants increased when supplied with nitrate, but decreased when supplied with ammonium under elevated CO\(_2\) (800 ± 50 ppm) compared to under ambient CO\(_2\) (350 ± 50 ppm); also, acid phosphatase activity increased in both roots and shoots in plants grown with nitrate under elevated CO\(_2\), and NO production in roots increased in nitrate-fed plants but decreased in ammonium-fed plants under elevated CO\(_2\) while a scavenger of NO inhibited root acquisition of P under elevated CO\(_2\). These results suggest that P uptake under elevated CO\(_2\) is affected by the form of N present in the growth media, and that NO may act as a signaling molecule in the acquisition of P (Niu et al. 2013a) (Fig. 4).

More than 100 genes are involved in plant response to P deficiency (Raghothama 1999), and over 300 independent genes are responsive to elevated CO\(_2\) in soybean plants (Ainsworth et al. 2006). Elevated CO\(_2\) may affect P acquisition via modifying root morphology. Plant hormone auxin transport genes are thought to be the most responsive to elevated CO\(_2\) and external P status (Santelia et al. 2005). Auxins regulate the initiation and elongation of root hairs, which are important for P acquisition (Pitts et al. 1998, Schiefelbein 2000, Ma et al. 2001). Elevated CO\(_2\) triggers the expression of auxin-specific genes likely involved in enhancing root hair growth in Arabidopsis (Niu et al. 2011). The expression of auxin-responsive genes responds to P deficiency by stimulating pericycle cells to produce lateral roots (Lopez-Bucio et al. 2005). P deficiency increased the expression of the auxin receptor TRANSPORT INHIBITOR RESPONSE 1 (TIR1), enhancing the sensitivity to auxins and increasing the emergence of lateral roots (Pérez-Torres et al. 2008). Therefore, CO\(_2\) may induce the expression of these plant genes and trigger molecular, physiological and cellular processes that modify root architecture for more P uptake (Gilroy and Jones 2000, Niu et al. 2013b).

K, along with N and P, is another important macronutrient. Mass flow of water in the soil facilitates diffusion and is important for root uptake of K (Fig. 4). Under elevated CO\(_2\), wheat plants acquired less K in dry soil, possibly due to a reduction in both plant water use and water flow in the soil, although over time, K acquisition may increase with greater root mass and higher soil moisture (Van Vuuren et al. 1997).

**Effect on root proteome, metabolome, exudation, rhizosphere microbes, and mycorrhizal production**

Roots of perennial creeping bentgrass exposed to 800 ppm CO\(_2\) showed up-regulation of proteins with roles in primary metabolism involving N metabolism (glutamine synthetase), energy metabolism (glyceraldehyde-3-phosphate dehydrogenase), and stress defense by antioxidant metabolism (ascorbate peroxidase, superoxide dismutase, and catalase) and protective chaperones that could mitigate drought stress, as well as down-regulated proteins with putative functions in metabolism, energy metabolism, cell growth and division, transcription, stress defense, and unclear classification (Burgess and Huang 2014). In Arabidopsis roots, elevated CO\(_2\) (800 ppm) downregulated genes related to amino acid conversion and reduced amino acid metabolism, but had no effect on root carbohydrate (fructose, sucrose, and starch) content (Jauregui et al. 2015). In tomato, elevated CO\(_2\) of 700 ppm changed the accumulation of 180 metabolites in the roots, some of which were species- and/or developmental stage-specific (Gray et al. 2020). In a recent review by Dong et al. (2021), elevated CO\(_2\) increased the efflux amount of root systems per plant by 31%, likely due to increased root biomass (29%). Elevated CO\(_2\) increased efflux rates of soluble sugars (47%), carboxylates (111%), and citrate (16%) but did not affect those of amino acids and malate (Dong et al. 2021).

The CO\(_2\)-induced root growth, particularly fine root production, correlates well with enhanced root
exudation of phenolic compounds, organic acids, amino acids, and other low molecular-weight organic compounds into the rhizosphere. These compounds have the effect of stimulating activities of soil microbes, including various bacteria and fungi. Microbial enzymes involved in decomposition of soil organic matter help to make minerals more available for root uptake, and mycorrhizae have an important role in plant nutrition (Fig. 5).

Elevated CO\textsubscript{2} often stimulates root exudation. The carboxylates in root exudate are thought to derive from the glycolytic pathway and the TCA cycle that occur in roots (Johnson et al. 1996, Massonneau et al. 2001). The TCA cycle accelerated under elevated CO\textsubscript{2}, accompanied by increased transcription of genes encoding enzymes of glycolysis and the TCA cycle (Ainsworth et al. 2006). Under elevated CO\textsubscript{2}, the activity of the principal phenolic biosynthetic enzyme in Senecio vulgaris increased (Hartley et al. 2000), and the concentration of phenolic compounds increased significantly in the rhizosphere of rice (Goufo et al. 2014). In response to elevated CO\textsubscript{2}, roots of short-leaf pine released 50\% more soluble C compounds after 34 weeks (Norby et al. 1987), Pinus sylvestris cultivated in nutrient solution released 1.2 to 1.6 times more low molecular-weight organic compounds and 2.5 times more amino acids after five weeks of growth (Johansson et al. 2009), and P. vulgaris exuded 1.77 times more malate after 18 days (Haase et al. 2007).

Root border cells are major contributors of root exudates in most crop plants. Under elevated CO\textsubscript{2}, the production of root border cells in pea seedlings increased (Zhao et al. 2000). Greater numbers of root border cells may lead to increased amounts of root exudates into the rhizosphere that stimulate soil microbial activities. In an agricultural ecosystem, soil bacterial respiratory activity was enhanced over time under free air CO\textsubscript{2} enrichment (FACE), most probably due to increasing C availability from rhizodepositions into the soil (Anderson et al. 2011). Mature loblolly pine trees grown under elevated CO\textsubscript{2} increased root exudation rates by 55\% during the primary growing season, and such increases in root-derived C were positively correlated with release of microbial enzymes involved in the breakdown of organic N in the rhizosphere, indicating that exudation stimulated microbial activity and accelerated the decomposition rate of soil organic matter and N uptake by plants (Drake et al. 2011, Phillips et al. 2011, 2012). In a grassland, after 10 years under elevated CO\textsubscript{2}, bacterial biomass was significantly increased, although fungal biomass was unaffected; microbial genes involved in labile C degradation, C and N fixation, and P utilization were upregulated (He et al. 2010). These changes may make the soil environment more favorable for plant growth and development in a high CO\textsubscript{2} environment.

Increased root exudation under elevated CO\textsubscript{2} may result in higher levels of mycorrhizal infection (Norby et al. 1987, O’Neill et al. 1987b). In a semiarid shrub-land ecosystem, fungal diversity increased in response to elevated CO\textsubscript{2}, with higher diversity found closer to plants, and the diversity was correlated with fine root production that may be involved in the release of root exudates (Lipson et al. 2014). Elevated CO\textsubscript{2} significantly increased the

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**Fig. 5.** Elevated CO\textsubscript{2} stimulates root exudation and mycorrhiza formation, which in turn affects mineral uptake.
intensity and magnitude of ectomycorrhizal symbiosis in *B. alleghaniensis* (Berntson et al. 1997). CO₂ enrichment increased mycorrhizal root tip production in deep soil but did not influence mycorrhizal production in shallow soil; however, survival of mycorrhizal tips was reduced in CO₂-enriched plots in deep soil, but was increased in shallower soil. Rhizomorph turnover was accelerated in shallow soil, but effects on survivorship in deep soil varied according to diameter (Pritchard et al. 2008). It is evident that many factors interact with CO₂ in affecting the formation of mycorrhizae.

**Conclusion and prospects**

Root form and function as affected by increasing atmospheric CO₂ is vitally important to the productivity of natural and agricultural ecosystems. Our understanding of root adaptation to an increasingly CO₂ enriched environment is progressing but still limited (Fig. 6). The performance of root system modified by CO₂ will affect plant’s ability to acquire water and minerals and cope with stress environments including drought, soil acidity, and toxicity of heavy metals such as Al, as well as the nutritional value of crops, and the composition of the natural ecosystem. Many important questions remain to be answered. We still need to investigate how elevated CO₂ affect root uptake efficiency of various nutrients by different species. As fine root production increases under elevated CO₂, its physiological capacity for nutrient and water uptake will likely change, and studies are needed to address this topic. We need to understand the implications of a larger root system with increased potential to acquire resources but at a declined acquisition efficiency. More work is needed to study how plants may change C allocation strategy for root growth, maintenance, nutrient uptake and exudation into the rhizosphere in response to CO₂, how CO₂-induced modifications to root system affect plant’s ability to cope with biotic and abiotic stresses, and how roots can be genetically engineered to store more C underground. It appears the genetic potentials for root system adaptation differ among species, and it is plausible that high CO₂ may lead to changes in global species composition and biodiversity in the future. As atmospheric CO₂ increases along with the associated climate change, the ability of the root system to adapt for better acquisition of water and nutrient is critical, and a greater understanding of the mechanisms involved in root architectural development under a complex web of interacting environmental conditions is needed for the breeding of improved crop varieties.

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**Fig. 6.** Elevated CO₂ stimulates shoot and root growth, increases root exudation and mycorrhiza formation, and affects water and nutrient uptake.
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Dr. Zhong Ma’s research interest is on various aspects of plant root biology, including gravitropism and root responses to nutrient deficiencies and heavy metal toxicities.