

The greenest revolution – harnessing the power of plants to help combat climate change

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As we continue searching for the technologies that will halt global warming, let us take a moment to think about plants. A key contributor to our climate crisis is the accumulation of carbon dioxide in the atmosphere. Plants have been capturing carbon dioxide for billions of years, making them the most tried and tested carbon capture machinery on the planet. Plants fix carbon dioxide as part of photosynthesis. After years of research, we now know the key regulators of this process and have the knowledge to start engineering plants with increased photosynthetic capacity. In addition to improving the efficiency of carbon fixation, we must also find a way to stably store the carbon captured by plants. To achieve this, we can look to the below-ground part of the plant body – the root system. Plant roots are packed full of carbon and also exude carbon-rich molecules into the soil. Engineering future plants with deeper, more extensive root systems, with enhanced chemical composition that increases carbon content and reduces the rate of biodegradation, offers a way to store atmospheric carbon fixed by plants below ground for years to come. With optimized root systems, these plants would also be better equipped to explore their surrounding soils for water and nutrients, which would ultimately improve plant performance. This approach also offers a way to replenish our carbon-depleted soils, which would increase soil quality by improving water and nutrient retention. Harnessing the plants' natural ability to capture carbon, thus provides a way to not only restore balance to the carbon cycle, but also improve soil quality and future crop performance.

A lesson from the Palaeozoic era

It's 2022, and we are now facing truly critical years for finding fast, effective and sustainable solutions for our on-going climate crisis. If carbon dioxide and other greenhouse gases continue to accumulate in our atmosphere, global temperatures *will* continue to rise. This has already and will continue to devastate life on Earth as we know it. For decades now, we have been searching for the breakthrough technologies that will allow us to remove and safely store atmospheric carbon. However, when faced with an uncertain future, we can often learn everything we need to know by looking to the past. Solving our climate change crisis seems to be no different.

Let us look back approximately 500m years, to the colonization of land by plants — now seen as one of the most transformative evolutionary events known to man. This event not only paved the way for animals and fungi on our world's land surfaces, but also fuelled a dramatic decrease in atmospheric carbon dioxide levels. Today, it is estimated that plants continue to hold as much as 450 gigatons of carbon – literally living proof that they

provide the most robust and efficient carbon pulldown solution on the planet. Finding ways to sequester only a small fraction of the plant-fixed carbon would help us to restore balance to the carbon cycle and prevent further accumulation of CO₂ in the atmosphere. As a result of past and on-going efforts in the plant research and plant breeding communities across the globe, we are already equipped with many of the tools we need to achieve this goal.

Engineering photosynthesis for enhanced carbon capture

Photosynthesis, the process utilized by plants for the production of sugars, which ultimately fuel their growth and development, results in carbon fixation. As a product of many years of active research, we now have a thorough understanding of the chemical reactions involved in photosynthesis, as well as the key catalysts and the genes that encode them. With this understanding, we have seen a number of research efforts aimed at fine-tuning the photosynthetic machinery to increase efficiency and maximize carbon capture. One engineering approach has

been to target key proteins, including SBPase, FBPA and GDC-H. These proteins play a central role in the Calvin cycle, which comprises a cascade of chemical reactions used by plants to fix carbon dioxide. Expression of these proteins at an increased level in our model plant species, *Arabidopsis thaliana*, resulted in increased efficiency of these chemical reactions and an increase in carbon fixation. In addition to finding ways to engineer plants that can fix carbon more efficiently, research has also been carried out with the aim of reducing plant respiration, during which plants release carbon dioxide back into the atmosphere. Photorespiration evolved as a way to eliminate a toxic by-product of the Calvin cycle called 2-phosphoglycolate, which forms when instead of reacting with carbon dioxide, the central enzyme, Rubisco, reacts with oxygen. However, there are photosynthetic systems that have evolved strategies that bypass photorespiration. For example, plant species, such as maize, or the so-called 'C4 plants', have evolved leaf anatomy that concentrates carbon dioxide around Rubisco, thus limiting the reaction of this enzyme with oxygen and eliminating the need for photorespiration. Recent progress has resulted from the engineering of rice plants expressing the *GLK* gene from maize. These rice plants display leaf anatomy more closely resembling that of C4 plants and represent a milestone in realizing the potential of engineering plants to more efficiently draw down carbon. However, despite the promise of research efforts such as these, as plants complete their life cycle and decompose, the carbon stored in much of the plant body is released back into the atmosphere. Thus, in addition to achieving more efficient pull down, we must also find a way to stably store the carbon captured by plants.

Building roots that increase soil carbon storage

One of the key drivers for the reduced levels of atmospheric carbon dioxide following the colonization of land by plants was the evolution of plant roots which provided a way to store carbon stably below ground for many years. Much like other plant materials, roots are carbon-rich structures. Plants use roots to explore their surrounding soils in search of water and nutrients. Several root characteristics have the potential to enhance carbon accumulation and lifetime in the soil. For instance, increasing root biomass will increase total carbon inputs into the soil. Other characteristics can increase the residence time of the root-derived soil organic carbon, which is key for plant-mediated soil carbon sequestration. One avenue for this is deeper roots, as carbon in deeper soil layers has a much longer residence time. Another root-associated factor that can

influence decomposability is root biochemistry; for instance, highly reduced organic compounds can't be readily degraded in oxygen-poor environments due to thermodynamic constraints. With this in mind, plant varieties with deeper, more extensive root systems, that have properties beneficial for greater and longer carbon storage, would contribute greatly to our goals in reducing atmospheric carbon and provide a long-term solution for carbon storage. In addition, given their vital role in the acquisition of both water and nutrients, a better developed root system of these future plants would also come with benefits for productivity in many areas, particularly under drought or nutrient-poor conditions.

Root mass and root depth have been altered many times during evolution and breeding. Several single genes for this have been identified that are capable of modulating these two plant characteristics. The majority of these studies have been the result of mutant analyses in *A. thaliana* (Figure 1a). Translation of gene discoveries from models into important crop species would provide a way to develop future plants with root systems optimized for increased carbon capture and storage.

In addition to the many discoveries to come from traditional, lab-based mutant analyses, more recently we have seen the exploration of natural variation as a powerful tool for gene discovery. Largely owing to vast decreases in the cost of genome sequencing, we can now screen many accessions/varieties of a given species at the sequence level and identify associations between variation in DNA sequence and variation in phenotypes of interest using methods such as Genome-Wide Association Mapping (Figure 1b). Using this approach, it becomes possible to not only locate causal genes, but identify the exact genetic variation that has driven phenotypic diversity in nature. This approach has allowed for the discovery of natural variation that regulates important carbon-capture traits including root depth and lateral root growth not only in *Arabidopsis* but also in important crop species such as maize and rice.

Suberin — finding optimism in a bottleneck

In addition to engineering future plants with deeper, more extensive root systems, we can also increase the carbon sequestration potential by focusing on the biochemical makeup of the root or its exudates. One very promising target is suberin. Suberin is a complex polyester biopolymer that is composed of long-chain fatty acids and polyaromatics. Several studies indicated that suberin can be preserved in soil for a long time and can be an important component of stable soil organic carbon. While the mechanism for this is not yet elucidated and the extent of it will be dependent on soil

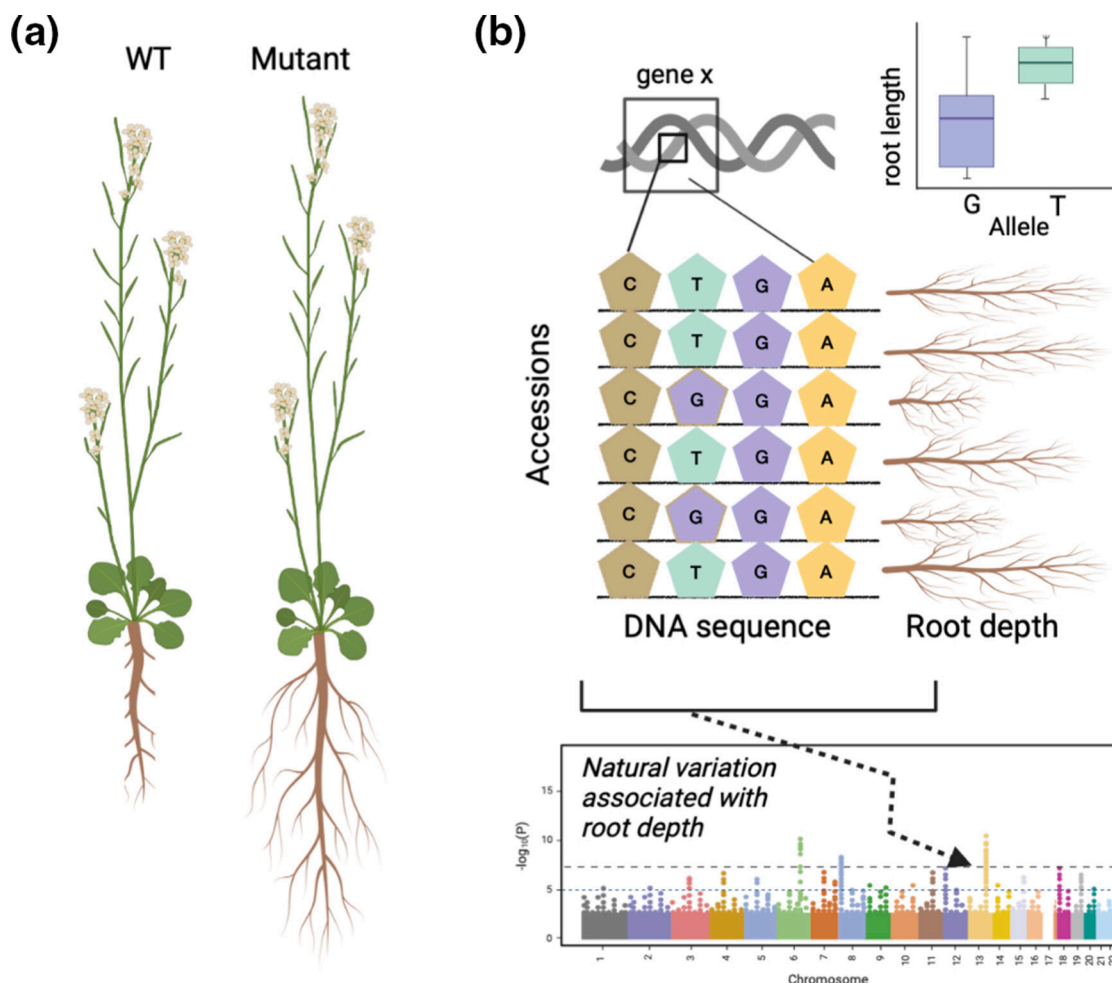


Figure 1. Through mutant analyses in our model plant *A. Thaliana* (a) and through exploration of natural variation in both model and crop species (b), we have identified several genes that regulate important carbon-capture traits in plants.

types, environmental conditions and depth within the soil profile, it most likely relates to its interaction with soil minerals and occlusion in topsoil microaggregates, as well as the thermodynamic constraints in breaking down reduced organic compounds as suberin under anaerobic conditions. Suberin is a well-known material as it is most abundantly produced in the cork oak tree, *Quercus suber*. The suberin layers harvested from these trees are widely utilized to produce the cork used to seal wine bottles, and for a wide variety of other applications ranging from home construction materials to insulation in deep space rocket boosters. But suberin is not only found in the trunk of the cork oak tree. Suberin also exists naturally in plant roots, where its recalcitrant and hydrophobic nature provides the perfect barrier to reduce water loss and limit the invasion of the root by soil pathogens. Thus, the development of roots rich in suberin not only provides an additional way to capture more carbon below-ground for longer, but also provides

a novel approach to overcome some of the biotic and abiotic stresses faced by plants.

Studies in cork oak have revealed many of the key enzymes involved in suberin biosynthesis. More recently, we have seen research focused on studying this process in the roots of *Arabidopsis*. These studies have revealed that the functions of many of the regulatory genes identified in cork oak are conserved in *Arabidopsis*. The genes encoding these regulators represent excellent targets for increasing suberization for enhanced carbon sequestration in the roots of future plants.

In plant roots, suberin is deposited within specialized cell types including the periderm and exodermis. In addition to building our understanding of how suberin is synthesized in plant roots, we are also beginning to understand how these cell types form. The periderm is a complex tissue comprising the phellogen meristem (also referred to as cork cambium), which produces the suberized phellem (cork) and the phelloderm cells. Studies

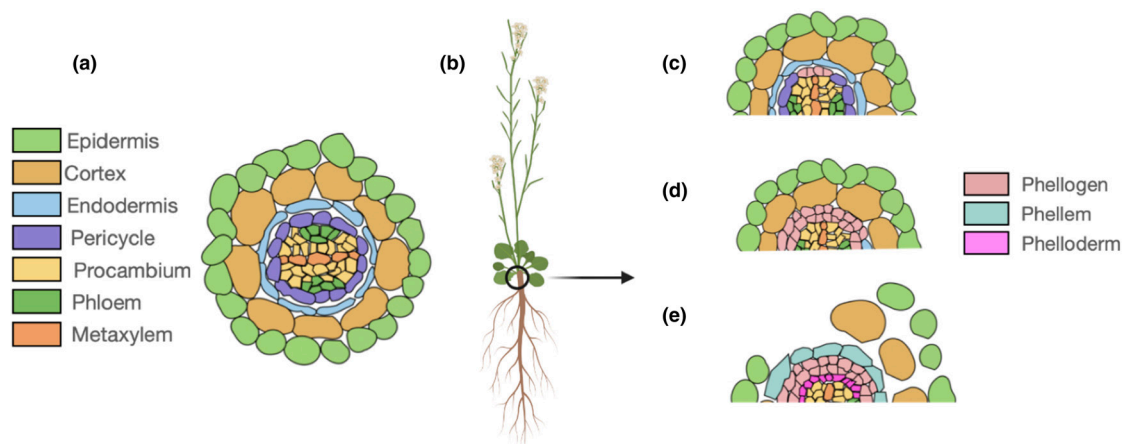


Figure 2. Suberin is deposited in specialised cell types such as the phellem in arabidopsis roots. Phellem cells originate from pericycle cells (a), which, in the mature part of the root (b), regain ability to divide to become phellogen (c). As these meristematic cells divide, the endodermis is lost through programmed cell death (d). The phellogen differentiates inwardly to form the phelloderm and outwardly to form the phellem. The phellem cells eventually undergo suberisation and as the cortex and epidermis dehisce, the phellem becomes the most outer cell layer of the mature root (e).

in *Arabidopsis* have shown that periderm cells originate from a cell type called the pericycle (Figure 2a). Unlike the majority of cell types, the pericycle is able to regain its ability to divide in the root maturation zone (b) to form a secondary meristem called the phellogen (c). As these cells develop, the endodermis cells undergo programmed cell death and are lost (d). The phellogen then divides into two different cell layers, the inner phelloderm and the outer phellem. The cortex and the epidermis dehisce and fall away leaving the phellem cells as the outer most cell layer in the mature root (e). These phellem cells will ultimately undergo suberization.

It was recently uncovered that the transition of these cells from pericycle to phellem is, as seen for other aspects of root development, under the regulation of the hormone auxin. In addition, transcriptional regulators, including *WOX4* and *KNAT1*, have been identified as having a key role in the development of these cells. Making use of these discoveries and continuing to build our knowledge of the genetic regulators underlying the development of these specialized cells and their suberization would allow us to produce future plants with improved potential for carbon sequestration and increased resistance to biotic and abiotic stresses.

Increased soil carbon – benefits beyond climate control

It is clear that there is great promise in increasing the carbon capture and soil storage ability of plants to mitigate climate change. However, some might wonder what might be the wider impact of increasing our soil carbon content

on biodiversity and ecosystems for example. Carbon-rich soils are not unknown to nature. In fact, since the dawn of agricultural efforts, we have seen a drastic loss of soil carbon and with this loss, a reduction in overall soil quality. Regions affected include the so-called ‘US corn belt’ and much of western Europe, which have been regions of high agricultural activity for many thousands of years. It is estimated that more than 133 gigatons of carbon in soils have been lost due to agricultural land uses. Given this, the idea of making use of plants to capture carbon in the soils is not only a powerful approach to mitigate climate change, but also offer a way to restore soils to their natural state. With this restoration effort, we can expect to see significant improvements in soil quality resulting from increased retention of water and nutrients, which will ultimately fuel an increase in crop productivity. Replenishing soil to their natural carbon-rich state thus has benefits that go far beyond our efforts to gain control of climatic change.

Conclusion and future perspectives

As a species we pride ourselves on our innovative thinking. In some cases however, this may leave us at risk of losing sight of the most accessible and simple solutions to a problem. Fine-tuning the plants’ natural ability to sequester carbon offers a way to gain some control of the on-going climate crisis in a way that is reliable, affordable and scalable. In addition to the outlined plant trait enhancements to do this (which is currently undertaken by the Salk Institute’s Harnessing Plants Initiative and others), there will be many already imagined or unimagined ways utilizing plants, microbes and agricultural practices alone



Figure 3. Using genome-editing technologies, such as Crispr-Cas9, we can now effectively translate discoveries from model to crop and between crop species with unparalleled precision.

or in combination, to store more of the carbon that is drawn down by plants in the soil and/or to avoid greenhouse gas emissions. The past, recent decades have seen enormous progress in our understanding of plant growth and development. Drops in the cost of genomic technologies mean that it is now feasible to identify the genetic causes of phenotypic variation across our crop species. This, together with advancements made in genome editing (including Crispr-Cas9) and single-cell functional genomic technologies, provides the tools required to engineer future plants with unparalleled precision (Figure 3). This will be key if plant breeders are to embrace engineering efforts to mitigate climate change, as any further genetic changes made to their crops would need to be achieved without yield penalties. However, while innovations in science have the power to make global change, as always, realizing the true impact of these ideas and discoveries requires a global effort. Key to this will be broad and active scientific and public debate to further our understanding of the opportunities in leveraging plants to address the climate

crisis. Many people still fail to see the transformative power of the plant kingdom. Sitting so quietly and humbly in the ground, it can be easy to overlook or forget the impact that plants have had and continue to have on our everyday lives. Shifting this perspective and realizing the ability of plants to transform their planet is an integral first step in harnessing plant-powered innovations to combat climate change.

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Further reading and viewing

- The harnessing plants initiative, Salk Institute: <https://www.salk.edu/harnessing-plants-initiative/>
- How supercharged plants could slow climate change | Joanne Chory. YouTube. <https://www.youtube.com/watch?v=pyFcr2WcOyo>

Deeper roots discovery:

- Ogura et al. (2019). Root System Depth in Arabidopsis Is Shaped by EXOCYST70A3 via the Dynamic Modulation of Auxin Transport. *Cell*. 178(2),400–412.e16. <https://www.sciencedirect.com/science/article/pii/S0092867419306841?via%3Dihub> The Realizing Increased Photosynthetic Efficiency (RIPE) project, University of Illinois: <https://ripe.illinois.edu/>

Historic changes in soil carbon and carbon capture by biomass:

- Sander et al. (2017). Soil carbon debt of 12,000 years of human land use. *PNAS*. 114(36) 9575–958. <https://www.pnas.org/doi/10.1073/pnas.1706103114>
- Erb et al. (2018). Unexpectedly large impact of forest management and grazing on global vegetation biomass. *Nature*. 553, 73–76. <https://www.nature.com/articles/nature25138>

Suberising cells:

- Xiao et al. (2020). Pluripotent Pericycle Cells Trigger Different Growth Outputs by Integrating Developmental Cues into Distinct Regulatory Modules. *Current Biology*. 30, 4384–4398. [https://www.cell.com/current-biology/pdf/S0960-9822\(20\)31243-4.pdf](https://www.cell.com/current-biology/pdf/S0960-9822(20)31243-4.pdf)
- Wunderling et al. (2018). A molecular framework to study periderm formation in Arabidopsis. *New Phytologist*. 219(1) 216–229. <https://nph.onlinelibrary.wiley.com/doi/full/10.1111/nph.15128>
- Photosynthesis research program: The RIPE project: <https://ripe.illinois.edu>

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