CENTER ON CONFLICT AND DEVELOPMENT
TEXAS A&M UNIVERSITY

EVOLUTIONARY STRATEGIES IN PLANTS

C-3, C-4 AND CAM

Spring 2016 | Taya Brown

There is no denying the importance plant sciences play in the health of human kind. We eat plants in whole and processed form, eat animals that eat plants, use plant material for paper, building materials and clothing, and create ethanol and other fuels from plant matter.

As we learned in the first week of class, 13 of the 15 CGIAR (Consultative Group for International Agricultural Research) centers are focused on specific crops because of their integral nature in subsistence around the world. Agriculture is increasingly important in the developing world, as "75 percent of poor people in developing countries still live in rural areas, where agriculture is critical to incomes and food security" (Messer, et al., 2001 p. 9). Norman Borlaug is accredited with fathering the Green Revolution and saving a billion lives due to his diligence in plant breeding, which produced dwarfed, non-lodging and disease resistant varieties of maize, wheat and rice (Godfray et al., 2010, p.815). The Norman Borlaug story exemplifies how an understanding of plant function facilitates effective management of the crops we rely on, directly aiding food production and other crucial industries. Plants also regulate oxygen and carbon cycles, both in microclimates and on the global scale, pulling CO_2 out of the atmosphere and literally creating the oxygen we breathe.

The better we understand the crops we grow, and plants in general, the better we are able to develop cultivars and management systems efficient and productive enough to feed the growing population. As science produces data on the physiology of adaptive crop species insight is gained that steers breeding programs, transgenic modifications, fertilizer and pest control applications, and many other agendas increasingly important to a food secure future.

Plants are static, meaning they do not have the mobility that insects and animals do, and cannot move themselves from one environment to another, or out of harms way. Yet, even with these severe limitations plants have adapted many eloquent ways to maintain life, health, and reproduction, some in the world's most inhospitable environments. Some adaptations lend a strong advantage over others in certain environments, and are therefore of great interest to crop scientists as they seek ways to raise efficiency and production levels. Here I will provide a general description of plant physiology, including three adaptive carbon fixation pathways employed by various species in order to thrive in otherwise inhospitable (generally hot and arid) environments.

PLANT PHYSIOLOGY BASICS

On a very basic level a plant is essentially a complex straw: One end is embedded in the soil, like the end of a drinking straw in a glass of water, and water is drawn up, through the plant, and into the atmosphere, like water is drawn up through a straw. In plants, this is analogous to a one-way circulatory system that relies on a water-potential gradient to draw water upwards.

The gradient works like this: there is *high* water potential in the soil because there is already water there, and *low* water potential in the air because it is relatively dry and can absorb water (see Figure 2). Soil-borne water moves across root membranes into the plant's vascular tissue, called xylem, and is pulled up through xylem tracheids (cells that resemble short drinking straws, see Figure 1), then exits the plant through small openings on leaf surfaces called stomata, all following the water-potential gradient. Stomata are pores where gas exchange takes place in plants, usually located on the bottom surface of leaves where they are protected from excessive heat, wind and rainfall. About 5% of the water up-taken by a plant takes part in metabolism within the organism and the remaining 95% is ultimately released into the environment.

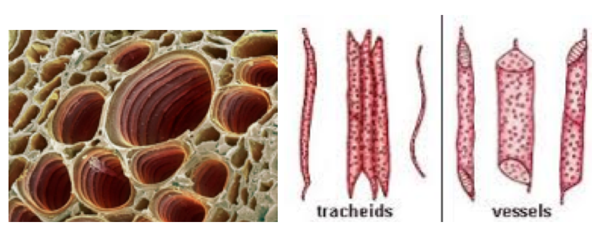

Figure 1. The photograph on the left shows a cross sectional view of Xylem tracheids. The drawings on the right depict the various types of straw-like xylem cells. Photo credit: Dr. David Furness, Keele Univ.

Plants are the only organisms on the planet (aside from a few photosynthetic bacteria) that can harness energy from photons of sunlight, which have travelled 150 million kilometers to reach the Earth's surface (Campbell and Reece, 2005, p. 181), and utilize this energy source to fuel the construction of organic matter. Through this process, known as photosynthesis, CO_2 from the air is taken into the plant and incorporated into short carbon chains, which are ultimately strung together, becoming the backbones of organic molecules we call carbohydrates. The carbon-based (aka organic) molecules provide material for the structure of plant tissues, including secondary cell walls, which keep plants rigid, and also fuel metabolic reactions. This process is truly an amazing feat. Take a minute to look around you and notice how much plant-based material there is, i.e. wood, paper, cotton, and consider that every plant, and every single plant-based product, is an assimilation of carbon that was pulled right out of thin air. Yes, even the largest redwood and sequoia trees, respectively the tallest and largest known organisms on the planet, are made almost entirely of carbon that was once *air*. Not only is it amazing but it is also incredibly useful. Organisms like cows, pigs, chickens and humans eat plants and metabolize the nutrients and energy embedded in them in order to fuel their own metabolic processes.

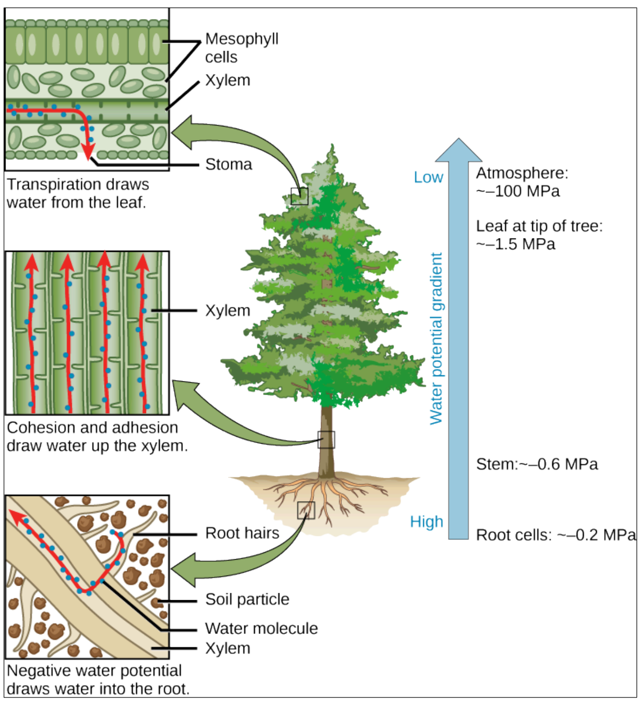

Figure 2. This diagram depicts water flow through a plant, from soil to atmosphere, by means of a water potential gradient.

Credit: UC Davis Bio Wiki

Photosynthesis is a two-step process: a "light cycle" and a "dark cycle" (See Figure 3). Step one is the "light cycle," in which photons of light are absorbed by proteins on the plant's surface and their energy used to break water (H_2O) molecules into atoms of hydrogen and oxygen. Oxygen is released back into the atmosphere, where organisms like humans (and most other terrestrial life) rely on it for respiration. Energy from the hydrogen-oxygen bonds is captured and stored within the bonds of simple molecules called ATP and NADPH. Both relatively small, ATP and NADPH are transported easily, carrying energy from place to place, and are key contributors in the vast majority of metabolic reactions within all organisms, including humans. Step two is known as the "dark cycle," or Calvin cycle, after Melvin Calvin, one of the scientists who first recognized this stage of photosynthesis. This step occurs when carbon from the air (in the form of CO_2) is drawn in through the stomata and incorporated into carbohydrates. Though this step relies on energy captured in the light cycle, these two cycles don't always occur simultaneously, as described below. Incidentally, carbon-carbon bonds are some of the strongest electro-chemical bonds that exist, which is why the human metabolism cannot break down many carbon chains or lattices. Carbohydrates, or "fibers" that we cannot metabolize, such as cellulose, form the basis of dietary fiber.

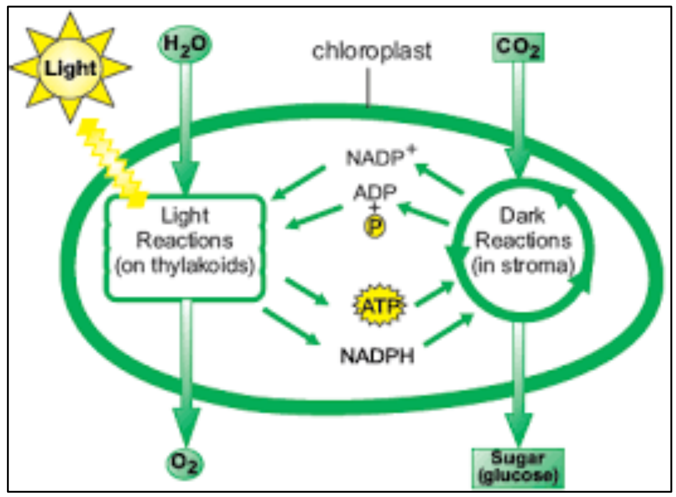

Figure 3. The two steps of photosynthesis: The light cycle and the dark cycle.

Credit: http://dev.elearn.punjab.gov.pk

Plants must play a delicate balancing act. The same pores from which water exits the plant, called stomata or stomates, must be open in order for CO_2 to be taken in. However, this causes a major dilemma: if stomates are open to allow CO_2 in, then they are also letting water out. In an arid climate, or on a hot sunny day when the air is very dry, the ambient environment has a strong affinity for absorbing H_2O molecules, and water may evaporate out of the plant at an unhealthy rate. This is exacerbated by the fact that, generally when and where it is hot and dry in the air, the soil is also hot and relatively dry, so there is less water available to replace what is lost. Stomates can be closed to protect the plant from losing too much water, but only for a certain period of time because the plant must also be taking in CO_2 with enough regularity to keep up carbon synthesis and metabolic functions (See Figure 4).

Due to this specific dilemma many plants have developed interesting adaptations to the photosynthetic process. By separating the two photosynthetic cycles carbon can be stored and assimilated while the stomata are closed losing less water throughout the photosynthetic process. Separation of light and dark cycles can be physical, where each takes place in a different location within the plant, or it can be temporal, where one takes place during the day, when photons are present and the other at night when ambient temperatures are cooler. The following are descriptions of the three most notorious photosynthetic pathways, two being adaptations to the first, along with examples of crops that utilize these methods.

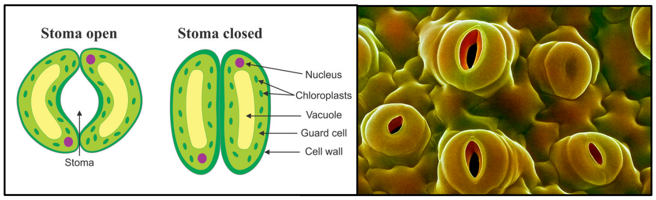

Figure 4. Left: This diagram shows stomate anatomy, which consists of two guard cells flanking the stomatal opening. When the guard cells are turgid, a differential between the cellular membrane causes disproportionate inflation, opening the space between them. Right: SEM photograph of open stomata on leaf surface.

PHOTOSYNTHETIC PATHWAYS

C-3 gets its name from the 3-carbon chains produced, and is the most common photosynthetic pathway. In C-3 plants like wheat, rice and soybean, both photosynthetic cycles occur at the same time. In terms of production, respectfully, these three crops were 2nd, 3rd, and 6th in the world in 2008, just behind maize (Goldschein, 2011). For these plants a hot climate means a dramatic reduction in carbohydrate production. When a C-3 plant senses heat, windiness or aridity, the reaction is to mitigate water loss by partially or fully closing stomata, which in turn slows or stops photosynthesis, reducing or halting carbon assimilation (Campbell and Reece, 2005, p. 195). C-3 plants perform much better in milder climates with some level of ambient humidity and relatively lower temperatures. In these climates stomata can remain open during the day, when the sun is out and photons are present, and continuously produce energy without losing too much water.

C-4 is named for the 4-carbon sugar produced as an interim molecule in the process of photosynthesis. Many grasses are C-4, including corn, the main ingredient in U.S. livestock feed, "accounting for 95% of total [U.S.] feed production" (USDA, 2015). With over 90 million acres planted annually in the United States and 130 million metric tons grown around the

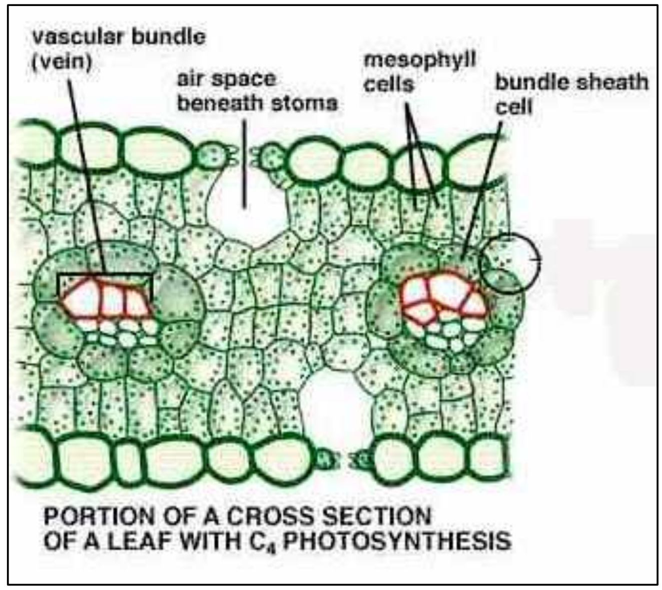

Figure 5. The special Kranz Anatomy of C-4 photosynthesis.

world (USDA, 2015), corn is an economically and nutritionally integral crop. In the U.S, corn is grown almost entirely within the heartland states, two thirds within Iowa and Illinois alone, where the summer growing season is hot and dry and there is little access to irrigation. Therefore C-4 processes are one of the main reasons these states are able to produce 10.8 billion bushels (NCGA, 2013) of corn each year.

A specific anatomical characteristic is associated with C-4 plants, called Kranz Anatomy (See Figure 5). This special anatomy facilitates the spatial separation of the light and dark cycles during photosynthesis. Mesophyll cells are loosely arranged just below the leaf surface and, within these cells, the interim four-carbon molecules are synthesized (Campbell and Reece, 2005, p. 196). These short carbon chains are then transported into, and concentrated within, cells called bundle sheath cells that are tightly packed in a ring around the vascular tissues. CO_2 from the 4-carbon chains is re-released inside these cells and the enzyme that synthesizes carbohydrates is bombarded. Because of the high concentration of CO_2 that builds up in the space around it, the enzyme functions much more efficiently (Campbell and Reece, 2005, p. 196).

CAM stands for crassulacean acid metabolism, named for the Crassulaceae plant family in which this process was first identified (Campbell and Reece, 2005, p. 197). CAM photosynthesis is most common in succulents, which have evolved high water holding capacity due to the extreme heat and aridity where they are naturally located,. CAM processes are found in important crops such as sugar cane, agave, and pineapple (Campbell and Reece, 2005, p. 197).

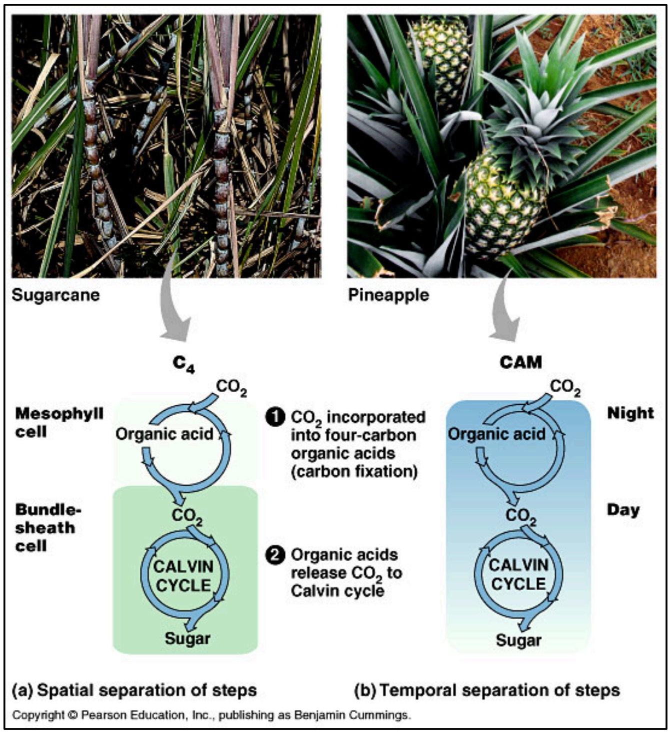

Figure 6. A visual depiction of the similarities and differences between C-4 and CAM; both have adapted to utilize the same four-carbon chain as an interim molecule, as seen in steps 1 and 2 in this diagram, facilitating separation of the two cycles, however C-4 compartmentalizes spatially utilizing mesophyll cells as the interim space while CAM relies on temporal separation.

The CAM pathway temporally separates the light and dark cycles, allowing stomata to open during the night, taking in CO_2 in the cooler nighttime temperatures, and remain shut during the hot days, greatly reducing water loss. "Typically, a CAM plant loses 50 to 100 grams of water for every gram of CO2 gained, compared with 250 to 300 grams for C4 plants and 400 to 500 grams for C3 plants" (Taiz and Zeger, 2010, p. 222). This pathway also utilizes an interim form of carbon storage, like C4 plants do, but stores these carbon chains within the same cell where the rest of photosynthesis also takes place. The interim carbon chains are stored until daylight, when photons are present and the light cycle commences.

CONCLUSION

These three photosynthetic pathways all produce the same end results – the plant processes CO_2, H_2O and sunlight, ultimately fixing carbon from the atmosphere and turning it into the structural energy containing molecules plant tissues are made of. There are clear advantages to each of the photosynthetic processes described here. Through understanding how these processes work, the various differences between them, and their respective advantages and disadvantages, scientists can improve production methods in currently produced crops and also breed or otherwise manipulate plant genetics to develop cultivars that will either produce more efficiently under current conditions and management, or function well in less than ideal climactic conditions. As the population continues to increase and humans tax the natural environment further with our demand for quality foods and other products, understanding plant physiology, including the various photosynthetic pathways, will become increasingly more important to the future of our species. ∞

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