Science & Society

OPEN ACCESS

EMBO reports

Plants, climate and humans

Plant intelligence changes everything

František Baluška[1] & Stefano Mancuso[2]

Global climate change is among the most urgent problems that science has to deal with in the 21st century. Scientists have developed ever more complex models in order to understand the driving factors of climate change and to predict future scenarios. Yet, for all their sophistication, these models might overlook a crucial factor with potentially enormous implications for predicting and dealing with climate change as they consider usually plants only as passive elements that convert atmospheric CO_2 into biomass. However, over the past decades, plant science has revealed that higher plants are much more than just passive carbon-fixing entities. They possess a plant-specific intelligence, with which they manipulate both their abiotic and biotic environment, including climate patterns and whole ecosystems. Considering plants as active and intelligent agents has therefore profound consequences not just for future climate scenarios but also for understanding mankind's role and position within the Earth's biosphere.

"Considering plants as active and intelligent agents has therefore profound consequences not just for future climate scenarios but also for understanding mankind's role and position within the Earth's biosphere."

Autotrophic plants as primary organisms

In terms of global carbon flux and food chains, autoptrophic plants are the most important organisms on Earth. Among all multicellular organisms, only plants have the ability to convert sunlight into organic substances via photosynthesis and are therefore able to live a more or less independent life, whereas all other organisms, including humans, fully depend on plants as primary producers of both food and oxygen. Moreover, most plants—perhaps with the few crop plant exceptions such as maize—would likely be able to survive if the humankind vanished. The opposite is clearly not true, unless we will develop novel efficient technologies of artificial photosynthesis to convert solar energy into organic matter.

"The fact that plant roots actively control carbon in the soil, further supports the view that plants may also be able to actively control climate."

When the first ancestors of terrestrial plants left the oceans to colonize the land, they joined fungi and bacteria to transform rocks and deserts into green ecosystems teeming with life. Ever since, they have been playing a crucial role in generating and maintaining the climatic conditions necessary to support terrestrial life [1,2]. Above the Earth's surface, photosynthetic leaf cells and tissues generate complex organic compounds from carbon dioxide and release oxygen into the atmosphere. Under the Earth's surface, plant roots shape and maintain the soil, a carbon-based ecosystem that provides a unique biosphere for microbial and fungal organisms.

Around 30% of all organic compounds generated via photosynthesis are released from root apices either as exudates [3] or as sugars to feed symbiotic fungi [4] in exchange for water, phosphate, nitrate and critical minerals (Fig 1). Exudates released into the rhizosphere also attract or repel microorganism to maintain the root microbiome, and shape the physico-chemical properties of the soil [3]. In particular, root exudates and mucilages induce biotic soil aggregation which is important for carbon stabilization within soil. Organic soil is not just the result of physical weathering rock and stones, but of the coordinated biological activities of fungi, bacteria and plant roots. Moreover, the large amounts of organic substances that flow from the roots to the microbiota generate huge networks via fungal hyphae that interconnect numerous plants and plant species into supra-organismal networks [3]. The fact that plant roots actively control carbon in the soil further supports the view that plants may also be able to actively control climate [3].

"Our tight co-evolution and the reliance of humans on plants to provide food, medicines and recreational drugs might raise the question of who actually domesticated whom."

Plants release also huge amounts of carbon-based volatiles into the Earth's atmosphere. These compounds are involved in plant–plant communication, as well as manipulation of their biotic and abiotic

1 University of Bonn, Bonn, Germany. E-mail: baluska@uni-bonn.de
2 University of Firenze, Firenze, Italy. E-mail: stefano.mancuso@unifi.it
DOI 10.15252/embr.202050109 | EMBO Reports (2020) 21: e50109 | Published online 27 February 2020

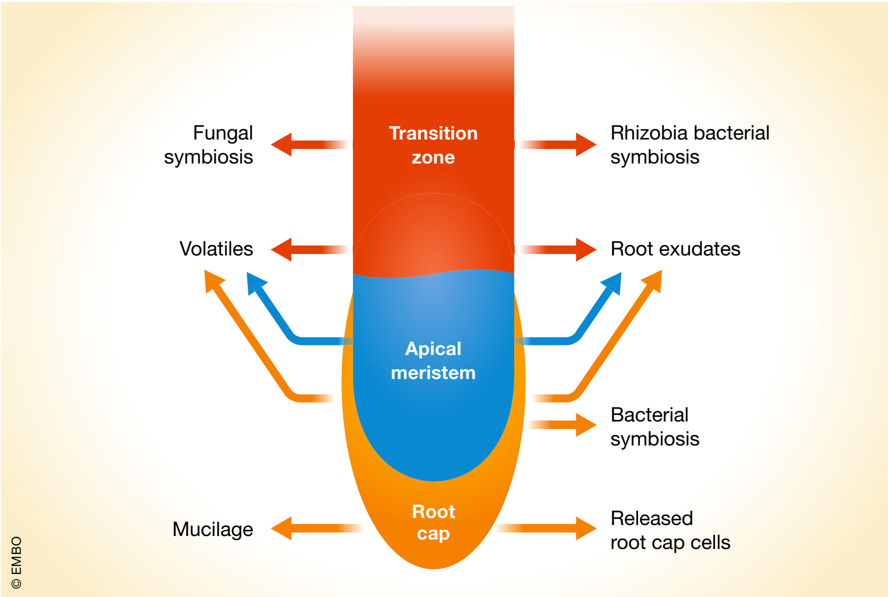

Figure 1. Functional organization of plant root apex.

The root apex actively releases carbon via several different pathways. Root cap cells secrete mucilage which facilitates root growth within soil. Peripheral root cap cells are released in large amounts; these cells often continue to live in, and actively manipulate, the rhizosphere. For example, root apices of *Gossypium hirsutum* shed up 10,000 cells in 24 h. Root apices also compound for manipulating the biotic and biotic rhizosphere environment as well as carbon-based volatiles and info-chemicals. Finally, root apices also provide large amounts of sucrose and lipids to feed their symbiotic fungal partners. The sheer abundance of root apices in the soil biosphere makes the plant root apex one of the most important plant organs.

environments, also by attracting or repelling insects and other organisms. By way of example, trees annually produce around 500 Gt of the highly reactive gas isoprene, along with large amounts of monoterpenes, sesquiterpenes and other biogenic volatile compounds. We still know very little about the biological role and mechanism of this chemical communication, but it is very likely that this huge amount of volatiles affects the composition of the atmosphere (Fig 2).

Co-evolution

The oldest mycorrhiza-root fossils are some 450 million years old—from the very beginning when ancient plants populated the land [5]. This fact shows that mycorrhizal symbiotic fungi co-evolved with the emerging roots of the ancient plants and that their tight association was essential for successfully colonizing a barren and hostile land [1]. Nowadays, many mycorrhizal fungi are so tightly integrated with plant roots that they are no longer able to exist or proliferate independently: their spores germinate only if roots are close enough to invade their

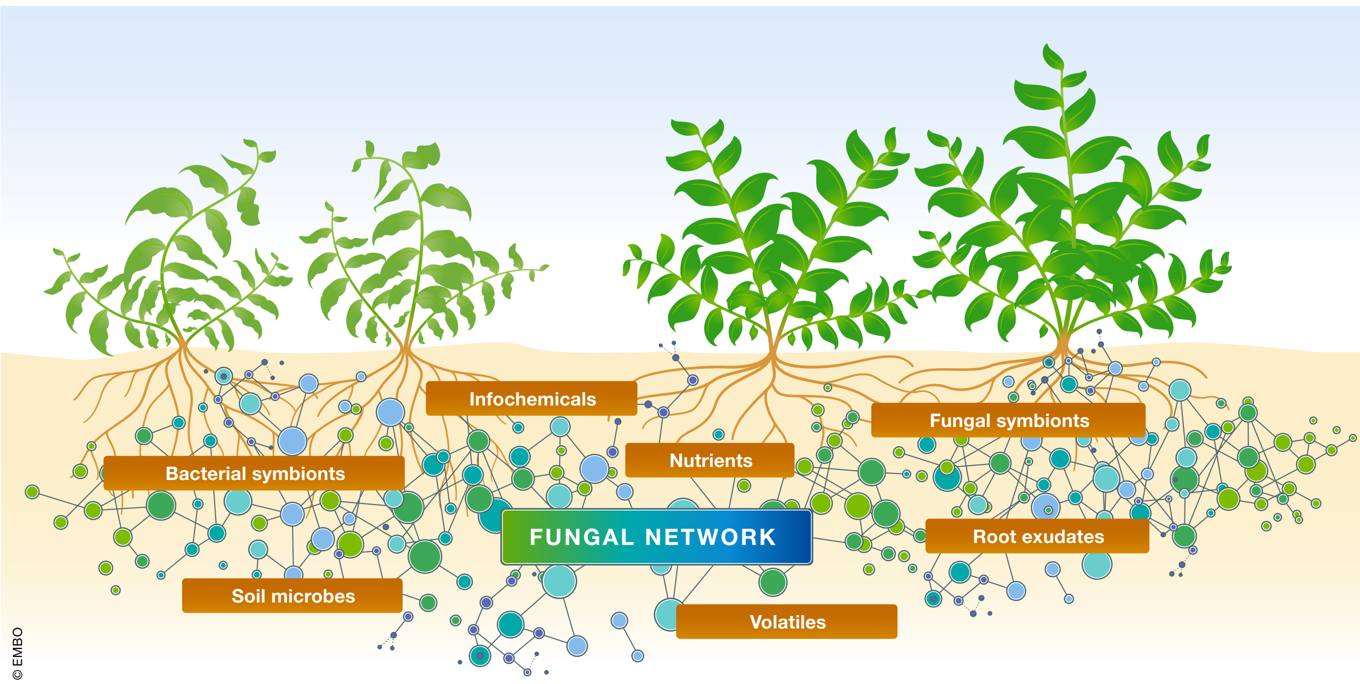

Figure 2. Root-fungal-microbial integrated networks.

Neighbouring plants communicate through their roots via exudates and volatile info-chemicals. Root apices also communicate with mycorrhiza fungi and organize integrated root-fungal networks. More than 90% of all plants, from liverworts up to angiosperms, form these symbiotic networks, which improve plant nutrition via providing plants with water and critical nutrients. These symbiotic fungi also improve plant performance under stress and allow plants to share messages and signals with neighbouring plants.

tissues. Intriguingly, mycelial networks demonstrate goal-directed, memory-based behaviour related to foraging with implications for carbon distribution in forest soils [4]. It seems that this behaviour of mycorrhizal fungi may assist plant roots to explore soils in their search for water and minerals.

All this means that plants are not just passive organisms that merely sit around and sequester CO_2 from the atmosphere until they are eaten. In contrast, plants display highly goal-oriented behaviour by constantly assessing and manipulating their environment to fit it to their needs. A striking example of this manipulation is the reproductive strategies of many flowering plants that rely on insects, birds or small mammals to distribute their pollen or seeds. Plants actively control these pollinators by attracting them using not only nectar as a food reward but also by manipulating the behaviour of insect pollinators via brain-altering chemicals [6]. This manipulation of animals achieves its highest level in the orchids that cheat and manipulate insect pollinators with such efficiency and elegance: the shape and colour of theirs flowers mimic insect females to fool males into copulation and thereby carry their pollen around. There are many more examples of how plants manipulate and control animals. To make sure that enslaved ants will stay loyal to their host trees and aggressively defend it, plants add brain-altering chemicals into nectar (Fig 3). Another drastic example of the supremacy of plants over animals is represented by tomato plants that induce cannibalism in caterpillars of the small mottled willow moth to reduce their herbivory (see Further Reading).

Albert Seward in his book *Plants: What They Are, What They Do* was among the first to speculate that plants might in fact be superior to many animal species. Ian T. Baldwin suggested that higher plants overcome their immobility constraints by their plant-specific environmental intelligence (see Further Reading). Humans are not excluded from plants' manipulative behaviour either. From the plant's perspective, domestication is not just subservience but rather co-evolution whereby both partners benefit from each other [6,7]. Crops and many medicinal plants produce chemicals that alter human brain chemistry, physiology and behaviour [6], similar to flowering plants that manipulate insects to become their pollinators and bodyguards. Our tight co-evolution and the reliance of humans on plants to provide food, medicines and recreational drugs might raise the question of who actually domesticated whom [7,8].

A new view of higher plants as cognitive and intelligent organisms that actively manipulate their environment to serve their needs [7–10] could therefore dramatically change our understanding of life on Earth and help us to better cope with climate changes. Better understanding of plant intelligence is relevant not only for maintaining life-supporting ecosystems and climate patterns, but also for understanding their co-evolution with insects and animals, as well

Figure 3. ***Lasius emarginatus*** **ant visiting extrafloral nectars of** ***Vicia sativa*** **(Photo by Daniele Giannetti).**

Figure 4. Vascular networks of a ***Plectranthus scutellarioides*** **(Coleus) leaf.**

as with humans since our modern, sophisticated civilization is utterly dependent on crop plants [7]. As history shows, failing crop production and resulting famines can easily spark social unrest, wars or even a total collapse of societies. Plants are therefore a crucial factor for addressing our environmental and social challenges [1,7–10].

Engineers of soil

Climate models have largely focused on the plant functions above ground, that is photosynthesis and carbon fixation. But, it is the root that generates and maintains ecosystems and that, together with symbiotic fungal networks and the rhizobiome, transfers around 60 Gt of carbon from the atmosphere into the soil each year. This root-fungal wood-wide-web below ground is estimated to sequester more carbon than the whole vegetation biomass and atmosphere together (see Further Reading). Unfortunately, the scale and the dynamics of carbon rhizodeposition remains largely unknown and it is not part of most climate models.

> *"... the scale and the dynamics of carbon rhizodeposition remains largely unknow and it is not part of most climate models."*

To achieve this impressive feat, roots actively decide with whom they interact and whom they shun. The root apices play a central role by recognizing, communicating with and controlling numerous bacteria, fungi, protozoa and many lower animals. They also actively search for water and minerals to supply photosynthesis in the leaves. Charles Darwin and his son Francis proposed as early as 1880 in the *Power of Movement in Plants* that the root apex acts as a brain of the plant in both cognitive and social aspects. Recent advances in cell and molecular plant biology strongly support this hypothesis. It is obvious that root apices actively engineer complex root-fungal networks which resemble both neuronal networks as well as the topology of the Internet: a forest wide web for sharing organic substances and information (Fig 2).

> *"In order to fully grasp the extent of Earth's climatic changes, a better understanding of vascular plants' cognitive and behavioral complexity is essential."*

Plants control their physiological activities—including water uptake and transport, water-use efficiency, photosynthesis, respiration, stomatal conductances and transpiration—adapting to CO_2 levels and temperature (see Further Reading). Vascular plants also increase carbon allocation to the root and root growth under increasing CO_2 levels. The critical organs are the root apices taking up water from soil, vascular tissues controlling the water transport to the leaves and the stomata complexes at the leaf surfaces controlling the fluxes of water and CO_2 (Fig 5). Importantly, both root apices and stomata complexes are rich in sensory systems and their activities are hormonally and electrically integrated (see Further Reading) via the vascular systems (Fig 4). Modern vascular plants show coordinated behaviour of their stomata similar to coordinated networks to optimize their gas exchange for their entire bodies (see Further Reading).

Plant intelligence and climate

Ever since plants conquered the land, they have invested huge amounts of their photosynthates, released from the roots as organic secretions, to actively shape the rhizosphere microbiome and the physico-chemical properties of soil [1,3]. In some sense, one can consider this enormous investment over millions of years as active niche construction. Plants are sessile organisms, unable to change their environment through moving around. Therefore, they manipulate their surroundings via physical and chemical activities that have a great impact on whole ecosystems and climate conditions (Figs 1 and 3).

By pumping water and mineral nutrients to shoot leaves, plants recycle immense amounts of water: one large rainforest tree can transpire around 1,200 liters of water into the atmosphere—even up to 2,000 liters in the case of redwood trees—on a single sunny summer day. These huge water flows not only cool the environment, but also impact on the atmosphere and the climate. Using their sensory root apices and stomatal complexes, vascular plants actively maintain the temperature of their bodies within a narrow range to optimize the activity of the RuBisCo enzyme for carbon fixation. Vascular plants are generally warmer than the surrounding air in cold areas and colder warm areas (see Further Reading). Plants thus act as a living air-conditioning system owing to their abilities to tightly control water and carbon fluxes on the global scales. In order to fully grasp the extent of Earth's climatic changes, a better understanding of vascular plants' cognitive and behavioural complexity is essential (Fig 5).

Current climate models rely on simplified representations of extremely complex phenomena, which contribute to the uncertainties of their predictions. Most models may overestimate future CO_2 levels due to insufficient understanding of how terrestrial and underground ecosystems react to increased CO_2 levels, and underestimation of photosynthetic carbon fixation into the

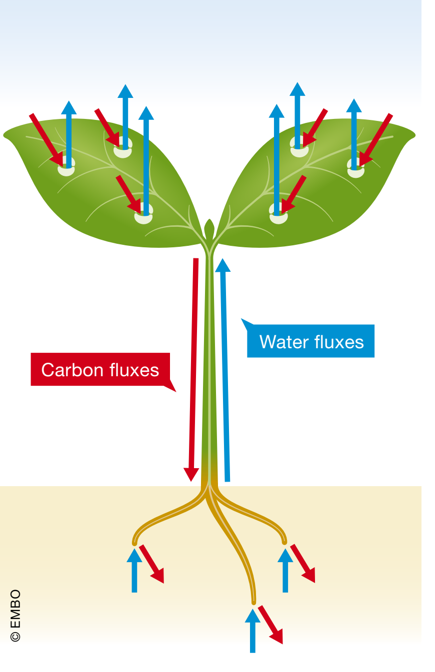

Figure 5. Root apices and leaf stomata integrated via vascular systems.
Root apices and stomata are integrated via plant-specific neuronal-like vascular networks that transport both water (blue arrows) and carbon (red arrows) fluxes along plants/trees bodies. Large trees control water and carbon fluxes on the global scales when integrated root apices and stomata activities play the crucial roles in the global control of these fluxes.

Further reading

Plant evolution and communication

Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM (2004) How plants communicate using the underground information superhighway. *Trends Plant Sci* 9: 26–32
Baluška F, Volkmann D, Hlavacka A, Mancuso S, Barlow PW (2006) Neurobiological view of plants and their body plan. In: *Communication in plants: neuronal aspects of plant life*. Springer, pp 19–35
Baluška F, Ninkovic V (2010) *Plant communication from an ecological perspective*. Springer
Bateman R, Crane PR, Dimichele W *et al* (1998) Early evolution of land plants: phylogeny, physiology, and ecology of the primary terrestrial radiation. *Ann Rev Ecol Evol Syst* 29: 263–292
Hedrich R, Salvador-Recatalà V, Dreyer I (2016) Electrical wiring and long-distance plant communication. *Trends Plant Sci* 21: 376–387
Selosse M-A, Le Tacon F (1998) The land flora: a phototroph–fungus partnership? *Trends Ecol Evol* 13: 15–20
Simard SW (2018) Mycorrhizal networks facilitate tree communication, learning and memory. In: *Memory and learning in plants*. Baluška F *et al* (eds), Springer, pp 191–213
Sussmilch FC, Schultz J, Hedrich R, Roelfsema MRG (2019) Acquiring control: the evolution of stomatal sgnalling pathways. *Trends Plant Sci* 24: 342–351

Plant roots in soil carbon cycling

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. *Annu Rev Plant Biol* 57: 233–266
Gill AL, Finzi AC (2016) Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. *Ecol Lett* 19: 1419–1428
Hawes MC, Brigham LA, Wen F, Woo HH, Zhu Y (1998) Function of root border cells in plant health: pioneers in the rhizosphere. *Annu Rev Phytopathol* 36: 311–327
Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant Soil* 321: 5–33
Pausch J, Kuzyakov Y (2018) Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Glob Chang Biol* 24: 1–12

Intelligent plants and climate

Bader MKF, Leuzinger S (2019) Hydraulic coupling of a leafless kauri tree remnant to conspecific hosts. iScience 19: 1238–124
Baldwin IT (2015) Rediscovering the bush telegraph. *Nature* 522: 282–283
Barlow P (2010) Plant roots: autopoietic and cognitive constructions. *Plant Root* 4: 40–52
Calvo P, Gagliano M, Souza GM, Trewavas A (2019) Plants are intelligent, here's how. *Ann Bot* 125: 11–28
Castells L (2017) Plants turn caterpillars into cannibals. *Nature* 10 July 2017
Hetherington AM, Woodward FI (2003) The role of stomata in sensing and driving environmental change. *Nature* 901–908
Keim B (2019) Never underestimate the intelligence of trees. Nautilus 77: 4
Kelly M (2015) Theory of 'smart' plants may explain the evolution of global ecosystems. https://www.princeton.edu/news/2015/12/01/theory-smart-plants-may-explain-evolution-global-ecosystems
Mancuso S (2018) *The revolutionary genius of plants: a new understanding of plant intelligence and behavior*. Atria Books
Michaletz ST, Weiser MD, Zhou J, Kaspari M, Helliker BR, Enquist BJ (2015) Plant thermoregulation: energetics, trait-environment interactions, and carbon economics. *Trends Ecol Evol* 30: 714–724
Negrutiu I, Frohlich MW. Hamant O (2020) Flowering plants in the anthropocene: a political agenda. *Trends Plant Sci* 25: In press
Pollan M (2013) The intelligent plant. The New Yorker, December 23 & 30

wood-wide networks of roots and symbiotic fungi. The most serious drawback, however, is that they do not take into account the fact that plants are intelligent organisms that actively shape and manipulate their ecological niches. We may not be aware of their active roles, as plants and their microbiotic networks likely "think" and act in timescales of months, years of even centuries. Nevertheless, it stands to reason that they will react to the global climate changes enacted by mankind with as yet unpredictable effects. Hopefully, their interests and actions will correspond with our human and the Earth's biosphere's needs.

References

1. Beerling D (2019) *Making Eden: how plants transformed a barren planet*. Oxford: Oxford University Press
2. Morton O (2007) *Eating the sun: how plants power the planet*. New York, NY: Harper-Collins Publishers
3. Canarini A, Kaiser C, Merchant A, Richter A, Wanek W (2019) Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Front Plant Sci* 10: 157
4. Fukasawa Y, Savoury M, Broddy L (2019) Ecological memory and relocation decisions in fungal mycelial networks: responses to quantity and location of new resources. *ISME J* 14: 380 – 388
5. Pirozynski KA, Malloch DW (1975) The origin of land plants: a matter of mycotrophism. *BioSystems* 6: 153 – 164
6. Kennedy DO (2014) *Plants and the human brain*. Oxford: Oxford University Press
7. Pollan M (2001) *The botany of desire: a plant's-eye view of the world*. New York, NY: Random House
8. Mancuso S, Viola A (2015) *Brilliant green: the surprising history and science of plant intelligence*. Washington, DC: Island Press
9. Trewavas A (2015) *Plant behavior and intelligence*. Oxford: Oxford University Press
10. Baluška F, Mancuso S, Volkmann D (2006) *Communication in plants: neuronal aspects of plant life*. Berlin: Springer Verlag

