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The effects of rising atmospheric carbon dioxide on shoot–root nitrogen and water signaling

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INTRODUCTION

Terrestrial higher plants are composed of roots and shoots, distinct organs that conduct complementary functions in dissimilar environments. For example, roots are responsible for acquiring water and nutrients such as inorganic nitrogen from the soil, yet shoots consume the majority of these resources. The success of such a relationship depends on excellent root–shoot communications. Increased net photosynthesis and decreased shoot nitrogen and water use at elevated CO2 fundamentally alter these source–sink relations. Lower than predicted productivity gains at elevated CO2 under nitrogen or water stress may indicate shoot–root signaling lacks plasticity to respond to rising atmospheric CO2 concentrations. The following presents recent research results on shoot–root nitrogen and water signaling, emphasizing the influence that rising atmospheric carbon dioxide levels are having on these source–sink interactions.

Keywords: carbon dioxide, nitrogen, nitrate assimilation, water, drought, salinity, chilling

For example, the dependence of photosynthesis on nitrogenous compounds and the inevitability of water loss during CO2 uptake (Field and Mooney, 1986) makes communicating N and water availability from roots to shoots essential to maintain shoot productivity (Bloom et al., 1985). Too little investment in roots leads to nutrient- or water-limited growth, whereas too much investment compromises shoot growth, reproduction, and photosynthesis. Excellent communications between roots and shoots are paramount for meeting the immediate demands of distal organs to optimize resource supply from them, while avoiding superfluous distribution of resources.

Atmospheric CO2 concentrations have remained relatively low, between 180 and 300 μmol mol−1 since 1800 from the burning of fossil fuels (Joos et al., 1999). This concentration has increased from 280 to 400 μmol mol−1 by the end of the century (Joos et al., 1999). This CO2 enrichment will increase photosynthesis in C3 plants and will decrease shoot N and water requirements for photosynthesis. This frequently results in increased biomass and productivity in the short-term that is not sustained in the long-term (Dukes et al., 2005; Korner, 2006; Kimball et al., 2007). Only after long-term growth at elevated CO2 do limitations from N deficiencies, carbohydrate transport, and altered shoot/root allocation patterns become apparent. Unknown is whether the mechanisms of long distance communication between roots and shoots that evolved under low CO2 will have the plasticity to optimize coordination of root and shoot growth under long-term exposure to elevated CO2.

The goal of this review is to describe shoot–root signaling for N and water and to examine the observed and predicted responses of these signaling mechanisms to rising atmospheric CO2 concentrations. First, we discuss shoot–root N signaling, changing C and N demand, and the breakdown of N signaling at elevated CO2. Then, we explore the common and distinctive features of drought, salinity, chilling, and high vapor pressure deficit and the opposing effects of elevated CO2 on chemical and hydraulic water stress signaling. Finally, we consider the effects of non-optimal shoot–root coordination on plant growth at elevated CO2.

NITROGEN: COMMUNICATING ROOT AVAILABILITY AND SHOOT DEMAND

For most plants, growth and productivity is highly dependent upon N obtained from root absorption of soil inorganic and organic N. In most temperate soils, the primary form of N available to plants is nitrate (NO3−; Epstein and Bloom, 2005). Therefore, this review focuses on this form.

Many studies have shown that elevated CO2 stimulates photosynthesis, plant growth, and demand for mineral nutrients.
High variability in plant growth and photosynthetic responses to elevated CO$_2$ may result from vast experimental differences in soil NO$_3^-$ concentration. In natural systems, soil NO$_3^-$ is typically around 1 mg and in fertilized agricultural soils, NO$_3^-$ can be much higher, ranging from 10 to 70 mg (Reisenauer, 1966). The negative charge of NO$_3^-$ prevents it from binding to most soil particles, and this contributes to substantial spatial and temporal heterogeneity in soil NO$_3^-$ availability (Jackson and Caldwell, 1993). Plants have responded to soil NO$_3^-$ variability with adaptations to increase NO$_3^-$ uptake rapidly when it is available. In response to high soil NO$_3^-$, individual roots increase NO$_3^-$ uptake (Forde, 2002a) and alter root hydraulic properties to increase mass flow (Gorska et al., 2008). These adaptations allow a few roots in a high NO$_3^-$ region of the soil to provide all the N that the shoot requires (Laine et al., 1995).

**ROOT TO SHOOT N SIGNALING**

Root to shoot communication of soil N availability may be as simple as NO$_3^-$ delivery from roots to shoots in xylem sap (Takei et al., 2002). When soil NO$_3^-$ is low, root C/N ratios are high and roots have sufficient carbohydrate to assimilate most of the NO$_3^-$, that they absorb (Andrews et al., 1992) and thus deliver little NO$_3^-$ to shoots. As soil NO$_3^-$ increases, a greater proportion of absorbed NO$_3^-$ remains unassimilated in the root and is transported to the shoot (Andrews, 1986a; Agrawal et al., 1994). Xylem sap NO$_3^-$ directly links soil availability to the shoot and thereby serves as an ideal signal for such a temporally and spatially variable nutrient. High shoot NO$_3^-$ stimulates shoot growth and low shoot NO$_3^-$ inhibits shoot growth even when total shoot N is high (Walch-Liu et al., 2000; Rahayu et al., 2005). Species that predominantly transport N from root to shoot as amino acids instead of NO$_3^-$ may not use xylem sap NO$_3^-$ for root to shoot N signaling (Sprent and Thomas, 1984). Indeed, leaf growth is not always proportional to leaf NO$_3^-$ concentration (Rahayu et al., 2005), indicating the importance of other signals such as phytohormones for root to shoot communication of root N supply.

One class of phytohormones involved in root to shoot signaling is cytokinins. Stimulation of leaf growth by N supply is associated with increased concentrations of active forms of cytokinins (Rahayu et al., 2005). Root cytokinin production and xylem sap delivery of cytokinins to shoots increases with NO$_3^-$ fertilization (Takei et al., 2001; Forde, 2002a). Cytokinins stimulate leaf growth, increase shoot sink strength (Werner et al., 2008), and delay leaf senescence (Gan and Amasino, 1995), while they inhibit root elongation. Xylem sap transport of cytokinins increases expression of N responsive genes in leaves (Sakakibara et al., 1999; Takei et al., 2001; Kiba et al., 2011; Ruffell et al., 2011). All of these responses to cytokinins suggest that these phytohormones serve as root to shoot signals for root N availability.

**ELEVATED CO$_2$ EFFECTS ON ROOT TO SHOOT N SIGNALS**

CO$_2$ enrichment influences root to shoot N signaling through its effects on xylem sap flow rate, NO$_3^-$ assimilation, and root allocation. Root to shoot signals of N availability depend upon xylem sap flow for rapid signal delivery, and elevated CO$_2$ affects xylem flow rates. Elevated CO$_2$ decreases transpiration rates between 5 and 20% as stomata close in response to higher intercellular CO$_2$ concentration (Leakey et al., 2009). Stomatal closure slows water uptake and thereby xylem sap flow rate. Decreased transpiration may impede mass flow of NO$_3^-$ in the soil solution to roots (McDonald et al., 2002), but this decrease may not slow delivery of N to shoots (Schulze and Bloom, 1984) because N concentration in the xylem sap increases as xylem sap flow decreases, maintaining N delivery rates (Shaner and Boyer, 1975; Schulze and Bloom, 1984). Increasing xylem loading of N in roots does not require substantial energy in that xylem solute N concentrations are relatively low. Xylem concentrations of cytokinins are in the nanomolar range (Fos et al., 2007), and so are even less likely to be affected by xylem sap flow rates.

Elevated CO$_2$ may disrupt root to shoot N signaling through shifting the location of NO$_3^-$ assimilation. Greater rates of photosynthesis at elevated CO$_2$ increase carbohydrate flux to roots (Grimmer and Komor, 1999). In the root, higher carbohydrates increase NO$_3^-$ assimilation (Matt et al., 2003), growth, and local demand for N (Kircher and Schopfer, 2012). Consequently, the root transports less NO$_3^-$ to the shoot, and xylem sap NO$_3^-$ becomes less effective as a signal of root N availability.

Plant allocation of carbohydrate to roots varies greatly with CO$_2$ enrichment (Rogers et al., 1996). For species in which carbohydrate flux to roots is insensitive to CO$_2$, the relationship among root NO$_3^-$ assimilation, root N utilization, and xylem sap NO$_3^-$ transport could indicate the potential for improving root to shoot N signaling at elevated CO$_2$. For species in which CO$_2$ enrichment increases carbohydrate flux, elevated CO$_2$ may disrupt cytokinin signaling. A low baseline level of root cytokinin production at low root available NO$_3^-$ (Samuelson and Larson, 1993) may result in greater root xylem cytokinin loading when root allocation is high under long-term growth at elevated CO$_2$ (Yong et al., 2000). High rates of cytokinin delivery to shoots could induce shoot growth in excess of what can be supported by root N supply. This could partially explain the decline in leaf N after prolonged exposure to elevated CO$_2$ (Orn et al., 2001). Additional study of xylem sap and leaf cytokinins at elevated CO$_2$ are necessary to determine if this disruption in cytokinin signaling is responsible for declining leaf N content.

**SHOOT TO ROOT N SIGNALING**

When soil NO$_3^-$ is high, a few roots – 3.5% of the root system in spring wheat (Robinson et al., 1991) and 12% in lettuce (Burns, 1991) – can supply leaves with all of their N. When leaf N becomes limiting, plants may enhance root uptake by increasing (1) root growth, (2) root transporters to absorb soil N, and (3) root exudation to stimulate soil microbe activity that accelerates mineralization (Hawkes et al., 2003). All of these N acquisition strategies expend carbohydrate exported from shoots, and coordination of these processes is essential for optimal plant growth. Signals that stimulate root growth when leaf N is low or that repress root growth when leaf N is high balance root N acquisition and shoot demand.

A significant portion of N transported to shoots is recycled to roots via phloem transport of amino acids (Forde and Clarkson, 1999). It has been hypothesized that this transport of amino acids from shoots to roots in phloem could allow for feedback inhibition...
of root growth and NO$_3^-$ assimilation (Marschner, 1986; Immundre and Touraine, 1994; Marschner et al., 1996). Although exogenously supplied amino acids can inhibit root growth and NO$_3^-$ uptake (Orel et al., 2002; Forde and Walch-Liu, 2009), composition and transport of amino acids in phloem often do not correlate with shoot N status or root NO$_3^-$ uptake (Forde, 2002a). In split root experiments, amino acids were preferentially transported to portions of root systems supplied with NO$_3^-$ rather than those deprived of exogenous N, and the roots receiving more amino acids had higher growth rates (Tillard et al., 1998). This supports that amino acids delivered via the phloem stimulate root growth rather than inhibit it (Marschner et al., 1996).

Auxins are primarily synthesized in shoots and inhibit shoot branching (Normanly et al., 1999; Liang et al., 2001). They are transported to roots through polar transport in the phloem (Baker, 2000) and promote proliferation of lateral roots. Phloem and root auxin concentrations decrease when plants are grown at high NO$_3^-$ (Caba et al., 2008; Tian et al., 2008) and increase in roots when N is limiting (Walch-Liu et al., 2006). Therefore, auxins are prime candidates for signals that communicate shoot NO$_3^-$ levels to roots (Forde, 2002b). Roots rely on photosynthesizing organs for carbohydrates, and thus, auxin-induced increases in root growth depend upon root carbohydrate supply (Reed et al., 1998; Bhalerao et al., 2002; Zhang et al., 2007).

The amount of carbohydrate transported in phloem sap from shoots to roots may also signal shoot N status, and this carbohydrate signaling mechanism appears to be independent of phloem transport of auxin (Bingham et al., 1998). At high leaf N, shoot growth acts as a sink for shoot produced carbohydrates and relatively little carbohydrate is transported to roots. If leaf N is low, shoot growth is limited and more carbohydrate is transported to roots (Brouwer, 1967; Brouwer and DeWit, 1969; Bloom et al., 2004). Turgor loss causes stomatal closure through integrative hydraulic signal of soil water potential that rapidly shuts off photosynthesis, shoot turgor, and shoot growth, plants under water stress rely on local root responses that increase water uptake as well as shoot responses that reduce water use.

During drought or salt stress, xylem tension acts as an integrative hydraulic signal of soil water potential that rapidly communicates soil water stress to leaves (Malone, 1993). Likewise, low root hydraulic conductance during root chilling results in rapidly increasing xylem tension and declining leaf turgor (Bloom et al., 2004). Turgor loss causes stomatal closure through either passive or active regulation (Tardieu and Davies, 1995) and inhibits leaf growth as leaf cell turgor declines below the threshold for cell wall expansion (Hisao and Acrevo, 1974). Smaller leaf area and stomatal closure resulting from decreased leaf turgor protect leaves from desiccation. During slowly developing soil drought, soil moisture content has substantial heterogeneity, but hydraulic signals are integrative; that is, xylem tension in leaves is affected by xylem tension in all connected roots. Roots in drier regions experience greater decreases in water potential before hydraulic signals are transmitted to leaves. Non-hydraulic

WATER STRESS SIGNALING
Photosynthesis in land plants results in the inevitable water loss during CO$_2$ uptake because both diffusion of CO$_2$ into leaves and water vapor out of leaves occur through stomata. Soil drought, salinity, and chilling can result in an inability of water transport from roots to match shoot water loss. To maintain leaf photosynthesis, shoot turgor, and shoot growth, plants under water stress rely on local root responses that increase water uptake as well as shoot responses that reduce water use.

ELEVATED CO$_2$ EFFECTS ON SHOOT TO ROOT N SIGNALING
Leaf N concentrations decline under prolonged growth at elevated CO$_2$ (Oren et al., 2011). Photosynthetic acclimation can account for some of this decrease (Long et al., 2004), but fertilization with NH$_4$NO$_3$ eliminates it (Crous et al., 2010; Liu et al., 2011), showing that increased N supply can compensate for the effects of elevated CO$_2$ through enhanced root N uptake and plant N assimilation. This suggests that elevated CO$_2$ interrupts shoot to root N signaling.

Amino acids in the phloem, potential signals of shoot N status, do not show a consistent response to elevated CO$_2$ (Docherty et al., 1997; Sicher, 2008). By contrast, leaf and root auxins increase under elevated CO$_2$ and stimulate root growth (Teng et al., 2006; Wang et al., 2009; Niu et al., 2011). Other processes, however, such as carbohydrate transport or shoot NO$_3^-$ assimilation, may limit the ability of increased root auxins to stimulate root N uptake.

Carbohydrate transport through the phloem is driven by a carbohydrate concentration gradient (van Bel, 2003). Higher rates of net photosynthesis under elevated CO$_2$ increase carbohydrate delivery to roots and can increase root respiration and root NO$_3^-$ assimilation (Bassirirad et al., 1996; Fonseca et al., 1997; Kruse et al., 2002). High carbohydrate delivery to roots of C$_3$ plants under long-term growth at elevated CO$_2$ can also increase root growth (Bernston and Baraz, 1996; Kimball et al., 2002) and root carbohydrate exudation (Bernston et al., 1997). Carbohydrate flow from shoots to roots, however, does not increase proportionally to photosynthesis at elevated CO$_2$. For example, elevated CO$_2$ increases photosynthesis in C$_3$ species, but carbohydrate export from the leaves may not increase proportional to this carbon fixation (Grozdinski et al., 1998). This probably derives from leaf carbohydrate production under elevated CO$_2$ exceeding phloem export capacity (Korner et al., 1999; Komor, 2000).

In most tropical and subtropical plants and in temperate plants at high soil NO$_3^-$, most NO$_3^-$ assimilation occurs in shoots because NO$_3^-$ photoassimilation in shoots is more energy efficient than respiratory-driven NO$_3^-$ and NO$_2^-$ reduction in roots (Andrews, 1986b). Elevated CO$_2$ inhibits shoot NO$_3^-$ assimilation in C$_3$ plants (Rachmilevitch et al., 2004; Bloom et al., 2010), necessitating a greater reliance on root NO$_3^-$ assimilation to maintain plant capacity for NO$_3^-$ assimilation. In tobacco, 3 weeks of CO$_2$ enrichment enhances root NO$_3^-$ assimilation and may compensate for decreasing shoot NO$_3^-$ assimilation when there is sufficient root carbohydrate (Kruse et al., 2002). A shift from shoot NO$_3^-$ assimilation to root NO$_3^-$ assimilation requires translocation of more carbohydrate to the roots to provide sufficient energy and carbon skeletons for these processes (Zheng, 2009). NH$_4^+$ fertilization decreases the limitations of phloem carbohydrate transport on plant N status because NH$_4^+$ assimilation requires less carbohydrate.

EASLON AND BLOOM SHOOT–ROOT NITROGEN AND WATER SIGNALING

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ABA and pH in xylem sap that also affect stomatal regulation (Bloom et al., 2002). For example, salts carried in the transpiration stream can also act as long distance root to shoot signals. Duration of root chilling tolerant species close stomata before declines in leaf water potential increases both root ABA production (Simonneau et al., 1998) and xylem sap transport of ABA from root to shoot (Zhang and Davies, 1989). ABA production also increases during chilling stress in the long-term (Melkonian et al., 2004), but the rapidity of stomatal closure during root chilling indicates that other, more rapidly produced root to shoot signals are involved in root chilling.

Abscisic acid-induced stomatal closure is not solely dependent on root ABA production. Shoot vascular tissue ABA production (Endo et al., 2008) and ABA uptake by leaf xylem also affect guard cell ABA concentration. Xylem sap pH increases with soil drought, salinity, and root chilling, slow leaf symplastic ABA uptake, and increases guard cell ABA concentration, thereby promoting stomatal closure (Vernieri et al., 2001; Wilkinson and Davies, 2002; Felle et al., 2005; Wilkinson et al., 2007).

Evidence is mounting for non-hydraulic signals other than ABA and pH in xylem sap that also affect stomatal regulation during water stress (Munns, 1992; Chen et al., 2002b; Hobberecht et al., 2002). For example, salts carried in the transpiration stream can also act as long distance root to shoot signals. Duration of root chilling tolerant species close stomata before declines in leaf water potential increases both root ABA production (Simonneau et al., 1998) and xylem sap transport of ABA from root to shoot (Zhang and Davies, 1989). ABA production also increases during chilling stress in the long-term (Melkonian et al., 2004), but the rapidity of stomatal closure during root chilling indicates that other, more rapidly produced root to shoot signals are involved in root chilling.

Shoot to root signaling is also important for responses to chilling and high vapor pressure deficit stresses that do not directly affect root water potential. During both of these stresses, transpiration exceeds the capacity for root water transport. High root ABA increases root hydraulic conductance and water flow during chilling or at high vapor pressure deficit to ameliorate shoot water deficit (Markhart, 1984; Kudoyanova et al., 2011). This increase in root ABA requires water stress signaling from shoots; for example, if leaf water potential is maintained during chilling, there is no increase in root ABA (Vernieri et al., 2001). Shoot to root communication of shoot water deficits may be communicated hydraulically or through phloem transport of ABA or other signals.

ELEVATED CO2 EFFECTS ON WATER STRESS SIGNALING

The primary effect of elevated CO2 on water stress signaling derives from stomatal closure in response to high intercellular CO2 and the resulting lower transpiration rates (Leakey et al., 2009). Lower transpiration rates under elevated CO2 may decrease both accumulation of ABA at sites of evaporation near guard cells (Zhang and Orlowski, 2001) and foliar ABA concentration in general (Teng et al., 2006). Moreover, stomatal closure in response to root ABA application and osmotic stress are greater at elevated CO2 (Leymarie et al., 1999) and may result from higher intercellular CO2. At ambient CO2, when stomata begin to close during water stress, low intercellular CO2 can partially reverse stomatal closure. At elevated CO2, intercellular CO2 remains high even after stomatal closure, and this can prevent reversal of stomatal closure.

Hydraulic signaling is also affected by lower transpiration rates at elevated CO2. Slower transpiration reduces leaf xylem tension and improves leaf water potential during drought (Xiao et al., 2005). This may mitigate midday declines in leaf water potential during early stages of drought that are necessary for shoot perception of water stress. Slower transpiration at elevated CO2 delays hydraulic signaling of declining root water potential, but does not delay non-hydraulic signaling. Non-hydraulic signals like ABA are still delivered to shoots at elevated CO2, decreasing shoot water use and further delaying hydraulic signaling of declining root water potential. Slower transpiration also minimizes development of leaf water deficit during chilling at elevated CO2 (Boese et al., 1997), which may inhibit root ABA production (Vernieri et al., 2001) that is important for root acclimation to chilling.

CONCLUSION

Leaf N concentration declines under prolonged growth at elevated CO2 (Oren et al., 2001) unless plants are heavily fertilized with NH4NO3 (Cousen et al., 2010; Liu et al., 2011). This suggests that mechanisms for long distance root–shoot communication of root N availability and shoot N status, which evolved under low CO2, may lack plasticity to maintain root–shoot coordination under elevated CO2. Leaf and root auxin concentrations increase in response to low leaf N under elevated CO2 which should increase root growth, root NO3 uptake, and root NO3 assimilation (Teng et al., 2006; Wang et al., 2009; Niu et al., 2011). However, root organic N supply to shoots may be limited by phloem carbohydrate transport from shoots to roots (Grozinski et al., 1998); although these effects may not affect growth until stored leaf N is depleted. The accumulation of non-structural carbohydrates in leaves at elevated CO2 that is often observed (Long et al., 2004) may result from an inability to transport carbohydrate out of leaves or to obtain enough N from roots for shoot growth. Photosynthetic acclimation, whereby carbon fixation per unit leaf area declines under prolonged exposure to elevated CO2, decreases leaf N requirements and increases leaf phloem export capacity. This may mitigate phloem carbohydrate export limitations and thus improve shoot–root N signaling.

The improvement in leaf water potential and water use efficiency resulting from higher intercellular CO2 concentration are predicted to benefit plant growth under elevated CO2, but productivity gains at elevated CO2 under water limitation are often lower than predicted (Nowak et al., 2004; Newingham et al., 2013). Slower transpiration impedes development of leaf water deficits important for shoot water stress perception as soil water potential declines. Plants generate ABA and other non-hydraulic signals of low root water potential, and these can decrease stomatal conductance and shoot growth before declines in leaf water potential.
Table 1 | Root-shoot N and water signal responses to elevated CO2.

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<thead>
<tr>
<th>Signal</th>
<th>Rule</th>
<th>Response to elevated CO2</th>
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<tbody>
<tr>
<td>NO3−</td>
<td>Root to shoot signal of root NO3− availability</td>
<td>Root NO3− assimilation, local root demand for N increase, and xylem transport of NO3− decreases</td>
</tr>
<tr>
<td>Cytokinin</td>
<td>Root to shoot signal of root NO3− availability</td>
<td>Cytokinin production and xylem transport increases even at low root available NO3−</td>
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<tr>
<td>Auxin</td>
<td>Shoot to root signal of leaf N availability</td>
<td>Auxin production and transport to roots increases in response to low leaf N</td>
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<tr>
<td>Carbohydrate</td>
<td>Shoot to root signal of leaf N availability</td>
<td>Increased carbohydrate delivery to roots, but delivery does not increase proportionally with leaf carbohydrate production</td>
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<tr>
<td>Xylem tension</td>
<td>Bidirectional signal of root or shoot water stress</td>
<td>Stomatal closure reduces leaf xylem tension delaying shoot perception of water stress</td>
</tr>
<tr>
<td>ABA</td>
<td>Bidirectional signal of root or shoot water stress</td>
<td>Transpirational accumulation of leaf and guard cell ABA decreases and stomatal sensitivity to ABA increases</td>
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potential occur. While stomatal closure from these non-hydraulic water stress signals has less negative impact on photosynthesis at elevated CO2 as compared to ambient CO2, these signals can still unnecessarily limit shoot growth (Leymarie et al., 1999). Greater stomatal sensitivity to osmotic and drought stress results in high water use efficiency and less negative leaf water potential, but more conservative shoot growth and lower potential productivity (Warren et al., 2011).

Shoot-root N and water signaling involves both resource and phytomolecule transport from source organs to distant sink organs to achieve a functional equilibrium between roots and shoots. Rising atmospheric CO2 concentrations will increase net photosynthesis, decrease water use, and may alter source–sink interactions beyond the capability of signaling mechanisms that evolved at the lower atmospheric CO2 concentrations, which have prevailed throughout recent history (Table 1). Critical assessment of limitations in shoot-root signaling at elevated CO2 and careful genetic manipulations of N and water signaling could enhance crop response to rising atmospheric CO2 and avoid declines in plant N.

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