Food production in an age of global warming and weirding

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Some estimates suggest that we will need to double food production by 2050, and do so despite the effects of climate change on crop yields. The competing demands of agriculture and human populations upon water supplies can only become more extreme with time and are likely to be exacerbated by the impact of increased evaporation due to global warming and changes to rainfall patterns. Therefore, this article will examine some of the ways that we can produce food using less water.

The world population passed 7 billion in 2011 and we anticipate that it may reach 9 billion by the year 2040. How will we feed so many? In addition to the simple increase in the number of mouths, many in the developing world, entirely reasonably, aspire to the lifestyles of populations in the developed world. Therefore, it has been estimated that by 2050 we may need to increase agricultural production to twice that of 2005, and we must achieve this without substantially adding to the area that we farm.

This cannot possibly be achieved if crop yields only improve at their current rate, and climate change is expected to make producing even what we do now more difficult. For example, models of the effects of increased temperature on wheat suggest that we can expect yields to fall by about 5% per 1°C of warming. Projections suggest that even if the signatories to the United Nations Framework Convention on Climate Change Paris Agreement stand by their commitments, the world will warm by between 2.6 and 3.1°C by 2100. Every bit as alarming is what has sometimes been called "global weirding." This refers to the effects of carbon emissions on weather patterns. It has almost become a cliché to greet each unexpectedly hot (or cold) day as a sign of global warming, but it seems that there has already been a significant increase in the frequency of ‘abnormal’ climatic events such as droughts and floods. We can expect that this tendency will become more extreme as temperatures continue to rise.

One of the primary ways that heat affects yields is by increasing water evaporation. Even now it seems that rainfall patterns may be altering as a result of climate change, and water supplies are under pressure as a result of the conflicting demands of agriculture and human populations. Supply of water to crops is still one of the main limitations upon agricultural productivity, but intensive irrigation can bring its own problems, such as the build-up of salts known as ‘salinization’, which may affect 70% of agricultural soils by 2050. For these reasons, the main focus of this article will be some of the ways that we might produce food using less water.

It may be worth initially considering why water is so important for agriculture. In photosynthesis, plants collect carbon dioxide from the air and convert it into carbohydrates. A small amount of water is used for photosynthesis itself and slightly more for growth, but the vast majority is simply evaporated, typically 97% or more of the total taken up. This is because carbon dioxide used in photosynthesis must first be absorbed by moist surfaces inside the leaves of the plant. If carbon dioxide can reach these surfaces from the atmosphere, water can also escape in the opposite direction. Plants restrict this loss by closing pores in their leaf surfaces, known as stomata, but if they do, they also prevent carbon dioxide getting in. Therefore, in land plants, water loss and photosynthesis are inextricably linked. To gain carbon (and in crops, that is what provides dietary calories) you must lose water.

**Turbocharged rice**

In plants, carbon dioxide is usually directly captured by an enzyme known as ribulose bisphosphate carboxylase/oxygenase or RuBisCO. The carboxylase conducts the reaction in which carbon dioxide is fixed, converting...
one molecule of ribulose bisphosphate and one of carbon dioxide into two molecules of phosphoglycerate. This is referred to as ‘C3 photosynthesis’ because phosphoglycerate, the first product in this process, has three carbon atoms. However, RuBisCO doesn’t distinguish well between carbon dioxide and oxygen. As a result, it will sometimes instead catalyse a reaction between ribulose bisphosphate and a molecule of oxygen, producing one molecule of phosphoglycerate and one of the two-carbon molecule, phosphoglycolate. The carbon in phosphoglycolate has to be recycled via a complex and wasteful series of reactions distributed between the cell’s chloroplasts, peroxisomes and mitochondria. Phosphoglycolate is formed by the ‘oxygenase’ activity of RuBisCO and this and the metabolic processes used to recycle it are referred to as photorespiration. This is a relatively limited problem at low temperatures, but evaporation increases approximately exponentially as the temperature increases, forcing plants to close their stomata to prevent water loss. As a consequence, carbon dioxide levels inside the leaf fall. At higher temperatures, RuBisCO differentiates less well between carbon dioxide and oxygen, and the ratio of dissolved carbon dioxide to oxygen is reduced. These effects mean that the rate of the oxygenase reaction rises and photorespiration becomes a greater and greater burden upon the plant as temperatures rise, potentially wasting 30% of the carbon fixed by C3 photosynthesis.

However, a number of species have evolved a solution to this. In these plants, carbon dioxide levels inside the leaf fall. At higher temperatures, RuBisCO differentiates less well between carbon dioxide and oxygen, and the ratio of dissolved carbon dioxide to oxygen is reduced. These effects mean that the rate of the oxygenase reaction rises and photorespiration becomes a greater and greater burden upon the plant as temperatures rise, potentially wasting 30% of the carbon fixed by C3 photosynthesis.

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However, a number of species have evolved a solution to this. In these plants, carbon dioxide (or more specifically bicarbonate) is initially combined with phosphoenolpyruvate (PEP) by the enzyme PEP carboxylase to form oxaloacetate. Oxaloacetate has four carbon atoms and so this is referred to as ‘C4 photosynthesis’. Note that C4 plants still use RuBisCO, but it is concentrated in specialized cells surrounding the leaf veins called ’bundle sheath cells’. The advantages of initially capturing carbon dioxide as oxaloacetate are that PEP carboxylase has a greater affinity for carbon dioxide than RuBisCO, and more importantly, that after conversion into malate or aspartate for transport, it can be concentrated in the bundle sheath cells. C4 plants thereby boost carbon dioxide levels around RuBisCO and virtually eliminate losses due to photorespiration. This makes them more productive at higher temperatures and they need less water because they can open their stomata less. Additionally, because they use their RuBisCO more efficiently they need less of it, and therefore less nitrogen for protein synthesis.

C4 species seem to have begun to evolve when carbon dioxide levels in the atmosphere dropped about 25 million years ago and expanded to dominate tropical grasslands across much of the Earth from about 15 million years ago when continental movements caused many areas to become more arid. Grasslands across the world today divide between those dominated by C3 and C4 species depending on their temperature and rainfall patterns. Perhaps unfortunately, the majority of our cereals originated from temperate C3 species. Some crop species carry out C4 photosynthesis, including maize, sugar cane and sorghum, but most do not, including wheat and rice. It has been estimated if rice could be modified to carry out C4 photosynthesis its yields could be increased by as much as 50%. We expect that this would reduce its water use, help it to withstand global warming, and perhaps also reduce fertilizer use (remember that C4 species need less nitrogen, and converting nitrogen for fertilizer itself contributes to global warming). About half of the world’s population depend on rice as a staple crop and so C4 rice could be a game changer. An international collaborative project funded in part by the Bill and Melinda Gates Foundation is underway to achieve this.

Unfortunately, when genes for the main enzymes required for C4 photosynthesis were simply inserted into rice, very little C4 carbon fixation resulted. Nor did the plants thrive. All of the metabolites involved in C4 photosynthesis are already present in plant cells and so it was not terribly surprising that adding new enzymes attuned to a different metabolic environment was disruptive.

However, C4 photosynthesis is one of the most striking instances of convergent evolution, having apparently arisen independently more than 60 times. Therefore, recapitulating this process in rice ought to be feasible and this has become one of the main thrusts of the C4 rice project. Interestingly, the evolutionary steps involved seem to start with a ‘streamlining’ of the photorespiratory reactions and so the problem may form part of the
solution. A recent report by Jane Langdale and colleagues describes replication of one of the early steps in this pathway, using maize transcription factors to bring about formation of enlarged chloroplasts and mitochondria in the cells surrounding the leaf veins in rice, as is seen in C4 species. This is a promising development, but the project is ambitious and will not reach its goal in the near future. Furthermore, even after C4 photosynthesis has been first achieved in one type of rice, it will have to be integrated into a range of other varieties for widespread use.

**Tricking crops into using less water**

Another approach that may bring benefits more quickly takes advantage of plant responses to water stress. It has been known since at least the 1940s that plants in drying soil conserve water by closing their stomata. However, it was not clear whether this happens when shoots and leaves of the plants directly experience water stress, or can be caused by a signal from their roots to prepare them for a reduced water supply before its effects start to bite. An elegant experiment was devised to test this in fruit trees grown with their roots split between two pots. They were kept hydrated by watering one pot, but the roots in the other pot were exposed to a drier environment. The trees closed their stomata even though water potential measurements showed that the aerial parts of the plant were receiving plenty of water. This seemed to confirm that the roots in the dry pot were indeed sending some sort of message that caused the shoots to conserve water. Particularly persuasive was that the test plants went back to behaving like the well-watered controls when the roots in the dry pot were cut off.

These experiments provided a useful insight into plant responses to water deficit, but it has turned out that the same methods can also be exploited to produce crops using less water. Researchers in Australia examined whether it would be possible to grow grapes for winemaking more efficiently by watering the roots on only one side of each row of vines while leaving roots on the other side unwatered. Their results were spectacular. The total grape harvest was the same but the vines used 30% less water and the grapes were better for wine making. The reason for this observation shed light on why the trick worked. It was because side shoots stopped growing and so more light was falling on the grapes, which consequently improved the quality of wine produced. As we would expect, when the vines closed their stomata it reduced photosynthesis and therefore total biomass accumulation, but the resources that they did have were directed to the fruit. Presumably, this is an adaptation to ensure that the plant reproduces despite environmental stresses. The degree to which this can occur is illustrated by the tomato plant in Figure 1. It was overlooked and left in a system that had been recording growth of one of the fruits when the investigator went on holiday. It was noticed that the fruit being tested was still growing when they returned 2 weeks later, even though the rest of the plant was obviously experiencing catastrophic water stress.
In many cases the reproductive tissues of our crops are the part we eat, whether these are fruits or seeds, and so we can often improve water efficiency by taking advantage of the way that plants protect their next generation. ‘Partial rootzone drying’ and other systems of ‘regulated deficit irrigation’ have now been shown to reduce the quantity of water required for food production without substantially decreasing the yield in a wide range of species, including tomato, sunflower, oilseed rape, mango and rice.

**Taking control of growth**

Water shortages can also affect plant development and we may also wish to control this in our crops. It will frequently be beneficial to maintain root growth to reach water supplies deeper beneath the soil, and keeping leaves and shoots growing to increase total photosynthesis may be the best strategy if there is a limited but reliable water supply. However, if conditions are more severe it could be better to reduce the leaf area from which water can be lost. Plant growth needs water because (as with all organisms) cells are mostly made of water, but for plant cells to expand their cell walls must also be stretched by turgor pressure. Their rate of growth can fall either if the pressure drops, which can result from reduced water availability, or if the walls become stiffer.

It seems that drought signals such as the plant hormone abscisic acid often reduce growth by causing cell walls to become less extensible in the tissues they affect. However, it has also become apparent that water plasticises plant cell walls, and that moderate stresses could in principle inhibit growth by pulling water out of them. Figures 2a and 2b illustrate that treatments equivalent to water stresses can reduce the water content of walls of sunflower hypocotyls and make them thinner, and Figure 2c shows that these treatments also affected the rate at which they could be stretched. It seems likely that the strength of this effect depends on how strongly the polysaccharides of the walls can hold onto water and therefore that wall composition could be used to control growth of plant tissues under water stress. This has not yet been explored but may offer a tool to influence crop physiology under drought conditions.

This article barely touches upon the wide and diverse range of approaches that researchers are exploring to protect our food production in light of the challenges that we face. Our odds of finding solutions will be best if we keep as many options in mind as possible, not least because different things may work best in different areas and for different crops. However, the success of at least some of these projects will be critical for the history of the 21st century.

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