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REVIEW

INTERACTIONS BETWEEN ABOVE AND BELOW GROUND PLANT STRUCTURES: MECHANISMS AND ECOSYSTEM SERVICES

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KEYWORDS

aerenchyma, carbon accumulation, hormones, phloem, xylem

HIGHLIGHTS

- Aboveground to belowground energy transfer.
- Importance of symplasmic nature of sieve tubes.
- Hydraulic, electrical and chemical energy transfer.
- Decreased soil organic C storage over 8000 years.

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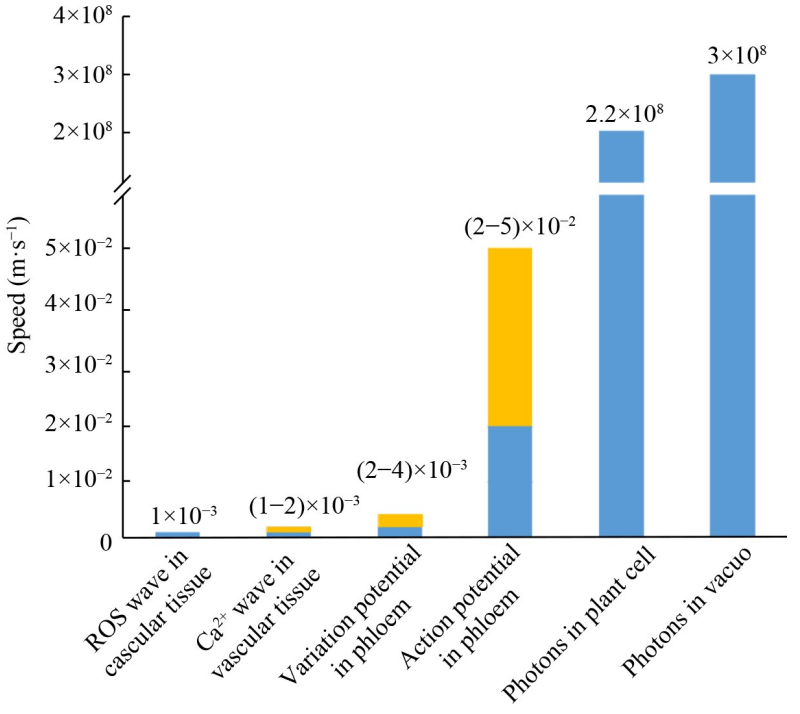
GRAPHICAL ABSTRACT



ABSTRACT

Interactions between above and below ground parts of plants can be considered under the (overlapping) categories of energy, material and information. Solar energy powers photosynthesis and transpiration by above ground structures, and drives most water uptake through roots and supplies energy as organic matter to below ground parts, including diazotrophic symbionts and mycorrhizas. Material transfer occurs as water and dissolved soil-derived elements transport up the xylem, and a small fraction of water moving up the xylem with dissolved organic carbon and other solutes down the phloem. The cytosolic nature of sieve tubes accounts for at least some of the cycling of K, Mg and P down the phloem. NO_3^- assimilation of above

ground parts requires organic N transport down phloem with, in some cases, organic anions related to shoot acid-base regulation. Long-distance information transfer is related development, biotic and abiotic damage, and above and below ground resource excess and limitation. Information transfer can involve hydraulic, electrical and chemical signaling, with their varying speeds of transmission and information content. Interaction of above and below ground plant parts is an important component of the ecosystem service of storing atmospheric CO_2 as organic C in soil, a process that has decreased since the origin of agriculture.

1 INTRODUCTION

Interactions between above and below ground structures involve energy, matter and information[1]. Occam's razor implies that the models initially considered should only involve energy and matter in determining allocation of resources between above and below ground structures. Such models can go some way to explaining the observed allocation of resources, for example, to water, carbon dioxide, light, and major nutrients acquisition, and the response to defoliation and root pruning[2–9]. However, such models are less successful when applied to minor nutrients, nutrient toxicity and temperature variations, and to reproduction and storage[4]. There are also differential above and below ground responses to competition[10]. Accordingly, as well as energy and matter in above and below ground interactions, it is also necessary to consider the flow of information.

2 ENERGY

Perhaps the most obvious means of transmitting energy from above ground to below ground structures is as photosynthate, i.e., organic carbon such as sucrose, sugar alcohols and/or oligosaccharides, moving down the phloem, thereby allowing catabolism below ground reducing NAD^+ or $NADP^+$ and phosphorylating ADP. Also, the driving force for Münch pressure flow from shoot to root is ATP-consuming proton ATPase, and sucrose-proton symporter in the companion cell-sieve tube element plasma membrane.

Energy is also transmitted via the tension generated by transpiratory water loss[11,12]. The latent heat of volatilization of water is supplied by photons absorbed by the photosynthetic structure and not stored in the products of CO_2, NO_3^-, SO_4^{2-} or O_2 photoreduction, fluoresced, or lost as longwave radiation. The liquid water that has been transpired is, in the steady-state, replaced by water moving up the xylem and, ultimately, from the root medium. The movement of water up the xylem when transpiration occurs, and in the absence of root pressure, is driven by water loss and transmitted by tension in the water column, dependent on the rigidity of the walls of xylem conduits that prevents collapse of the conduits, and the absence of pores in the cell wall large enough to allow air from intracellular spaces to enter the xylem under the observed pressure difference between the gas space and the water under tension. In the root system, the negative pressure in the xylem (less negative than in the shoot) drives water flux to the xylem from the soil solution. In addition to the water lost in transpiration, tension in the xylem conduit driven by transpiration supplies water used in cell expansion, as a substrate for photosynthesis, and water cycling down the phloem in Münch pressure flow[13,14].

Under conditions of limited or no transpiration, water can be moved up the xylem by root pressure, supporting cell expansion, guttation and water cycling down the phloem in Münch pressure flow especially in the case of nutrient transport to the shoot when nutrients are only supplied in the daily dark period[13]. The widely accepted mechanism of root pressure is the accumulation of solutes in the xylem conduits, decreasing the water potential in the xylem sap relative to that in the root medium. There is some evidence that a component of root pressure can, in some cases, be active water transport, i.e., energized movement of water against a water potential difference[15].

In addition to tension-driven flow in xylem, and pressure-driven flow in phloem and xylem (root pressure), there are other possibilities of energy transfer from above ground to below ground structures. One is transmission of light along plant axes from illuminated shoots to darkened roots, i.e., light piping, Light transmission along shoot and root axes has been

for woody plants[16] and for herbaceous plants[17]. Wavelengths usable in photosynthesis were attenuated by about an order of magnitude over a path of 10 mm, with rather less attenuation of 730 nm radiation absorbed by the far-red form of phytochrome[16,17]. However, energetic use of light in photosynthesis is less likely, granted attenuation of radiation by an order of magnitude per cm: by 30 mm the noon incident 40–700 nm photon flux density of ~2 $mmol \cdot m^{-2} \cdot s^{-1}$ is decreased to ~2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, less than the light compensation point for net photosynthesis in vascular plants. Below ground structures of terrestrial plants are not photosynthetic, but roots of dark-grown *Zea mays* seedlings contain protochlorophyllide that can be converted to chlorophyll by red light, although this was applied to the whole seedlings[18]. A further possibility of energy transfer between above and below ground structures is transmission of electrochemical potential differences, typically as proton motive force, along membranes between photochemical, redox reaction or ATPase-driven primary active transport at one location and the sites of proton motive force use in cotransport[19]. However, this transmission is unlikely to occur over more than a few 100 μm at most[19]. As with light, axial transmission of information by electrochemical potential differences by ions in action potentials or variation potentials, for example, along phloem, can occur over much long distances than transmission of proton motive force.

3 MATTER: XYLEM AND PHLOEM TRANSPORT OF WATER AND SOLUTES

The apoplasmic xylem conduits transport soil-derived water and solutes from the below ground to the above ground parts of vascular land plants; acquisition of nutrients from the above ground environment is minimal in most natural environments[20,21]. The driving force for most of the xylem flux is transpiratory water loss ultimately powered by solar radiation, directly through absorption by photosynthetic structures, and indirectly via wind. This transpiratory loss is much smaller in the dark in C_3 and C_4 plants even when stomata are open. Plants expressing Crassulacean acid metabolism have the highest stomatal conductance at night when dark CO_2 assimilation occurs. Transpiration-driven xylem flux involves negative pressure in the conduits. In contrast, root pressure, involving higher solute concentrations in the xylem conduits than in the root medium and, arguably, with active water transport, involves much slower solution movement in the xylem than in transpiratory water flux in the light, albeit with a higher solute concentration. The apoplasmic nature of the transport pathway imposes fewer constraints on the solute composition than in the symplasmic phloem, especially since the total solute concentration in the xylem is less than that in the phloem. Most of the water transported up the xylem is transpired; the rest is used in the hydration of growing cells, and less is used as the source of electrons in photosynthesis with production of O_2. The universal solute transport role of xylem is movement of solutes derived from the soil to transpirational termini with, for some solutes, transfer to the phloem for transport to growing above ground tissues with limited transpiratory water loss[22]. As will be seen below, some of these solutes, particularly NH_4^+, N_2 and sometimes NO_3^-, are subject to metabolic transformation in below ground structures. Water transport up the xylem occurs at up to 0.8 $m \cdot s^{-1}$ (Table 1) in *Triticum aestivum* trimmed so that only one seminal root remains[24].

The cytosolic phloem sap in phototrophically growing vascular moves solutions from sites carrying out net photosynthetic carbon gain over the diel cycle to sites that are net chemoorganotrophic over the diel cycle, for example, growing structures above ground and, from the viewpoint of this paper, the below ground structures. There is also phloem-xylem exchange of solutes[22]. The energization of flow from source to sink is, according to the widely accepted Münch pressure flow mechanism, the higher concentration of solutes at the source end of the pathway than at the sink end of the pathway[34–38]. The speed ($m \cdot s^{-1}$) of phloem transport is generally invariant with path length, despite limits on the maximum driving force (osmotic pressure difference), and the small observed difference in driving force with path length, between the source and sink end[35–37] (Table 1). Decreased resistance to flow with greater path length, for example, through larger sieve pore diameter, can apparently account for the relative constancy of sap of flow with path length[36]. If this does not always occur, it may be useful to reexamine the relay hypothesis whereby the length of sieve tubes is shorter than the path length, allowing additional energy input where solutes are unloaded at the end on one sieve tube and energized loading into the next sieve tube[37]. The relay hypothesis only applies to the apoplasmic loading pathway. Although the most commonly recognized function of the phloem is transport of photosynthate, most commonly as sucrose, other solutes are also transported. As is discussed below, the symplasmic nature of the pathway not only constrains the amounts of certain solutes (e.g., Ca^{2+} and H^+) that can be transported, but that there could be solutes necessarily present at relatively high concentrations (e.g., K^+ and HPO_4^{2-}) because they are needed for functioning of the pathway. Importantly, relatively few plants yield pure phloem sap when cut; a cautionary case is that of the Cucurbitaceae

Table 1 Speed of transmission of matter and signals in vascular plants

Process	Speed ($m \cdot s^{-1}$)	Reference
Photons in vacuo	3×10^8	[23]
Photons in plant cell	2.2×10^8	[23]
Water and solute flux root to shoot in xylem conduits	$\leqslant 0.8$	[24]
Water and solute flux shoot to root in phloem sieve tubes	$\leqslant 1.7 \times 10^{-3}$	[25]
	$\leqslant 0.33 \times 10^{-3}$	[26]
Basipetal polar auxin transport in parenchyma	$(0.33–5) \times 10^{-6}$	[27]
Solutes in cytoplasmic streaming	7×10^{-6}	[28]
Pressure wave in xylem	$\leqslant 1.5 \times 10^3$	[29]
Action potential in phloem	$(20–50) \times 10^{-3}$	[30,31]
Variation potential in phloem	$(1–4) \times 10^{-3}$	[32]
Ca^{2+} wave in vascular tissue	$(1–2) \times 10^{-3}$	[32]
ROS wave in vascular tissue	1×10^{-3}	[32,33]

where the copious exudate has only a small fraction of phloem sap[39]. Excised stylets of sap-feeding insects yields pure phloem sap, but in very small quantities[39]. Transport of solutions down the phloem occurs at up to 1.7 $mm \cdot s^{-1}$ (Table 1) in *T. aestivum* trimmed so that only one seminal root remains[25].

4 MATTER: CYCLING AND RECYCLING OF WATER AND NUTRIENTS BETWEEN ROOTS AND SHOOTS

Moving photosynthate and other solutes from the shoot to the roots in phloem requires movement of water as the solvent; in land plants this water must previously have been moved to the shoot in the xylem. This Münch counterflow accounts for up to 10% of the water moving up the xylem in the light, and up to 54% in the dark, in C_3 plants[13,14,40]. The maximal 10% value for the Münch counterflow in the light is compatible with the slightly higher maximum speed of water movement in the phloem (Table 1) in view of the larger area of cross-section of xylem lumens than of sieve tubes resulting in a greater mass flow per axis in xylem than phloem[14,17].

Cycling and recycling of elements between root and shoot plants has been reviewed[41]. For the normal functioning of vascular land plants, C and some of the O are obtained as CO_2 from the atmosphere whereas (in decreasing order of mol of each element) H, O, N, P, S, Mg, Ca, Cl, Fe, Cu, Mn, Mo, Zn and Ni are obtained from the pedosphere. In the simplest case the soil-derived elements are either retained in the root or transported to the shoot in proportion to their requirement for growth of the two structures whereas photosynthate derived from atmospheric CO_2 and H_2O from the pedosphere is retained in the shoot or transferred to the root in proportion to the requirement for growth and maintenance of the respective structures. However, when NO_3^- is the N source and less NO_3^- is reduced and assimilated in roots than is needed for root growth, some of the organic N from NO_3^- reduced and assimilated in the shoots is cycled to roots[42]. Also, the common S source SO_4^{2-} is predominantly reduced in the shoot, and organic S is cycled to the shoot[42]. It should be that noted that excised root systems of some plants are able to assimilate both NO_3^- and SO_4^{2-}[43], and that some intact plants assimilate essentially all NO_3^- in their roots[44,45].

As well as this cycling, there is also recycling of phloem-mobile ions, especially K^+, Mg^{2+} and inorganic orthophosphate, as well as Cl^-[41,46–51]. In this process the ions are taken up by roots and transferred to the shoot in the xylem in excess of shoot demand, with the excess transferred back to the roots in the phloem, with some of these ions reloaded into the xylem and transported again to the shoot[41]. Although various suggestions have been made for the role of this recycling, here the possibility is considered that the presence in, and movement along, sieve tubes of K^+, Mg^{2+} and inorganic phosphate is a necessary consequence of the cytosolic nature of sieve tube sap whereas Cl^- and K^+ are needed for transmission of action potentials along the sieve tube-companion cell complex.

5 MATTER: IMPLICATION FOR SOLUTE TRANSPORT OF THE CYTOSOLIC NATURE OF SIEVE TUBE SAP

The argument given here is that the cytosolic nature of the sieve tube sap means that they not only have constraints on the maximum concentration of some solutes, but also require a minimum concentration of some solutes for their functioning. All solutes in the sieve tube sap are swept along in the Münch pressure flow and consequently must be added at the source end and removed at the sink end, with exchange between the sieve tube sap and the cytosol of symplasmically connected companion cells. This statement must be modified for solutes as a whole with respect to solute exchange between sieve tube-companion cell complexes and xylem and other cells, but the concept of upper and lower limits of particular solutes is unchanged.

Dealing first with the upper limit of solute concentration in cytosol/sieve tube sap, two key solutes are H^+ and Ca^+[52]. The free H^+ concentration in cytosol and sieve tube sap are in the same range, between pH 7 and 8, i.e., 10–100 μmol·m^{-3}, and the OH^- concentration is 100–1000 μmol·m^{-3}[52]. The free Ca^{2+} concentration in the plant cytosol is 50–100 μmol·m^{-3}[53], whereas that in the sieve tube sap, using three independent methods, is almost three orders of magnitude higher, i.e., 13–63 mmol·m^{-3}[54].These higher sieve tube free Ca^{2+} concentrations may have implications the functioning of the symplasmically connected companion cells[54,55].

The capacity for transport of H^+, OH^- and Ca^{2+} along phloem depends not only on the concentration of the free ions but also of the mobile buffer capacity for the ions with the over the range of free ion concentrations known within the sieve tube sap[52]. There are no published values of buffer capacity for H^+/OH^- (mol bound H^+/OH^- m^{-3} (pH unit)$^{-1}$ or Ca^{2+} (mol bound Ca^{2+} m^{-3} (pCa unit)$^{-1}$). This means translating the free H^+/OH^- and free Ca^{2+} concentrations relative to sucrose concentration in sieve tube sap into the capacity for H^+/OH^- and Ca^{2+} transport requires assumptions as to the concentration of mobile buffers relative to that of the soluble carbohydrates providing the driving force for Münch pressure flow[52]. Assuming no pH or pCa gradient along sieve tubes, H^+/OH^- and Ca^{2+} would be loaded into the sieve tubes in parallel with the buffer compounds at the source end of the pathway, and likewise unloaded from sieve tubes at the sink end. Even considering buffering, the H^+/OH^- transport capacity of phloem is insufficient to transport to the roots the excess H^+ that would be produced from the assimilation of NH_4^+ into organic matter (~1.3 H^+ per N) using carbohydrate in the shoot following NH_4^+ and Cl^- from the soil to the shoot in the xylem[52,56,57]. The same is the case for the excess OH^- generated from the assimilation of NO_3^- into organic matter using carbohydrate in the shoot (~0.7 per N) following K^+ and NO_3^- transport from the soil to the shoot in the xylem[52,56,57]. These conclusions still stand when the much smaller (relative to the H^+ or OH^- production in combined inorganic N assimilation) OH^- production during SO_4^{2-} assimilation[56]. NH_4^+ assimilation is limited to the root of land plants, with the excess H^+ lost to the soil solution, with organic N needed for shoot growth transported in the xylem[56,58]. There is no biochemical means of disposing of the quantity of H^+ that would be generated from NH_4^+ assimilation in the shoot[59]. An alternative allowing mechanism allowing NH_4^+ assimilation into organic C in the shoot, i.e., transport of one NH_4^+ and 0.5 malate^{2-} plus ~0.3 K^+ and 0.15 malate^{2-} up the xylem following malic acid synthesis from sucrose and CO_2 in the root, with H^+ loss to the root medium in exchange for NH_4^+ and K^+[56]. This does not seem to be a major pathway, although there is more malate^{2-} in the xylem sap of *Ricinus* communis grown with NH_4^+ than when grown with NO_3^-[60]. Roots are the sole or predominant site of NO_3^- assimilation in some vascular land plants, with 0.7 OH^- excreted to the root medium for one NO_3^- and 0.3 K^+ entering As with root NH_4^+ assimilation, organic N used in shoot growth is transported up the xylem. In other plants shoots are the sole or predominant site of NO_3^- assimilation. One K^+ and one NO_3^- from soil is transported up the xylem, where NO_3^- assimilated into organic N producing ~0.7 OH^-[56,58,61–63]. This is neutralized by 0.35 malate^{2-} whereas the remaining 0.3 K^+ charge balances the net negative charge on organic compounds. The 0.7 K^+ and 0.35 malate^{2-} is sometimes accumulated in shoot cell vacuoles[56]. Alternatively, the 0.7 K^+ and 0.35 malate^{2-} is transported to the root in the phloem where 0.35 malate^{2-} is metabolized generating 0.7 OH^- which is excreted to the root medium in exchange for 0.7 NO_3^-[56,64]. This 0.7 NO_3^- moves up the xylem with the 0.7 K^+ that accompanied 0.35 malate^{2-} down then phloem, with a further 0.3 K^+ and 0.3 NO_3^- from the soil solution[56]. In the case of diazotrophic symbioses, the typical location of nodules (with the paraphyletic rhizobia or other proteobacterial symbionts such as *Burkholderia*) or rhizothamnia (*Frankia* symbionts) is below ground[56,65]. Here the measured H^+ excreted to the medium is greater[62,63]; than the predicted 0.3 H^+ per N predicted from NO_3^- assimilation[56], so additional organic anion synthesis is required, some of which could be accumulated as within the plant, secreted[62,63,66,67] suggested that diazotrophic nodule initiation and growth is, at least in part, regulated by phloem N.

The acid-base regulation of plants with diazotrophic stem nodules (*Aeschynomene*, *Discolobium*, *Neptunia* and *Sesbania*) is not known, although the nodules can form under water as well as in humid air[68].

The enucleate state of mature sieve tube elements in flowering plants potentially poses problems for their functioning in view of the need for proteins in sieve tubes for their functioning in the face of protein damage from reactive oxygen species (perhaps limited by hypoxia in phloem) and, in shoots, ultraviolet radiation[55,69,70]. However, subsequent results show that some proteins (less than 20 kDa) can pass symplasmically from nucleate companion cells to enucleate sieve tube elements[71], so it is possible that damaged proteins in sieve tube elements can be replaced. Although some mRNAs occur in sieve tube sap[72,73], they cannot be translated in mature sieve tubes since they lack ribosomes[73,74].

In addition to the macromolecules, small molecules are needed for the functioning of the sieve tube element-companion cell complex in maintenance of the long-distance transport pathway, loading and unloading of solutes via the apoplasmic pathway, and conversion of sucrose to raffinose and verbascose in one variant of symplasmic loading, and recouping of leaked solutes[75]. These small molecules include K^+ and Mg^{2+} as enzyme cofactors, and the ATP-ADP-AMP-inorganic phosphate system of energy transduction and transmission[76,77]. It is possible that most of the functions of these small molecules occur in the nucleate companion cells, for example, apoplasmic phloem loading, recouping of leaked, sucrose, with symplasmic transfer of the sucrose to the sieve tubes. However, it seems that there is no mechanism that prevents symplasmic transfer of the catalytically active small molecules from the companion cells to the sieve tubes, and their movement is consequently by mass flow along sieve tubes. In *Solanum lycopersicum* the sieve tube elements and companion cells have essentially identical inside-negative electrical potential differences across their plasma membranes, i.e., are electrically connected[78,79]. The phloem parenchyma cells have smaller electrical potential difference across the plasma membrane[78]. Similar results were found for the difference in electrical potential difference across the plasma membrane of sieve tube elements and phloem parenchyma for *R. communis* and *Salix alba*[80]. Electrical isolation of the sieve tube element-companion cell complex agrees with measurements of plasmodesmatal frequency distribution in the wells separating sieve tube elements and companion cells, sieve tube elements and phloem parenchyma cells, companion cells and phloem parenchyma cells, and between phloem parenchyma cells, and the spread of Lucifer yellow injected into individual cells[75,80]. Plants with apoplasmic phloem loading have more negative electrical potentials across the sieve tube/companion cell complex plasma membrane than is the case for phloem parenchyma; in plants with symplasmic loading the electrical potential across the plasma membranes of sieve tube/companion cell complex and that of phloem parenchyma are more similar[75].

The solutes in sieve tubes carrying solutes (and water) from shoot to root necessarily include photosynthate, usually sucrose, needed by the non-photosynthetic roots and proving much of the driving force for Münch pressure flow, and organic N and S when root-derived NO_3^- and SO_4^{2-} are reduced and assimilated entirely or predominantly in the shoots so that root growth requires organic N and S from the shoot[42]. However, in addition to these compounds there are inorganic solutes derived from the root medium, for example, K^+, Mg^{2+}, inorganic phosphate and Cl^-[51]. Table 2 lists the concentration of these for inorganic ions for sieve tube sap. The flux of these solutes down the phloem appears to be a futile cycle since the roots can obtain all the K^+, Mg^{2+}, inorganic phosphate and Cl^- they need for their growth as well as what is transported up the xylem supplying requirements for shoot growth[51]. In NO_3^--grown *R. communis* sieve tube sap the concentration of K^+ is 66.0 mol·m^{-3}, Mg^{2+} is 4.1 mol·m^{-3} and inorganic phosphate is 4.2 mol·m^{-3}[81]. Earlier work found 91.9 mol·m^{-3} K^+, 1.5 mol·m^{-3} Mg^{2+} and 4.4 mol·m^{-3} inorganic phosphate in NH_4^+-grown *R. communis*; for NO_3^-- grown *R. communis* the concentrations are 110 mol·m^{-3} K^+, 1.4 mol·m^{-3} Mg^{2+} and 9.1 mol·m^{-3} inorganic phosphate[60]. Again for NO_3^--grown *R. communis*, sieve tube sap concentrations of K^+ is 67.1 mol·m^{-3}, Mg^{2+} is 3.7 mol·m^{-3} and inorganic phosphate is 6.6 mol·m^{-3}[51].

In comparison, the concentration of K^+ in the cytoplasm of a range of glycophytic flowering plants using a diversity of methods is 58–126 mol·m^{-3}[83–86]. Some of the methods, for example, compartmental analysis using $^{42}K^+$, may include the K^+ in the other, non-vacuolar, compartments[83]. Using $^{42}K^+$ compartmental analysis to measure cytosolic (including non-vacuolar intracellular compartments) K^+ concentration in *Hordeum vulgare* roots, a range of 40–130 mol·m^{-3} was found; the lowest values correspond to high external NH_4^+ concentrations[87]. Using K^+-sensitive electrodes, the activity (~90% of concentration) of K^+ in the cytosol of *H. vulgare* root epidermal and cortical cells is 38–75 mol·m^{-3}[88]. The concentration of Mg^{2+} in the cytosol of flowering plants, determined by ^{31}P nuclear magnetic resonance estimation of Mg^{2+} binding phosphate compounds, ionophores, and the kinetics of the enzyme adenylate kinase, is 0.25–0.9 mol·m^{-3}[89–91], with rather higher free Mg^{2+} in mitochondria (1–3 mol·m^{-3}) and

chloroplasts (0.2–5 mol·m^{-3})[90]. The concentration of inorganic phosphate in cytosol of *Acer pseudoplatanus* and *A. thaliana* culture cells, measured using ^{31}P nuclear magnetic resonance is 0.055–0.080 mol·m^{-3}[92]. The most reliable estimate of cytosol Cl^- involves the use of Cl^--specific microelectrodes yielded concentration of 11 mol·m^{-3} Cl^- whereas compartmental analysis of tracer Cl^- efflux yielded values of 5.7–21 mol·m^{-3} Cl^-; all of these values are for non-salinized glycophytes[93,94].

Although K^+ concentrations in cytosol and phloem are similar, Mg^{2+} and inorganic phosphate concentration in the cytosol (given above) are much lower than those in phloem (Table 2). Although the values for the sieve tube sap and the cytosol involved different plant species and (except for K^+) different analytical methods, the differences between sieve tube sap concentration and cytosol concentrations for Mg^{2+} and, especially, inorganic phosphate suggest that there is a higher concentration of these two solutes in the sieve tube sap than would be the case if the sieve tube sap concentrations reflected that of cytosol. Although more measurements are needed, it is possible that the concentrations of inorganic phosphate and Mg^{2+} exceed in sieve tubes that needed for functioning of the symplasmically connected companion cells whereas the K^+ concentration in sieve tube sap can be accounted for as the concentration associated with cytosol, in this case companion cell plus sieve tube element. Accordingly, the futile cycling of K^+ down the phloem can be accounted for by the concentration needed for functioning of the sieve tube-companions cell symplasmic entity. In contrast, the greater concentration of inorganic phosphate and Mg^{2+}, and, perhaps, Cl^- in sieve tube sap than in cytosol suggests that the high concentration of these solutes in sieve tube sap cannot explain futile cycling in terms of the minimum concentrations needed for companion cell-sieve tube complex function. The role of phloem in transmission of action potentials requires the presence of K^+ and Cl^- in sieve tube sap[30,95].

Another approach to the question of futile cycling in phloem from shoot to root is to examine the composition of sieve tube sap from phloem supplying growing vegetative and reproductive shoot structures for comparison with the composition of sieve tube sap from phloem supplying roots. Such comparisons should be within a genotype and grown under the same conditions. If there is no constraint on the composition of phloem sap, the default assumption on composition would be that the solutes in sieve tube sap moving from shoot to roots move photosynthate as sugar, and, when all NO_3^- and SO_4^{2-} are assimilated in shoots, organic N and S. For the phloem sap moving from transpirational termini in photosynthetic tissue to growing vegetative and reproductive structures with 24-h photosynthesis less than respiration and limited transpiration, the phloem would move the complete suite of organic C and other nutrient elements needed for growth of the structures, including the organic N needed for respiration used for growth and maintenance. However, there seem to be no such data.

A further role of K^+, and also Cl^-, in the sieve tube sap is in action potentials transmitted along the plasma membrane of the sieve tube-companion cell complex[30,95–98], discussed in more detail below (section 7). After initial influx of Ca^{2+} from the phloem apoplasm, the Cl^- efflux causes the depolarization of the inside-negative electrical potential, and subsequent K^+ efflux causes repolarization[30,95]. More detailed discussion of this is given below (section 7). The sieve tube-companion cell complex lack the photosynthetic apparatus that is one of the main processes in oxygenic photosynthetic organisms that require catalytic Cl^-[93,94].

Cl^-, and Na^+, in the phloem sap have a limited role in removing NaCl that has been transported to above ground parts of glycophytes subject to salinization. Not more than 10% of the NaCl from salinized soil that reaches the shoot of glycophytes is returned to the root in the phloem[99–102]. Osmotic and hydraulic coupling of xylem and phloem are

Table 2 Concentrations (mol·m^{-3}) of K^+, Mg^{2+}, $H_2PO_4^-/HPO_4^{2-}$ and Cl^- in sieve tube sap of *Ricinus communis*

Growth conditions	K^+	Mg^{2+}	$H_2PO_4^-/HPO_4^{2-}$	Cl^-	Reference
External K^+ is 0.4 mol·m^{-3} with NO_3^- as N source	47.0	1.5	5.0	10.9	[81]
External K^+ is 1 mol·m^{-3} with NO_3^- as N source	66.0	4.1	4.2	11.4	[81]
NO_3^- as N source	68.1	3.9	7.6	8.9	[82]
NH_4^+ as N source	41.9	1.5	4.4	26.0	[60]
NO_3^- as N source	110.0	1.4	9.1	Not detected	[60]
NO_3^- as N source	67.1	3.7	6.6	12.0	[51]

important in salinization[103]. There are limited data on the sieve tube sap of halophytes[104].

6 MATTER: GAS PHASE MOVEMENT IN AERENCHYMA

Intercellular gas spaces are a key component of the functional anatomy of embryophytic land plants[105,106]. In the context of above-below ground interactions, an important role of intercellular gas spaces is in supplying O_2 to below ground structures in waterlogged soils and flooding[105–111]. In non-waterlogged soils the O_2 supply to below ground structures of plants is mainly by gas phase diffusion from the atmosphere through soil pores[105,107,112]. The diffusion coefficient of O_2 in water is only 10^{-4} of that in air, and diffusive O_2 supply from the atmosphere to below ground structures through waterlogged soils at a rate sufficient for aerobic functioning of these structures is not possible[105,107,110]. Plants that are tolerant of waterlogging have increased development of intercellular gas spaces in the form of aerenchyma, with individual longitudinally-running gas spaces of radii that are a significant fraction of the root radius[107–110]. There is a negligible role of the phloem in dissolved O_2 transport from above ground to below ground plant structures[69].

Waterlogging-tolerant plants also have barriers to lateral diffusion of O_2 from aerenchyma to waterlogged, hypoxic or anoxic, soils in the form of a suberized exodermis with lignified underlying sclerenchyma[108–110,113]. This barrier presumably also limits uptake of water and nutrient solutes[108], and may also restrict entry of toxins, such as high concentrations of Fe^{2+}, generated in anoxic soil[114]. In plants growing in non-waterlogged soil, such a barrier would limit diffusion of O_2 from the soil solution into root[105]. O_2 leakage, and water and nutrient uptake can occur through lateral roots growing in a less deoxygenated basal region of the root and also, perhaps, through rhizodermal passage cells[108,111].

In addition to diffusion, O_2 movement by convection (mass flow of gas) can occur when there are two or more above water structures linked by aerenchyma in a rhizome[108,115]. Convection depends on different structure and/or function among the two (or more) above water structures, including death of one of the structures, and can be driven by differences in water vapor pressure, by thermo-osmosis, or by the venturi effect[108,115]. Other mechanisms of mass flow can only increase the O_2 flux to below ground structures in flooded *Oryza sativa* by up to 6% relative to the diffusive O_2 flux[108,116,117].

As well as the role of aerenchyma in internal O_2 transport from the atmosphere (and photosynthesis in illuminated shoots) to below ground structures in waterlogging-tolerant plants, there is also a flux of CO_2 from respiration of below ground structures to above ground structures in aerenchyma. Root respiration in the presence of aerenchyma and the lateral barrier to diffusion of O_2 (and other gases) leads to a significant CO_2 flux to the shoot from root respiration[108,111]. When the CO_2 concentration in the waterlogged soil exceeds that in the root, entry of CO_2 (not HCO_3^-) by diffusion contributes to the CO_2 flux up aerenchyma[108,111] or in the xylem stream[111]. Although CO_2 flux to above ground structures of the waterlogging-tolerant *O. sativa* from waterlogged soil in the light amounts to 20% of measured photosynthesis, leakage through lenticels mean that a much smaller fraction of the below ground derived CO_2 is assimilated in shoot photosynthesis[111]. In emergent wetland plants CO_2 obtained through below ground parts accounts for less than 0.1% of shoot photosynthesis in the C_3 *Phragmites australis*[118] and less than 0.25% in the C_3 *Schoenoplectus lacuustris* (as *Scirpus lacustris*) and C_4 *Cyperus papyrus*[119]. However, up to 10% of photosynthesis by emergent leaves of the C_4 tidal marsh *Sporobolus alterniflorus* (as *Spartina alterniflora*) is supplied from below ground structures[120]. Further work is needed. The CO_2 concentration in the xylem sap is higher than that in atmosphere-equilibrium solutions even in plants growing in non-waterlogged soils, and leakage from above ground stem structures to the atmosphere is lower in trees than in herbs[121]. Aerenchyma is also a conduit for methane transfer to the atmosphere for plants in waterlogged soils[108,111].

7 INFORMATION TRANSFER MECHANISMS

Apart from the well-recognized biochemical mechanisms of transfer of information between above and below ground parts of plants as hormones, peptides and small RNAs in xylem and phloem sap, and polar auxin transport from shoot to root, there are also mechanisms involving action potentials, variation potentials, Ca^{2+} waves, reactive oxygen species waves, hydrostatic waves and, possibly, light piping within the plant from the illuminated shoot to below ground parts[29,30,95,122–133].

Hydraulic pressure waves in xylem water can in principle travel at the speed of sound in water, i.e., 1500 $m \cdot s^{-1}$[29] (Table 1). How these pressure waves in the apoplasm are perceived by target cells is not clear; mechanosensitive ion channels are a clear possibility, although knockouts of the relevant genes lacks

a clear phenotype[134]. Hydraulic transmission has been suggested as the mechanism by which, for example, sudden decreases in water potential of the root medium influences leaf growth in grasses[122,124]. The osmoticum polyethylene glycol added to the root medium of *Z. mays* decreases leaf growth within 2 min of the decrease in root medium water potential[122]. Experiments in which the decrease in xylem pressure resulting from the added osmoticant (polyethylene glycol or, more similar to nature, salt) was offset by pressurizing the root system in a pressure chamber showed that effect on leaf growth was prevented[124]. The results were not a result of artifacts such as injection of the aqueous medium into the root gas spaces, and showed that the decreased leaf growth was related to the decreased pressure in the xylem rather than a chemical messenger[124]. However, these experiments do not appear to exclude the possibility of a pressure difference-induced electrical signal transmitted along the phloem. Also, a sudden increase in root medium osmotic potential (decreased water potential) of the magnitude used in these experiments do not occur in the natural environment[122,124]. Whether acoustic signals, of the kind used by investigators to detect embolism of individual xylem conduits, are used for within-plant signaling deserves investigation[135].

Light travels at 2.2×10^8 m·s^{-1} in plant cells[23] (Table 1). Light piping through files of cells is known to occur in vascular land plants[16,17,136]. Light can also penetrate to a limited extent into soil[137]. For both plants and soil exposed to sunlight, far-red light penetrates further than red light, which penetrates further than blue light[137]. Correspondingly, the blue light absorbing photoreceptor, phototropin, is expressed in roots near the hypocotyl whereas the red to far-red absorbing phytochromes are expressed near the root apex[130,137]. Phytochrome in root tips was activated by light incident on shoots and transmitted along the root tip, with photomorphogenetic effects on growth and gravitropism; however, the length of the roots is not stated, so the distance in the root over which light sufficient to act on phytochrome is transmitted is not known[130]. A retinal binding protein is involved in the oscillatory mechanism (root clock) that regulates the origin of lateral roots in *A. thaliana*[138], but there is no evidence as to a role of light absorption by retinal such as occurs in phototaxis by some flagellate algae[139].

Other means of information transfer are the Ca^{2+} wave and the reactive oxygen species (ROS) wave[126–128,131,132,140]. The Ca^{2+} wave involves a two-pore Ca^{2+} channel in the plasma membrane, and also glutamate receptor-like proteins 3.3 and 3.6, and travels at about 0.4 mm·s^{-1}[127,128,141] (Table 1). The ROS wave involves increased activity of a NADPH oxidase generating ROS in the apoplasm, and travels at about 1.4 mm·s^{-1}[126,128,140] (Table 1). These waves may involve electrical transmission resulting from plasma membrane depolarization by apoplasmic ROS or by Ca^{2+}[126,131,142].

The Ca^{2+} wave and the ROS wave are transmitted faster than the mass flow in most measurements in the phloem (0.33 mm·s^{-1}[26,35]: but at a similar speed to the highest measured value of 1.7 mm·s^{-1}[25] (Table 1)). Also, they can move in either direction rather than just shoot to root as for mass flow in the phloem. The Ca^{2+} and ROS waves move much more rapidly than the 7.2 μm·s^{-1} speed of cytoplasmic streaming, in *A. thaliana*[28] (Table 1). Even when *A. thaliana* myosin XI-2 was made chimeric with the giant-celled alga, *Chara corallina*, myosin XI, giving streaming speeds in *C. corallina* up to 100 μm·s^{-1}, the streaming speed of *A. thaliana* is only increased to 16 μm·s^{-1}[28]. Finally, diffusion[143,144] of Ca^{2+} or ROS to activate, respectively, Ca^{2+} channels and NADPH oxidases, increasing the concentration of Ca^{2+} in the cytosol and of ROS in the apoplasm, in propagating, the wave by a relay mechanism, is far to too slow to account for the wave speeds.

Electrical transmission of information can occur as action or variation potentials along the phloem, involving depolarization of the inside-negative electrical potential difference by limited Ca^{2+} influx and greater Cl^- efflux, followed by repolarization K^+ efflux[30,95–98,123]. Table 2 shows that, at least in *R. communis*, the K^+ concentration is sieve tube sap ranges from 47 to 110 mol·m^{-3} whereas the Cl^- concentration is 8.9–26 mol·m^{-3} with the exception of the finding[60] for NO_3^--grown *R. communis* of no detectable Cl^-. Much work has been carried out on action potentials using giant intermodal cells of the Characeae; these are algal members of the Streptophyta, the clade to which flowering plants belong[144,145]. However, internally perfused internodal cells of *Chara* and showed that normal action potentials were found with cytosol Cl^- concentrations from 0.01 to 29 mol·m^{-3} Cl^-[146]. If a cytosol Cl^- concentration as low as 0.01 mol·m^{-3} allows action potentials in *R. communis*, then the absence of detectable Cl^- in the sieve tube sap NO_3^- grown *R. communis*[60] may have been compatible with the occurrence of 0.01 mol·m^{-3} Cl^- in the sieve tube sap. More work is needed.

The speed of transmission of action potentials in phloem is 20–50 mm·s^{-1}[30,98] (Table 1) whereas angiosperm tree and herb phloem mass flow is at 0.17 mm·s^{-1}[26,35] and up to 1.7 mm·s^{-1}[25] (Table 1). Variation potentials travel at 1–4 mm·s^{-1}[32] (Table 1). Although the direction of mass flow in phloem is determined by source-sink relations, action

potentials can be transmitted in either direction. However, action potentials carry little information relative to the multitude of informational molecules transported by mass flow in phloem and, to a lesser extent, in xylem.

Importantly, Fichman and Littler[132] show that glutamate receptor-like proteins 3.3 and 3.6 integrate electrical, Ca^{2+}, reactive oxygen species and hydraulic systemic signals. Also, reactive oxygen species-enhanced signaling involves a plasmodesma-located protein, providing an additional link between systemic signaling and symplasmic transport[147].

Transport of low molecular mass hormones, peptides and miRNA can occur in xylem and/or phloem[132,148–150]; there is also the possibility that the increase in root xylem sap pH in response to drought also has a signaling function[151]. Auxin (indoleacetic acid) is subject to shoot-root (basipetal) polar transport in parenchyma at 0.33–5 $\mu m \cdot s^{-1}$[27] (Table 1). The polar transport involves $indoleacetate^{-}$:H^{+} cotransport into cells at the source end, and $indoleacetate^{-}$ efflux through PIN channels driven by the inside-negative electrical potential difference across the plamalemma generated by H^{+} efflux using a H^{+} P-ATPase. The higher speeds may require cytoplasmic streaming, though inhibition by streaming inhibitors such as cytochalasin is complicated by effects on the polar distribution of transport proteins in the upstream and downstream ends of the cell[152].

Long-distance transport of hormones in xylem and/or phloem has been reported for abscisic acid (ABA), cytokinin, strigolactone, and the precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) of the gaseous ethylene[149]. Although the ABA transported to shoots in the xylem in response to drought has been reported as being synthesized in roots, movement of ABA up the xylem to stomata would give slow stomatal response to changes in the root medium[153], and later results show that ABA can be synthesized in shoot vascular tissue in response to drought, and ABA can be synthesized in guard cells in response to low relative humidity[149]. Different cytokinins can transported acropetally in the xylem and basipetally in the phloem[149]. ACC can also move in both xylem and phloem[149].

Variation in xylem sap pH in response to below ground conditions might transmit information to the shoot, either directly or by influencing the uptake in the shoot of hormones, especial those that are weak acids and bases such as ABA and cytokinins[151,154–156]. Drought increases the xylem sap pH which would, if reflected in the leaf apoplasm, increase stomatal aperture, but, via effects on ABA distribution between apoplasm and symplasm in the leaf leading to a higher apoplasmic ABA concentration, and thereby causes stomatal closure[155]. Increased xylem pH is apparently also involved in decreased stomatal aperture when plants are grown with conspecifics and competition for water and nitrogen are eliminated[157].

Finally, innovative use in information transfer has been made of the flowering plant holoparasite, *Cuscuta campestris*, that parasitizes a range of euphyllophytes through haustoria on above ground parts[97,158]. For a *C. campestris* individual parasitizing two hosts of different species it was) shown that systemic wound signals could be transmitted between dicot and monocot hosts, and between dicot and fern hosts, consistent with similar signals being used throughout euphyllophytes (ferns and seed plants)[158]. A systemic signal of N-deprivation in *Glycine max* was transmitted via *C. campestris* to N-replete *Cucumis sativa* where NO_3^- uptake was stimulated, again showing commonality of the N-deprivation signal of the two hosts[97].

8 ECOSYSTEM SERVICES

Ecosystem services covers a wide range of ecosystem effects that influence human beings[159]. Here agroecosystems are emphasized, where obvious benefits to humanity are the food, fiber and fuel that have obvious economic value, and clearly involve above and below ground interactions irrespective of whether the harvested crop is above ground, such as *T. aestivum* grain, or below ground, such as *Solanum tuberosum* tubers. However, the other outcomes of agroecosystems that influence humanity need be considered.

Organic C from photosynthesis transferred to below ground structures, and subsequently respired to CO_2 can contribute to CO_2 sequestration as inorganic carbon in soil via recalcitrant plant components, and as HCO_3^- by respired CO_2 whose diffusive loss to the atmosphere is limited, chemically weathering Ca and Mg silicates and carbonates in Eq. (1) (calcite), Eq. (2) (forsterite) and Eq. (3) (anorthite)[160].

$$CaCO_3 + CO_2 + H_2O \rightarrow Ca^{2+} + 2HCO_3^- \quad (1)$$

$$Mg_2SiO_4 + 4CO_2 + 4H_2O \rightarrow 2Mg^{2+} + 4HCO_3 + H_4SiO_4 \quad (2)$$

$$CaAl_2Si_2O_8 + 2CO_2 + 3H_2O \rightarrow Ca^{2+} + 2HCO_3^- + Al_2Si_2O_5(OH)_4 \quad (3)$$

Such weathering was greatly enhanced with the origin of rooted embryophytic plants over 400 million years ago[161], and is a major source of HCO_3^- to the ocean. However, this oceanic HCO_3^- is not a very long-term CO_2 sink since biological

$CaCO_3$ precipitation occurs with release of CO_2 (Eq. (4)), the reverse of Eq. (1):

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O \quad (4)$$

However, enhanced HCO_3^- production is soil water by addition of silicate minerals to soils is a plausible role of below ground metabolism of plants in CO_2 sequestration in the ocean, unless the rate of calcification, largely by coccolithophores and foraminifera, in the ocean increases to an extent that compensates for HCO_3^- input[160,162,163].

Storage of CO_2 as organic C in soil can occur as recalcitrant polymers from dead plants such as lignin and, from above ground parts, cutin. Polymeric carbohydrates (pectins, arabinogalactans, xyloglucans from plant roots, and the glomalin thought to be produced by root-symbiotic arbuscular mycorrhizal fungi[164] are important agents of soil aggregation[165]. Production of combined N by symbiotic and non-symbiotic diazotrophy, and mobilization and movement through soil of combined N, P and Fe, in the soil, all depend on organic C from shoot photosynthesis[166,167]. All of these effects are larger per m^2 soil area with vascular plant vegetation, with their greater volumetric penetration into the soil, than with cyanobacteria, algae and bryophytes[161,165,168]. To the extent that crops have a higher productivity than the vegetation that would otherwise occur on that area there is the potential for enhanced soil ecosystem services; however, fertilizer input can alter the ecosystem processes. It is not clear what effect the soil aggregates ultimately produced by plant organic C have on water flow in soil and allocation of precipitation into liquid water transfer to ground water, streams and the ocean, to evaporation, and to transpiration, with their effects on humanity through the supply of potable water and on local weather[169,170].

One important ecosystem service related to organic C transport from shoots to below ground parts is accumulation of organic C in soil[19,171–175]. The decrease in atmospheric CO_2 and CH_4 in the pre-agricultural Holocene was reversed about 8000 years ago for CO_2, paralleling the widespread occurrence of agriculture and associated deforestation, and for CH_4 about 5000 years ago with introduction of irrigation rice production and domesticated[176]. Agriculture, and wetland degradation, have been causally related to these reversals of decreases in atmospheric greenhouse gas[171]. The decrease in organic C in soil and above ground biomass over the past 8000 years is 38 Pmol C[171]. Agriculture has resulted in a global reduction of 9.7 Pmol organic C in the top 2 m of global soils, i.e., an ecosystem disservice[172]. The global reduction of soil organic C from a meta-analysis of peer-reviewed literature yielded a value of 11.3 Pmol C[173]. Methods have been suggested by which this loss of soil organic C in agricultural land could be reversed[173,174]; however, the warming resulting from additional CO_2 and CH_4 from agriculture has exerted a positive feedback by decreased CO_2 solubility in a warmer ocean[175].

The discussion of the impact of agriculture on sequestration in soil of organic C produced from atmospheric CO_2 above shows that soil organic C is significantly below what would have occurred from continuation of the pre-agricultural vegetation.

9 CONCLUSIONS

Some aspects of the balance of above and below ground growth of vascular land plants can be rationalized by the models considering the rate of acquisition of resources supplied from the aerial environment (light and CO_2) and the soil (H_2O, essential elements other than C and some O). However, such models do not account, for example, for storage in reproductive structures in shoots and below ground storage structures, and information flow as well as resource flow between above and below ground plant parts is needed. There is wide acceptance of the cohesion-tension hypothesis for the mechanism of transpiratory flow of water and dissolved solutes derived from the soil from roots to shoot in the xylem, and of the Münch pressure flow of transport of dissolved carbohydrates and other solute from shoot to below ground structures in the phloem. However, some aspects need further research, such as the possibility of active water transport in contributing to root pressure under low transpiration conditions. The cytosolic nature of the contents of sieve tube elements and symplasmically connected companion cells imposes constraints on the transport from shoots to roots of buffered H^+/OH^- generated by metabolism in the shoot with implications for the location of the assimilation of inorganic N. A further, less investigated, constraint on phloem transport is that there is a minimum concentration of cytosolic ions such as K^+, Mg^{2+} and $H_2PO_4^-/HPO_4^{2-}$ as well as ATP and ADP to operate and maintain the transport system, and mass flow of solution means that these solutes must originate in the shoot and be delivered to the roots. This explains, in part, the futile cycling of root-derived nutrients returned from the shoot to the root, and constraints on how much NaCl delivered to the shoot in the xylem from saline soils can be returned to the roots. Aerenchyma, and barriers to radial O_2 loss, are important in supplying O_2 to below ground structures in waterlogged soil.

Above-below ground interactions also involve information

transfer used for integration of growth of plant parts and, in the short-term, communication of abiotic and biotic damage and environmental changes. As well as the obvious transfer of phytohormones in xylem and phloem, faster communication can occur through pressure waves and electrical (variation and action potentials) signals, the latter apparently including Ca^{2+} waves and ROS waves.

Agriculture has decreased the ecosystem benefit of organic C accumulation in soil and consequently decreased CO_2 removal from the atmosphere, i.e, an ecosystem disservice The incorporation of atmospheric CO_2 into soil, and eventually into the ocean, can be stimulated by spreading particulate silicate minerals on agricultural soils. This accumulation of atmospheric C as dissolved inorganic C is an ecosystem service.

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REFERENCES

1. Weigelt A, Mommer L, Andraczek K, Iversen C M, Bergmann J, Bruelheide H, Fan Y, Freschet G T, Guerrero-Ramírez N R, Kattge J, Kuyper T W, Laughlin D C, Meier I C, Plas F, Poorter H, Roumet C, Ruijven J, Sabatini F M, Semchenko M, Sweeney C J, Valverde-Barrantes O J, York L M, McCormack M L. An integrated framework of plant form and function: the belowground perspective. *New Phytologist*, 2021, **232**(1): 42–59
2. Thornley J H M. A balanced quantitative model for root: shoot ratios in vegetative plants. *Annals of Botany*, 1972, **36**(2): 431–441
3. de Wit C T, de Vries F W T P. Crop growth models without hormones. *Netherlands Journal of Agricultural Science*, 1983, **31**(4): 313–323
4. Wilson J B. A review of evidence on the control of shoot:root ratio, in relation to models. *Annals of Botany*, 1988, **61**(4): 433–449
5. Thornley J H M, Parsons A J. Allocation of new growth between shoot, root and mycorrhiza in relation to carbon, nitrogen and phosphate supply: teleonomy with maximum growth rate. *Journal of Theoretical Biology*, 2014, **342**: 1–14
6. Feller C, Favre P, Janka A, Zeeman S C, Gabriel J P, Reinhardt D. Mathematical modelling of the dynamics of shoot-root interactions and reserve partitioning in plant growth. *PLoS One*, 2015, **10**(7): e0127905
7. Nagel K A, Schurr U, Walter A. Dynamics of root growth stimulation in *Nicotiana tabacum* in increasing light intensity. *Plant, Cell & Environment*, 2006, **29**(10): 1936–1945
8. Walter A, Nagel K A. Root growth reacts rapidly and more pronounced than shoot growth towards increasing light intensity in tobacco seedlings. *Plant Signaling & Behavior*, 2006, **1**(5): 225–226
9. Tognetti J A, Pontis H G, Martínez-Noël G M A. Sucrose signaling in plants: a world yet to be explored. *Plant Signaling & Behavior*, 2013, **8**(3): e23316
10. Murphy G P, Dudley S P. Above- and below-ground competition cues elicit independent responses. *Journal of Ecology*, 2007, **95**(2): 261–272
11. Steudle E. The cohesion-tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology*, 2001, **52**(1): 847–875
12. Jones H G. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology. 3rd ed. Cambridge: *Cambridge University Press*, 2014
13. Tanner W, Beevers H. Transpiration, a prerequisite for long-distance transport of minerals in plants. *Proceedings of the National Academy of Sciences of the United States of America*, 2001, **98**(16): 9443–9447
14. Hölttä T, Vesala T, Sevanto S, Perämäki M, Nikinmaa E. Modelling xylem and phloem water flows in trees according to cohesion tension and Münch hypothesis. *Trees*, 2006, **20**(1): 67–78
15. Wegner L H. Root pressure and beyond: energetically uphill water transport into xylem vessels. *Journal of Experimental Botany*, 2014, **65**(2): 381–393
16. Sun Q, Yoda K, Suzuki M, Suzuki H. Vascular tissue in the stem and roots of woody plants can conduct light. *Journal of Experimental Botany*, 2003, **54**(387): 1627–1635
17. Sun Q, Yoda K, Suzuki H. Internal axial light conduction in the stems and roots of herbaceous plants. *Journal of*

Experimental Botany, 2005, **56**(409): 191–203
18. Björn L O. The state of protochlorophyll and chlorophyll in corn roots. *Physiologia Plantarum*, 1976, **37**(3): 183–184
19. Raven J A. Determinants, and implications, of the shape and size of thylakoids and cristae. *Journal of Plant Physiology*, 2021, **257**: 153342
20. Peuke A D, Jeschke W D, Dietz K F, Schreiber L, Hartung W. Foliar application of nitrate of ammonium as sole nitrogen supply in *Ricinus communis*-I. Carbon and nitrogen uptake and inflows. *New Phytologist*, 1998, **138**(4): 675–687
21. Otto R, Marques J P R, Pereira de Carvalho H W. Strategies for probing absorption and translocation of foliar-applied nutrients. *Journal of Experimental Botany*, 2021, **72**(13): 4600–4603
22. Aubry E, Dinant S, Vilaine F, Bellini C, Le Hir R. Lateral transport of organic and inorganic solutes. *Plants*, 2019, **8**(1): 20
23. Slavík B. The relation of the refractive index of plant cell sap to its osmotic pressure. *Biologia Plantarum*, 1959, **1**(1): 48–53
24. Passioura J B. The effect of root geometry on the yield of wheat growing on stored water. *Australian Journal of Agricultural Research*, 1972, **23**(5): 745–752
25. Passioura J B, Ashford A E. Rapid translocation in the phloem of wheat roots. *Australian Journal of Plant Physiology*, 1974, **1**(4): 521–527
26. Liesche J, Windt C, Bohr T, Schulz A, Jensen K H. Slower phloem transport in gymnosperm trees can be attributed to higher sieve element resistance. *Tree Physiology*, 2015, **35**(4): 376–386
27. Kramer E M, Rutschow H L, Mabie S S. AuxV: a database of auxin transport velocities. *Trends in Plant Science*, 2011, **16**(9): 461–463
28. Tominaga M, Kimura A, Yokota E, Haraguchi T, Shimmen T, Yamamoto K, Nakano A, Ito K. Cytoplasmic streaming velocity as a plant size determinant. *Developmental Cell*, 2013, **27**(3): 345–352
29. Malone M. Hydraulic signals. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 1993, **341**(1295): 33–39
30. Fromm J, Bauer T. Action potentials in maize sieve tubes change phloem translocation. *Journal of Experimental Botany*, 1994, **45**(4): 463–469
31. Fromm J, Eschrich W. Electric signals released from roots of willow (*Salix viminalis* L.) change transpiration and photosynthesis. *Journal of Plant Physiology*, 1993, **141**(6): 673–680
32. Johns S, Hagihara T, Toyota M, Gilroy S. The fast and the furious: rapid long-range signaling in plants. *Plant Physiology*, 2021, **185**(3): 694–706
33. Fichman Y, Miller G, Mittler R. Whole-plant live imaging of reactive oxygen species. *Molecular Plant*, 2019, **12**(9): 1203–1210
34. van Bel A J E. The phloem, a miracle of ingenuity. *Plant, Cell & Environment*, 2003, **26**(1): 125–149
35. De Schepper V, De Swaef T, Bauweraerts I, Steppe K. Phloem transport: a review of mechanisms and controls. *Journal of Experimental Botany*, 2013, **64**(16): 4839–4850
36. Knoblauch M, Knoblauch J, Mullendore D L, Savage J A, Babst B A, Beecher S D, Dodgen A C, Jensen K H, Holbrook N M. Testing the Münch hypothesis of long distance phloem transport in plants. *eLife*, 2016, **5**: e15341
37. Raven J A. Evolution and palaeophysiology of the vascular system and other means of long-distance transport. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 2018, **373**(1739): 20160497
38. Gersony J T, McClelland A, Holbrook N M. Raman spectroscopy reveals high phloem sugar content in leaves of canopy red oak trees. *New Phytologist*, 2021, **232**(1): 418–424
39. Zhang C, Yu X, Ayre B G, Turgeon R. The origin and composition of cucurbit "phloem" exudate. *Plant Physiology*, 2012, **158**(4): 1873–1882
40. Windt C W, Vergeldt F J, de Jager P A, van As H. MRI of long-distance water transport: a comparison of the phloem and xylem flow characteristics and dynamics in poplar, castor bean, tomato and tobacco. *Plant, Cell & Environment*, 2006, **29**(9): 1715–1729
41. Marschner H, Kirkby E A, Cakmak I. Effect of mineral nutritional status on shoot-root partitioning of photoassimilates and cycling of mineral nutrients. *Journal of Experimental Botany*, 1996, **47**(Special Issue): 1255–1263
42. Herschbach C, Gessler A, Rennenberg H. Long-distance transport and plant internal cycling of N- and S-compounds. In: Lüttge U, Beyschlag W, Büdel B, Francis D, eds. Progress in Botany 73. Berlin, Heidelberg: *Springer*, 2012, 161–188
43. Sheat D E G, Fletcher B H, Street H E. Studies on the growth of excised roots. *New Phytologist*, 1959, **58**(2): 128–141
44. Andrews M, Morton J D, Lieffering M, Bisset L. The partitioning of nitrate assimilation between root and shoot of a range of temperate cereals and pasture grasses. *Annals of Botany*, 1992, **70**(3): 271–276
45. Andrews M, Condron L M, Kemp P D, Topping J F, Lindsey K, Hodge S, Raven J A. Will rising atmospheric CO_2 concentration inhibit nitrate assimilation in shoots but enhance it in roots of C_3 plants. *Physiologia Plantarum*, 2020, **170**(1): 40–45
46. Dieter Jeschke W, Atkins C A, Pate J S. Ion circulation via phloem and xylem between root and shoot of nodulated white lupin. *Journal of Plant Physiology*, 1985, **117**(4): 319–330
47. Jeschke W D, Pate J S. Modelling of the uptake, flow and utilization of C, N and H_2O within whole plants of *Ricinus communis* L. based on empirical data. *Journal of Plant Physiology*, 1991, **137**(4): 488–498
48. Jeschke W D, Pate J S. Cation and chloride partitioning through xylem and phloem within the whole plant of *Ricinus communis* L. under conditions of salt stress. *Journal of Experimental Botany*, 1991, **42**(9): 1105–1116
49. Jeschke W D, Kirkby E A, Peuke A D, Pate J S, Hartung W. Effects of P deficiency on assimilation and transport of nitrate and phosphate in intact plants of castor bean (*Ricinus*

communis L.). *Journal of Experimental Botany*, 1997, **48**(1): 75–91

50. Jeschke W D, Hartung W. Root-shoot interactions in mineral nutrition. *Plant and Soil*, 2000, **226**(1): 57–69
51. Peuke A D. Correlations in concentrations, xylem and phloem flows, and partitioning of elements and ions in intact plants. A summary and statistical re-evaluation of modelling experiments in Ricinus communis. *Journal of Experimental Botany*, 2010, **61**(3): 635–655
52. Raven J A. H^+ and Ca^{2+} in phloem and symplast: relation of relative immobility of the ions to the cytoplasmic nature of the transport paths. *New Phytologist*, 1977, **79**(3): 465–480
53. Costa A, Navazio L, Szabo I. The contribution of organelles to plant intracellular Calcium signalling. *Journal of Experimental Botany*, 2018, **69**(17): 4175–4193
54. Brauer M, Zhong W J, Jelitto T, Schobert C, Sanders D, Komor E. Free calcium ion concentration in the sieve-tube sap of *Ricinus communis* L. seedlings. *Planta*, 1998, **206**(1): 103–107
55. Otero S, Helariutta Y. Companion cells: a diamond in the rough. *Journal of Experimental Botany*, 2017, **68**(1): 71–78
56. Raven J A, Smith F A. Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. *New Phytologist*, 1976, **76**(3): 415–431
57. Feng H, Fan X, Miller A J, Xu G. Plant nitrogen uptake and assimilation: regulation of cellular pH homeostasis. *Journal of Experimental Botany*, 2020, **71**(15): 4380–4392
58. Kirkby E A, Mengel K. Ionic balance in different tissues of the tomato plant in relation to nitrate, urea, or ammonium nutrition. *Plant Physiology*, 1967, **42**(1): 6–14
59. Raven J A. Biochemical disposal of excess H^+ in growing plants. *New Phytologist*, 1986, **104**(2): 175–206
60. Allen S, Raven J A. Intracellular pH regulation in *Ricinus communis* grown with ammonium or nitrate as N source: the role of long distance transport. *Journal of Experimental Botany*, 1987, **38**(4): 580–596
61. Dijkshoorn W. Metabolic regulation of the alkaline effect of nitrate utilization in plants. *Nature*, 1962, **194**(4824): 165–167
62. Raven J A, Farquhar G D. The influence of N metabolism and organic acid synthesis on the natural abundance of isotopes of carbon in plants. *New Phytologist*, 1990, **116**(3): 505–529
63. Raven J A, Franco A A, de Jesus E L, Jacob-Neto J. H^+ extrusion and organic-acid synthesis in N_2-fixing symbioses involving vascular plants. *New Phytologist*, 1990, **114**(3): 369–389
64. Zioni A B, Vaadia Y, Lips S H. Nitrate uptake by roots as regulated by nitrate reduction products of the shoot. *Physiologia Plantarum*, 1971, **24**(2): 288–290
65. Allen S, Raven J A, Sprent J I. The role of long-distance transport in intracellular pH regulation in *Phaseolus vulgaris* grown with ammonium or nitrate as nitrogen source, or nodulated. *Journal of Experimental Botany*, 1988, **39**(5): 513–528
66. Parsons R, Stanforth A, Raven J A, Sprent J I. Nodule growth and activity may be regulated by a feedback mechanism involving phloem nitrogen. *Plant, Cell & Environment*, 1993, **16**(2): 125–136
67. Parsons R, Raven J A, Sprent J I. Translocation of iron to the N_2-fixing stem nodules of *Sesbania rostrata* (Brem). *Journal of Experimental Botany*, 1995, **46**(3): 291–296
68. Martina C M, Borges W L, de Sousa Costa Júnior J, Rumjanek N G. Rhizobial diversity from stem and root nodules of *Discolobium* and *Aeschynomene*. *Acta Scientiarum*: *Agronomy*, 2015, **37**(2): 163–170
69. Raven J A. Long-term functioning of enucleate sieve elements: possible mechanisms of damage avoidance and damage repair. *Plant, Cell & Environment*, 1991, **14**(2): 139–146
70. van Dongen J T, Schurr U, Pfister M, Geigenberger P. Phloem metabolism and function have to cope with low internal oxygen. *Plant Physiology*, 2003, **131**(4): 1529–1543
71. Fisher D B, Wu Y, Ku M S B. Turnover of soluble proteins in the wheat sieve tube. *Plant Physiology*, 1992, **100**(3): 1433–1441
72. Doering-Saad C, Newbury H J, Bale J S, Pritchard J. Use of aphid stylectomy and RT-PCR for the detection of transporter mRNAs in sieve elements. *Journal of Experimental Botany*, 2002, **53**(369): 631–637
73. Kehr J, Buhtz A. Long distance transport and movement of RNA through the phloem. *Journal of Experimental Botany*, 2008, **59**(1): 85–92
74. Cronshaw J. Phloem structure and function. *Annual Review of Plant Physiology*, 1981, **32**(1): 465–484
75. Hafke J B, van Amerongen J K, Kelling F, Furch A C U, Gaupels F, van Bel A J E. Thermodynamic battle for photosynthate acquisition between sieve tubes and adjoining parenchyma in transport phloem. *Plant Physiology*, 2005, **138**(3): 1527–1537
76. Gardner D C J, Peel A J. The effect of low temperature on sucrose, ATP and potassium concentrations and fluxes in the sieve tubes of willow. *Planta*, 1972, **102**(4): 348–356
77. Gardner D C J, Peel A J. Some observations on the role of ATP in sieve tube translocation. *Planta*, 1972, **107**(3): 217–226
78. van der Schoot C, van Bel A J E. Glass microelectrode measurements of sieve tube membrane potential in internode disks and petiole strips of tomato (*Solanum lycopersicum* L.). *Protoplasma*, 1989, **149**(2–3): 144–154
79. Wright J P, Fisher D B. Measurement of the sieve tube membrane potential. *Plant Physiology*, 1981, **67**(4): 845–848
80. van Bel A J E, Kempers R. Symplastic isolation of the sieve element-companion cell complex in the phloem of *Ricinus communis* and *Salix alba* stems. *Planta*, 1991, **183**(1): 69–76
81. Mengel K, Haeder H E. Effect of potassium supply on the rate of phloem sap exudation and the composition of phloem sap of *Ricinus communis*. *Plant Physiology*, 1977, **59**(2): 282–284
82. Smith J A C, Milburn J A. Osmoregulation and the control of phloem-sap composition in *Ricinus communis* L. *Planta*, 1980, **148**(1): 28–34

83. Leigh R A, Wyn Jones R G. A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. *New Phytologist*, 1984, **97**(1): 1–13
84. Korolev N. How potassium came to be the dominant biological cation: of metabolism, chemiosmosis, and cation selectivity since the beginnings of life. *BioEssays*, 2021, **43**(1): e2000108
85. Britto D T, Coskun D, Kronzucker H J. Potassium physiology from Archean to Holocene: a higher-plant perspective. *Journal of Plant Physiology*, 2021, **262**: 153432
86. Raven J A. The potential effect of low cell osmolarity on cell function through decreased concentration of enzyme substrates. *Journal of Experimental Botany*, 2018, **69**(20): 4667–4673
87. Kronzucker H J, Szczerba M W, Britto D T. Cytosolic potassium homeostasis revisited: ^{42}K-tracer analysis in *Hordeum vulgare* L. reveals set-point variations in K^+. *Planta*, 2003, **217**(4): 540–546
88. Walker D J, Leigh R A, Miller A J. Potassium homeostasis in vacuolate plant cells. *Proceedings of the National Academy of Sciences of the United States of America*, 1996, **93**(19): 10510–10514
89. Hermans C, Conn S J, Chen J, Xiao Q, Verbruggen N. An update on magnesium homeostasis mechanisms in plants. *Metallomics*, 2013, **5**(9): 1170–1183
90. Kleczkowski L A, Igamberdiev A U. Magnesium signaling in plants. *International Journal of Molecular Sciences*, 2021, **22**(3): 1159
91. Yamagami R, Sieg J P, Bevilacqua P C. Functional roles of chelated magnesium ions in RNA folding and functions. *Biochemistry*, 2021, **60**(31): 2374–2386
92. Pratt J, Boisson A M, Gout E, Bligny R, Douce R, Aubert S. Phosphate (Pi) starvation effect on the cytosolic Pi concentration and Pi exchanges across the tonoplast in plant cells: an in vivo 31P-nuclear magnetic resonance study using methylphosphonate as a Pi analog. *Plant Physiology*, 2009, **151**(3): 1646–1657
93. Raven J A. Chloride: essential micronutrient and multifunctional beneficial ion. *Journal of Experimental Botany*, 2017b, **38**(3): 359–367
94. Raven J A. Chloride involvement in the synthesis, functioning and repair of the photosynthetic apparatus *in vivo*. *New Phytologist*, 2020, **227**(2): 334–342
95. Fromm J, Spanswick R. Characteristics of action potentials in willow (*Salix viminalis* L.). *Journal of Experimental Botany*, 1993, **44**(7): 1119–1125
96. van Bel A J E, Furch A C U, Will T, Buxa S V, Musetti R, Hafke J B. Spread the news: systemic dissemination and local impact of Ca^{2+} signals along the phloem pathway. *Journal of Experimental Botany*, 2014, **65**(7): 1761–1787
97. Zhang J, Xu Y, Xie J, Zhuang H, Liu H, Shen G, Wu J. Parasite dodder enables transfer of bidirectional systemic nitrogen signals between host plants. *Plant Physiology*, 2021, **185**(4): 1395–1410
98. Fromm J, Hajirezaei M R, Becker V K, Lautner S. Electrical signaling along the phloem and its physiological responses in the maize leaf. *Frontiers in Plant Science*, 2013, **4**: 239
99. Munns R, Fisher D B, Tonnet M L. Na^+ and Cl^- transport in the phloem from leaves of NaCl-treated barley. *Australian Journal of Plant Physiology*, 1986, **13**(6): 757–766
100. Wolf O, Munns R, Tonnet M L, Jeschke W D. Concentrations and transport of solutes in xylem and phloem along the leaf axis of NaCl-treated *Hordeum vulgare*. *Journal of Experimental Botany*, 1990, **41**(9): 1133–1141
101. Munns R, James R A, Läuchli A. Approaches to increasing the salt tolerance of wheat and other cereals. *Journal of Experimental Botany*, 2006, **57**(5): 1025–1043
102. Munns R, Tester M. Mechanisms of salinity tolerance. *Annual Review of Plant Biology*, 2008, **59**(1): 651–681
103. Perri S, Katul G G, Molini A. Xylem-phloem hydraulic coupling explains multiple osmoregulatory responses to salt stress. *New Phytologist*, 2019, **224**(2): 644–662
104. Downing N. The regulation of sodium, potassium and chloride in an aphid subjected to lonic stress. *Journal of Experimental Biology*, 1980, **87**(1): 343–350
105. Armstrong W. Aeration in higher plants. *Advances in Botanical Research*, 1980, **7**: 225–332
106. Raven J A. Into the voids: the distribution, function, development and maintenance of gas spaces in plants. *Annals of Botany*, 1996, **78**(2): 137–142
107. Armstrong W, Justin S H F W, Beckett P M, Lythe S. Root adaptation to soil waterlogging. *Aquatic Botany*, 1991, **39**(1–2): 57–73
108. Colmer T D. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment*, 2003, **26**(1): 17–36
109. Colmer T D, Cox M C H, Voesenek L A. Root aeration in rice (*Oryza sativa*): evaluation of oxygen, carbon dioxide, and ethylene as possible regulators of root acclimatizations. *New Phytologist*, 2006, **170**(4): 767–778
110. Yamauchi T, Colmer T D, Pedersen O, Nakazono M. Regulation of root traits for internal aeration and tolerance of waterlogging-flooding stress. *Plant Physiology*, 2018, **176**(2): 1118–1130
111. Kirk G J D, Boghi A, Affholder M C, Keyes S D, Heppell J, Roose T. Soil carbon dioxide venting through rice roots. *Plant, Cell & Environment*, 2019, **42**(12): 3197–3207
112. Glinski J, Stepniewski W. Soil Aeration and its Role for Plants. Boca Raton: *CRC Press*, 1985
113. Kotula L, Ranathunge K, Schreiber L, Steudle E. Functional and chemical comparison of apoplastic barriers to radial oxygen loss in roots of rice (*Oryza sativa* L.) grown in aerated or deoxygenated solution. *Journal of Experimental Botany*, 2009, **60**(7): 2155–2167
114. Snowden R E D, Wheeler B D. Iron toxicity to fen plant species. *Journal of Ecology*, 1993, **81**: 35–46
115. Wegner L H. Oxygen transport in waterlogged plants. In:

Mancuso S, Shabala S, eds. Waterlogging Signalling and Tolerance in Plants. Berlin, Heidelberg: *Springer*, 2021, 3–22

116. Raskin I, Kende H. How does deep water rice solve its aeration problem. *Plant Physiology*, 1983, **72**(2): 447–454
117. Raskin I, Kende H. Mechanism of aeration in rice. *Science*, 1985, **228**(4697): 327–329
118. Brix H. Uptake and photosynthetic utilization of sediment-derived carbon by *Phragmites australis* (Cav.) Trin ex Steudel. *Aquatic Botany*, 1990, **38**(4): 377–389
119. Singer A, Eshel A, Agami M, Beer S. The contribution of aerenchymal CO_2 to the photosynthesis of emergent and submerged culms of *Scirpus lacustris* and *Cyperus papyrus*. *Aquatic Botany*, 1994, **49**(2–3): 107–116
120. Hwang Y H, Morris J T. Fixation of inorganic carbon from different sources and its translocation in *Spartina alterniflora* Loisel. *Aquatic Botany*, 1992, **43**(2): 137–147
121. Salomón R L, De Roo L, Bodé S, Boeckx P, Steppe K. Efflux and assimilation of xylem-transported CO_2 in stems and leaves of tree species with different wood anatomy. *Plant, Cell & Environment*, 2021, **44**(11): 3494–3508
122. Chazen O, Neumann P M. Hydraulic signals from the roots and rapid cell-wall hardening in growing maize (*Zea mays* L.) leaves are primary responses to polyethylene glycol-induced water deficits. *Plant Physiology*, 1994, **104**(4): 1385–1392
123. Fromm J, Fei H. Electrical signaling and gas exchange in maize plants of drying soil. *Plant Science*, 1998, **132**(2): 203–213
124. Munns R, Passioura J B, Guo J, Chazen O, Cramer G R. Water relations and leaf expansion: importance of time scale. *Journal of Experimental Botany*, 2000, **51**(350): 1495–1504
125. Sachs T. Auxin's role as an example of the mechanisms of shoot/root relations. *Plant and Soil*, 2005, **268**(1): 13–19
126. Miller G, Schlauch K, Tam R, Cortes D, Torres M A, Shulaev V, Dangl J L, Mittler R. The plant NADPH oxidase RBOHD mediates rapid systemic signaling in response to diverse stimuli. *Science Signaling*, 2009, **2**(84): ra45
127. Choi W G, Toyota M, Kim S H, Hilleary R, Gilroy S. Salt stress-induced Ca^{2+} waves are associated with rapid, long-distance root-to-shoot signaling in plants. *Proceedings of the National Academy of Sciences of the United States of America*, 2014, **111**(17): 6497–6502
128. Gilroy S, Suzuki N, Miller G, Choi W G, Toyota M, Devireddy A R, Mittler R. A tidal wave of signals: calcium and ROS at the forefront of rapid systemic signaling. *Trends in Plant Science*, 2014, **19**(10): 623–630
129. Huber A E, Bauerle T L. Long-distance plant signaling pathways in response to multiple stressors: the gap in knowledge. *Journal of Experimental Botany*, 2016, **67**(7): 2063–2079
130. Lee H J, Ha J H, Park C M. Underground roots monitor aboveground environment by sensing stem-piped light. *Communicative & Integrative Biology*, 2016, **9**(6): e1261769
131. Ko D, Helariutta Y. Shoot-root communication in flowering plants. *Current Biology*, 2017, **27**(17): R973–R978
132. Fichman Y, Mittler R. Integration of electric, calcium, reactive oxygen species and hydraulic signals during rapid systemic signaling in plants. *Plant Journal*, 2021, **107**(1): 7–20
133. Verhage L. Alert! Alert! Stress-induced systemic signals unraveled. *Plant Journal*, 2021, **107**(1): 5–6
134. Basu D, Haswell E S. Plant mechanosensitive ion channels: an ocean of possibilities. *Current Opinion in Plant Biology*, 2017, **40**: 43–48
135. Gagliano M. Green symphonies: a call for studies on acoustic communication in plants. *Behavioral Ecology*, 2013, **24**(4): 789–796
136. Mandoli D F, Briggs W R. The photoperceptive sites and the function of tissue light-piping in photomorphogenesis of etiolated oat seedlings. *Plant, Cell & Environment*, 1982, **5**(2): 137–145
137. Mo M, Yokawa K, Wan Y, Baluška F. How and why do root apices sense light under the soil surface. *Frontiers in Plant Science*, 2015, **6**: 775
138. Dickinson A J, Zhang J, Luciano M, Wachsman G, Sandoval E, Schnermann M, Dinneny J R, Benfey P N. A plant lipocalin promotes retinal-mediated oscillatory lateral root initiation. *Science*, 2021, **373**(6562): 1532–1536
139. Jékely G. Evolution of phototaxis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 2009, **364**(1531): 2795–2808
140. Glauser G, Dubugnon L, Mousavi S A R, Rudaz S, Wolfender J L, Farmer E E. Velocity estimates for signal propagation leading to systemic jasmonic acid accumulation in wounded *Arabidopsis*. *Journal of Biological Chemistry*, 2009, **284**(50): 34506–34513
141. Toyota M, Spencer D, Sawai-Toyota S, Jiaqi W, Zhang T, Koo A J, Howe G A, Gilroy S. Glutamate triggers long-distance, calcium-based plant defense signaling. *Science*, 2018, **361**(6407): 1112–1115
142. Martins T V, Evans M J, Woolfenden H C, Morris R J. Towards the physics of calcium signalling in plants. *Plants*, 2013, **2**(4): 541–588
143. Nobel P. Physicochemical and Environmental Plant Physiology. 4th ed. Amsterdam: *Academic Press/Elsevier*, 2009
144. Beilby M J. Action potential in charophytes. *International Review of Cytology*, 2007, **257**: 43–82
145. Beilby M J, Casanova M T. The Physiology of Characean Cells. Berlin, Heidelberg: *Springer*, 2014
146. Shimmen T, Tazawa M. Intracellular chloride and potassium ions in relation to excitability of *Chara* membrane. *Journal of Membrane Biology*, 1980, **55**(3): 223–232
147. Fichman Y, Myers R J Jr, Grant D G, Mittler R. Plasmodesmata-localized proteins and ROS orchestrate light-induced rapid systemic signaling in *Arabidopsis*. *Science Signaling*, 2021, **14**(671): eabf0322
148. Baker D A. Long-distance vascular transport of endogenous hormones in plants and their role in source: sink relation. *Israel Journal of Plant Sciences*, 2000, **48**(3): 199–203
149. Park J, Lee Y, Martinoia E, Geisler M. Plant hormone

transporters: what we know and what we would like to know. *BMC Biology*, 2017, **15**(1): 93

150. Oldroyd G E D, Leyser O. A plant's diet, surviving in a variable nutrient environment. *Science*, 2020, **368**(6486): eaba0196
151. Hartung W, Radin J. Abscisic acid in the mesophyll apoplast and in the xylem sap of water-stressed plants: the significance of pH gradients. *Current Topics in Plant Biochemistry and Physiology*, 1989, **8**: 110–124
152. Muday G K, DeLong A. Polar auxin transport: controlling where and how much. *Trends in Plant Science*, 2001, **6**(11): 535–542
153. Huber A E, Bauerle T L. Long-distance plant signaling to multiple stressors: the gap in knowledge. *Journal of Experimental Botany*, 2016, **67**: 2062–2079
154. Wilkinson S, Corlett J E, Oger L, Davies W J. Effects of xylem pH on transpiration from wild-type and flacca tomato leaves. A vital role for abscisic acid in preventing excessive water loss even from well-watered plants. *Plant Physiology*, 1998, **117**(2): 703–709
155. Wilkinson S. pH as a stress signal. *Plant Growth Regulation*, 1999, **29**(1/2): 87–99
156. Geilfus C M. The pH of the apoplast: dynamic factor with functional impact under stress. *Molecular Plant*, 2017, **10**(11): 1371–1386
157. Vysotskaya L, Wilkinson S, Davies W J, Arkhipova T, Kudoyarova G. The effect of competition from neighbours on stomatal conductance in lettuce and tomato plants. *Plant, Cell & Environment*, 2011, **34**(5): 729–737
158. Lei Y, Xu Y, Zhang J, Song J, Wu J. Herbivory-induced systemic signals are likely to be evolutionarily conserved in euphyllophytes. *Journal of Experimental Botany*, 2021, **72**(20): 7274–7284
159. La Notte A, D'Amato D, Mäkinen H, Paracchini M L, Liquete C, Egoh B, Geneletti D, Crossman N D. Ecosystem services classification: A systems ecology perspective of the cascade framework. *Ecological Indicators*, 2017, **74**: 392–402
160. Renforth P, Henderson G. Assessing ocean alkalinity for carbon sequestration. *Reviews of Geophysics*, 2017, **55**(3): 636–674
161. Raven J A, Edwards D. Roots: evolutionary origins and biogeochemical significance. *Journal of Experimental Botany*, 2001, **52**(Spec Issue suppl_1): 381–401
162. Bach L T, Gill S J, Rickaby R E M, Gore S, Renforth P. CO_2 removal with enhanced weathering and ocean alkalinity enhancement: potential risks and co-benefits for marine pelagic ecosystems. *Frontiers in Climate*, 2019, **1**: 7
163. Vakilifard N, Kantzas E P, Edwards N R, Holden P B, Beerling D J. The role of enhanced rock weathering deployment with agriculture in limiting future warming and protecting coral reefs. *Environmental Research Letters*, 2021, **16**(9): 094005
164. Irving T B, Alptekin B, Kleven B, Ané J M. A critical review of 25 years of glomalin research: a better mechanical understanding and robust quantification techniques are required. *New Phytologist*, 2021, **232**(4): 1572–1581
165. Raven J A. How long have photosynthetic organisms been aggregating soils? *New Phytologist*, 2018, **219**(4): 1139–1141
166. Soper F M, Taylor B N, Winbourne J B, Wong M V, Dynarski K A, Reis C R G, Peoples M B, Cleveland C C, Reed S C, Menge D N L, Perakis S S. A roadmap for sampling and scaling biological nitrogen fixation in terrestrial ecosystems. *Methods in Ecology and Evolution*, 2021, **12**(6): 1122–1137
167. Lambers H. Phosphorus acquisition and utilization in plants. *Annual Review of Plant Biology*, 2022, **73** [Published Online] doi:10.1146/annurev-arplant-102720-125738
168. Edwards D, Cherns L, Raven J A. Could land-based early photosynthesizing ecosystems have bioengineered the planet in mid-Palaeozoic times. *Palaeontology*, 2015, **58**(5): 803–837
169. Evaristo J, Jasechko S, McDonnell J J. Global separation of plant transpiration from groundwater and streamflow. *Nature*, 2015, **525**(7567): 91–94
170. Wei Z, Yoshimura K, Wang L, Miralles D G, Jasechko S, Lee X. Revisiting the contribution of transpiration to global terrestrial evapotranspiration. *Geophysical Research Letters*, 2017, **44**(6): 2792–2801
171. Ruddiman W F. Plows, Plagues, and Petroleum: How Humans Took Control of Climate. Princeton: *Princeton University Press*, 2005
172. Sanderman J, Hengl T, Fiske G J. Soil carbon debt of 12,000 years of human land use. *Proceedings of the National Academy of Sciences of the United States of America*, 2017, **114**(36): 9575–9580
173. Lal R. Digging deeper: a holistic perspective of factors affecting soil organic carbon sequestration in agroecosystems. *Global Change Biology*, 2018, **24**(8): 3285–3301
174. Lal R, Smith P, Jungkunst H F, Mitsch W J, Lehmann J, Nair P K R, McBratney A B, de Moraes Sá J C, Schneider J, Zinn Y L, Skorupa A L A, Zhang H L, Minasny B, Srinivasrao C, Ravindranath N H. The carbon sequestration potential of terrestrial ecosystems. *Journal of Soil and Water Conservation*, 2018, **73**(6): 145A–152A
175. Ruddiman W F, He F, Vavrus S J, Kutzbach J E. The early anthropogenic hypothesis: a review. *Quaternary Science Reviews*, 2020, **240**: 106386
176. Ruddiman W F. The anthropogenic greenhouse era began thousands of years ago. *Climatic Change*, 2003, **61**(3): 261–293