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Optofluidics of plants

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Optofluidics is a tool for synthesizing optical systems, making use of the interaction of light with fluids. In this paper we explore optofluidic mechanisms that have evolved in plants where sunlight and fluidic control combine to define most of the functionality of the plan. We hope that the presentation of how plants function, from an optofluidics point of view, will open a window for the optics community to the vast literature of plant physiology and provide inspiration for new ideas for the design of bio-mimetic optofluidic devices. [http://dx.doi.org/10.1063/1.4947228]

The plant in Figure 1 is a *calathea* and it lives in the house of one of the authors (DP). The picture in Figure 1(a) was taken in the middle of the day when ample sunlight was coming through the window. Figure 1(b) was taken at 9 pm when it was dark. The plant spreads its leaves at dawn, as the sun rises. In the evening, the plant collects its leaves into a tight bundle and seemingly goes to sleep. What triggers this daily transformation? One possible mechanism is an internal clock analogous to the circadian rhythm cycles that prevent us from sleeping at night when we are jet lagged.[1] Another possibility is that the plant "wakes up" when the light reaches its leaves. This must be at least partially true for the calathea plant since when exposed to bright artificial light in the middle of the night, it spreads its leaves. This daily reorientation of the leaves in response to the sun is a form of heliotropism[2] or more precisely diaheliotropism when we refer to the movement of leaves rather than flowers.[3] Such movements are generally initiated by optically induced flows of water in and out of special cells, modifying their mechanical properties (stiffness) causing the stem of the leaves to bend. The resulting movement automatically reorients the leaves so that more light is absorbed.[4] Lacking a central nervous system, plants rely on such light-fluid interactions in a distributed, autonomous way, in order to carry out many of the tasks necessary for their survival. In this paper, we highlight examples where the flows of fluid in plants are controlled by light and also examples where the optical properties of plants are modified with fluidics.

Photosynthesis,[5] the most important and extensively studied plant-light interaction, harvests solar energy to manufacture the fuel that plants use to grow and reproduce. Incidentally, this process is the source for all the food that animals and humans consume, directly or indirectly. While photosynthesis is primarily a photochemical process, it also relies on important optofluidic processes since the incident light induces fluidic flow and the photosynthetic cycle is driven by light induced flow of fluids (liquids and gases).

Photosynthesis takes place in an intricate network of membranes inside the cells of leaves.[6] These membranes divide the cell interior into compartments filled with fluids (mostly water) containing somewhat different chemical composition (Figure 2). Incident photons are absorbed by light sensitive molecules (chlorophyll pigments)[7] embedded at the membrane of intracellular compartments. These compartments are called thylakoids. This process releases hydrogen ions[8] into the inner compartments of the thylakoids.[9] At the same time oxygen gas and other molecules are

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FIG. 1. *Calathea* plant. (a) In the middle of day, the plant spreads its leaves. (b) At night, the plant closes into a tight bundle.

released to the outside of the thylakoid. This process disturbs the balance between the liquids that reside on opposite sides of the thylakoid membrane. Since the membrane is permeable, protons, water molecules, and other molecules cross the membrane to restore the balance.[10] A consequence of the cross-membrane flow is that some of the energy of the absorbed photons is ultimately transferred to the chemical bonds of hydrocarbons that the plant can readily use as fuel.[11] At the same

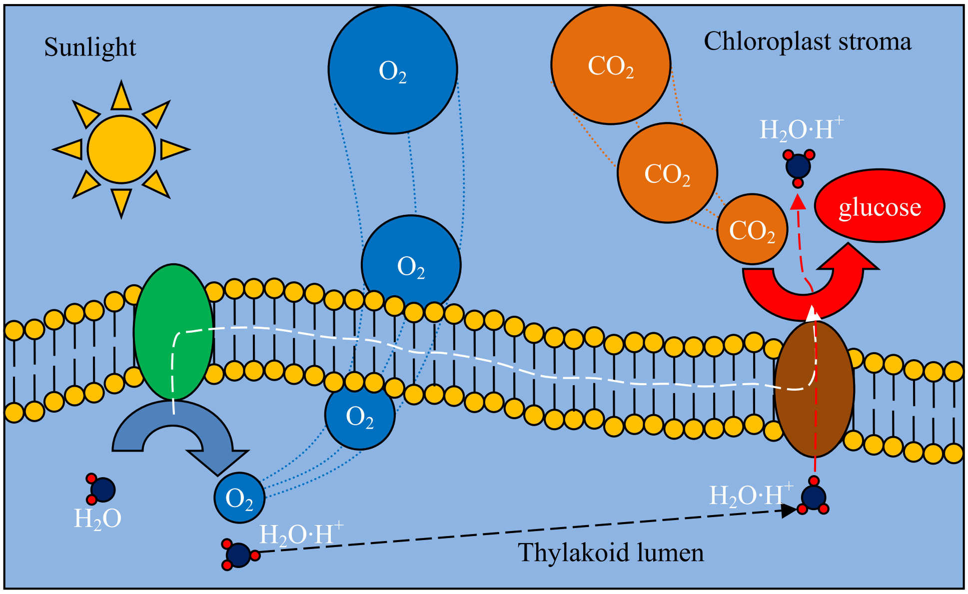

FIG. 2. Diagram of photosynthesis, which occurs at the thylakoid membrane inside the chloroplast. At the chlorophyll pigment, energy from sunlight is used to split water into protons and oxygen gas. The proton is used to split carbon dioxide gas into glucose.

FIG. 3. Image of a *Ficus elastica* leaf. The complex microfluidic network can be seen clearly.

time, the flow across the membrane alters the chemical composition, the acidity, the pressure, and the shape of the different fluidic compartments inside the cell.[12] The changing shape of the cell can alter the optical properties (cross section, scattering properties, lensing, waveguiding) of the tissue they are part of.

Leaves contain a complex, intricate microfluidic network (Figure 3).[13] The main channels (veins) are clearly visible in most leaves. Smaller microfluidic channels branch out from the main veins to reach the various organelles inside the leaf (chloroplasts containing the photosynthetic thylakoid membranes, mitochondria).[14] The finer veins (Figure 3) are microfluidic channels that range from 10 to 30 μm in diameter and are spaced 10–100 μm apart.[15] This extensive microfluidic network distributes through the leaf water that is absorbed by the roots or through the surface of the leaves. A separate set of microfluidic channels takes water containing nutrients generated through photosynthesis to other parts of the plant where they are either stored or consumed. The part of the microfluidic network that brings water up from the ground is called the xylem. The upward transport of water is driven by light induced evaporation or transpiration.[16] Capillary action does the rest of the job.[17] The portion of the light that is not used by photosynthesis is converted to heat and raises the temperature of the liquid in and around the cell leading to water evaporation.[18] The water vapor finds an outlet to the outside through openings in the leaf membrane. These openings are called stomata. Stomata are remarkable optically controlled valves. We will discuss them further later on. A mature tree can pump up to 50 kg of water on a sunny day.[19] Assuming that the tree is 5 m tall, the potential energy needed to raise the water is only 5.4 MJ. This is a small portion of the energy delivered to the tree by the sun.

How much energy does the sun deliver to a typical tree? Assuming the surface area of the tree foliage is 12.5 m^2 (Figure 4) and the light intensity of the sun is 1 kW/m^2 then the energy incident over 6 h on a sunny day is 270 MJ. About half the light is reflected in a typical leaf leaving 135 MJ absorbed. A simple calculation shows that the energy needed to evaporate 50 kg of water is roughly equal to 114 MJ. Comparing this value to the 5.4 MJ increase in potential energy required to raise

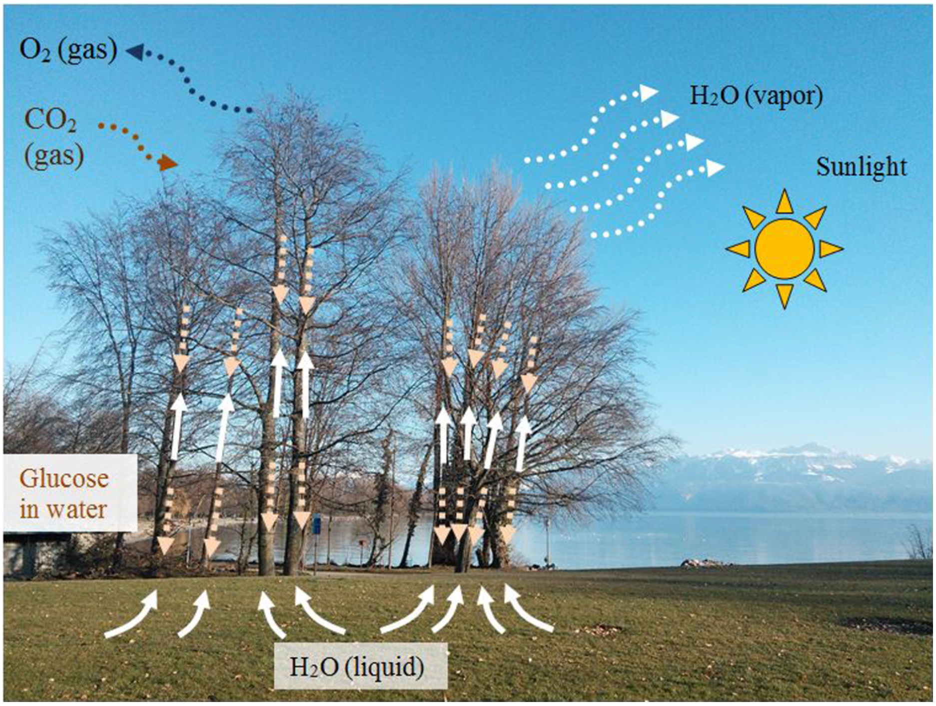

FIG. 4. Photograph of trees near Lake Geneva overlaid with a diagram showing fluidic flows. The energy required to pump water from the roots to the leaves is partially provided by the sun. At the leaves, most of the water evaporates. Additionally, some of the water is used with carbon dioxide to produce oxygen and glucose. Glucose makes its way back down to the roots for storage.

the water by 5 m in the example above, we conclude that the tree uses most of the energy it receives from the sun to heat and evaporate water.[20]

The efficiency of photosynthesis is low. Typically only 1%-3% of the absorbed light is converted to chemical energy even though it can be as high as 8% in plants such as the sugar cane.[21] It is interesting to ponder why the tree spends so much of the solar energy available to it for heating and pumping water. A possible answer may be found in the observation that the leaves in trees found as far north as southern Alaska and as far south as Mexico have the same temperature: 21.4 °C, near the optimum temperature for photosynthesis.[22,23]

Light also plays a significant role in the control of the flow in the portion of the microfluidic network that transports the fluids from the leaves to other parts of the plant (the phloem).[24] The phloem distributes the fuel generated through photosynthesis to multiple destinations in the plant. Most scientists believe that plants do this by adopting a strategy that economists might approve of: Supply and demand. If there is excess concentration of a particular substance in a region adjacent to part of the phloem, then, water flows into that region to balance things out.[25] The process for management in the microfluidic networks of plants (the xylem and the phloem) is explained with the help of the diagram in Figure 5. The concentration of the various chemicals in the tissues that surrounds the phloem is determined by many interrelated chemical processes. At the leaves in particular, sunlight generates excess concentration of nutrients through photosynthesis. Therefore, flow in the phloem at the leaves is ultimately driven at by light induced chemical gradients.

During the day, plants import CO_2 from the atmosphere and water primarily through the roots[26] and release oxygen in the atmosphere, a byproduct of photosynthesis. At the same time, plants during the day release large amounts of water vapor through the leaves. At night, most plants cease the exchange of fluids with the outside.[27] The openings on the leaf that control the fluidic flow are called stomata (Figure 6). In the presence of light, the stomata open up (Figure 6(a)) and

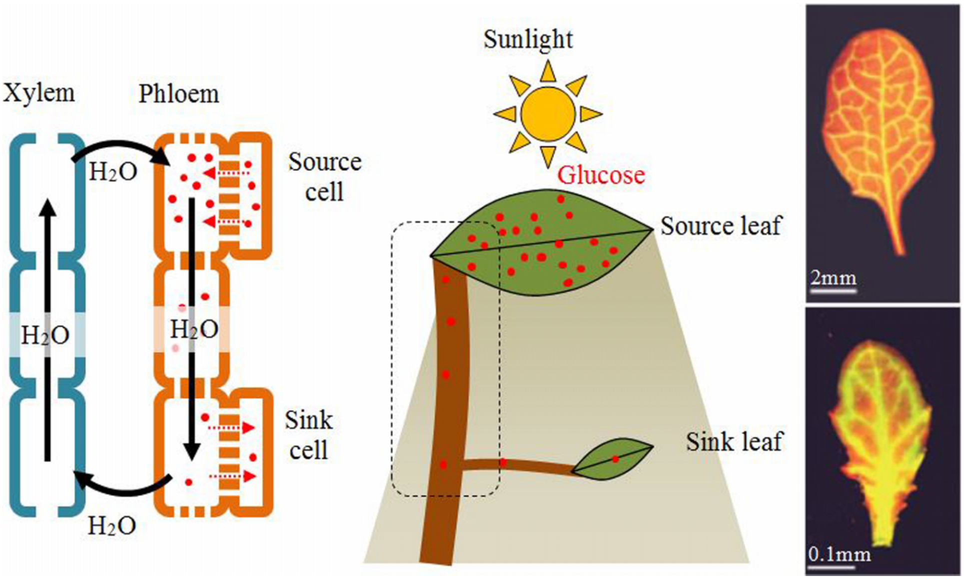

FIG. 5. Phloem network. Osmotic flow of water into the cells of the phloem near the source cell increases the pressure locally. This drives the excess glucose away from the high concentration region through the phloem network. If, at the same time, this same substance is consumed at another leaf and its concentration locally drops, then the process is reversed: Water flows out of the phloem cells through osmosis (the low concentration is the same as too much water) and the pressure at that location drops. In this way, nutrients are delivered from source to sink, as they become available and as they are needed. On the right, photographs of a source leaf (top) and a sink leaf (bottom) belonging to transgenic *Arabidopsis* plants expressing green fluorescent protein (GFP) on the companion cell (CC)-specific *AtSUC2* promoter are shown. Since the *AtSUC2* promoter is a source leaf specific activity, no GFP is produced at the sink leaf. The GFP can move from the source leaf to the sink leaf via the phloem [reprinted with permission from Stadler *et al.*, Plant J. **41**, 319-331 (2005). Copyright 2005 Wiley].[48]

in the dark, they close again (Figure 6(b)) in order to prevent moisture from escaping the plant unnecessarily.

Each of the stomata consists of a pair of special cells on the epidermis (the skin) of the leaf called *guard cells*.[28,29] The guard cells have an asymmetry in the mechanical stiffness of their membranes. The membranes that touch each other are stiffer. When light hits the two guard cells, protons are generated in a process similar to photosynthesis and they are released from inside the cells. The proton gradient drives potassium ions into the cells. The positive charge of the potassium ions attracts negative ions from the fluid surrounding the cell (typically chloride ions), which penetrate the membrane and induce an excess salt concentration inside. This triggers osmotic water flow into the guard cells to compensate for the increase in salt concentration. The increased osmotic pressure (referred to as turgor) puffs up the guard cells like small balloons and the asymmetry in the stiffness of the membranes causes the inner membrane to deform in such a way that it opens up a passage for fluids to enter and exit the leaf interior (see Figure 6). This remarkable sequence of events relies on an intricate interaction of the optical, mechanical, and fluidic properties of the guard cells.

Most leaves are semitransparent in the visible range of the electromagnetic spectrum (Figure 3).[30] Their scattering, reflection, birefringent, and absorption properties are determined by the fluids and tissues inside the leaf. Leaves also exhibit various forms of intensity dependent optical properties (i.e., non-linearities) that generally depend on the levels of solar illumination.[31] An example of this is shown if Figure 7 which is a photograph of a *Philodendron leaf*. A pattern was recorded on this leaf by illuminating it for 10 min with radiation at wavelength 488 nm and intensity 0.1 W/cm^2. The illuminated areas become lighter as if the absorbing pigments that are responsible for the green color of the leaf have been bleached. Closer examination by imaging at higher magnification reveals that the discoloration is not due to bleaching but due to movement of the organelles inside the cytoplasm of the cells.[32] The green colored organelles visible in Figure 8 are the chloroplasts discussed earlier. The absorption of light in the blue and red by the pigments involved in

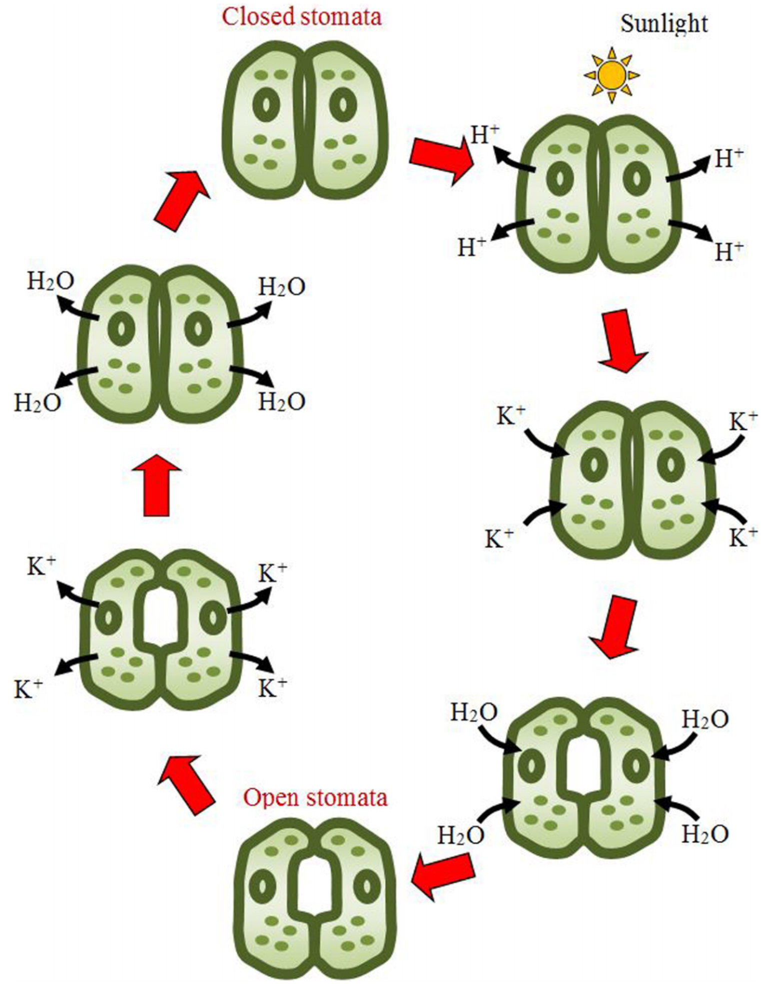

FIG. 6. Image of stomata. For a closed stomata, sunlight drives a proton pump. The proton gradient drives a potassium ion pump. The potassium ions bring chlorine ions with it, resulting in an osmotic pressure differential. Water goes into the cell, changing the shape of the guard cell into opening stomata.

photosynthesis filters the incident white light, leaving the green part of the spectrum to dominate in the backscattered light. This explains the green color of most leaves. With bright illumination, the chloroplasts aggregated near the side membrane of the cell in this top view, whereas the chloroplasts appear evenly distributed in the cells that have not been exposed to light. As they aggregate near the membrane, the chloroplasts shade each other and reduce dramatically the absorption cross section of the cell. Avoidance of thermal damage, photobleaching, and other possible negative side effects due to high light intensity are the reason for this nonlinear optical behavior.[33] This physiological response mechanism under intense illumination has been experimentally observed recently and termed "chloroplast avoidance motion."[33]

How do chloroplasts move? Chloroplasts were originally independent single cell organisms that developed the ability to harvest solar energy through photosynthesis just as algae do.[34] Plants in the very beginning of the evolution process relied on metabolizing chemical energy from nutrients obtained from their environment or possibly heat from hot springs.[35] At some point, chloroplasts entered the cytoplasm of cells and their ability to provide a "free" energy boost from solar energy (in the form of the coenzymes adenosine triphosphate - ATP - and nicotinamide adenine dinucleotide - NADH) was so welcome to the host that essentially all existing plants today use photosynthesis and contain cells with chloroplasts. Their independent origins explain the mobility of chloroplasts within the cytoplasm. But how do they swim in response to light illumination? When

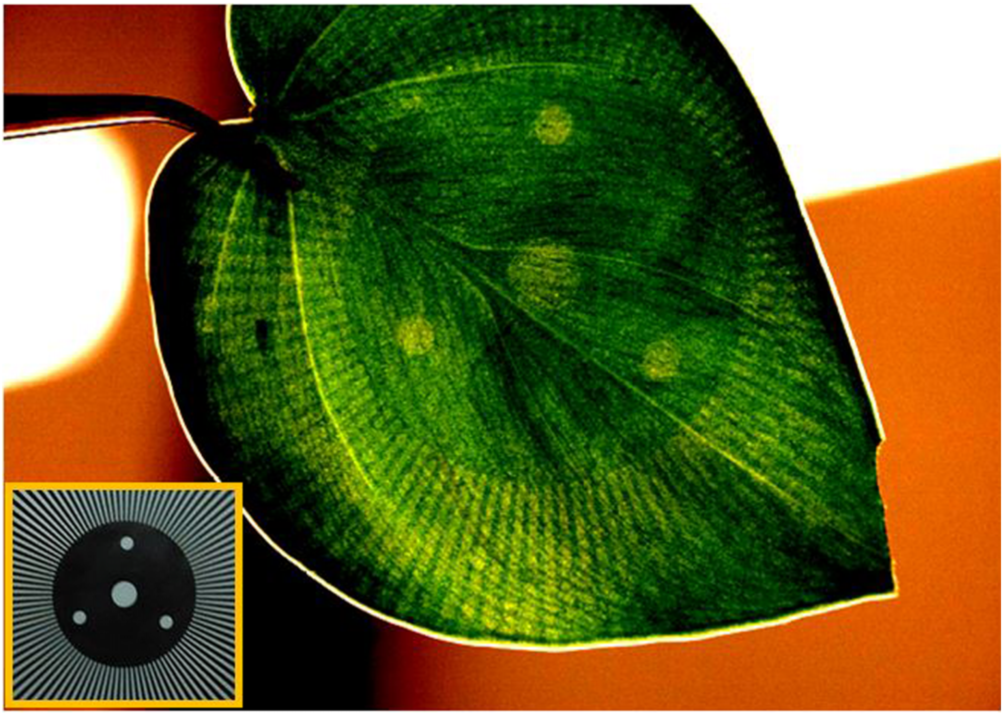

FIG. 7. *Philodendron* leaf exposed 10 min with a 488 nm laser at 10^3 W/m^2 covered by a transmission mask. Inset shows mask pattern.

light is absorbed by chlorophyll, fuel is produced in the form of ATP and the cofactor dihydronicotinamide - adenine dinucleotide phosphate (NADPH) in the thylakoid of the chloroplast. Specific to ATP production, this is produced by the generation of excess hydrogen cations, which are then transferred across the thylakoid membrane. This transfer process generates an electrochemical proton gradient, which is catalyzed by the ATP synthase enzyme to generate ATP.[49] ATP then powers the molecular motors that move chloroplasts along the cytoskeleton of the cell.[36] The chloroplasts

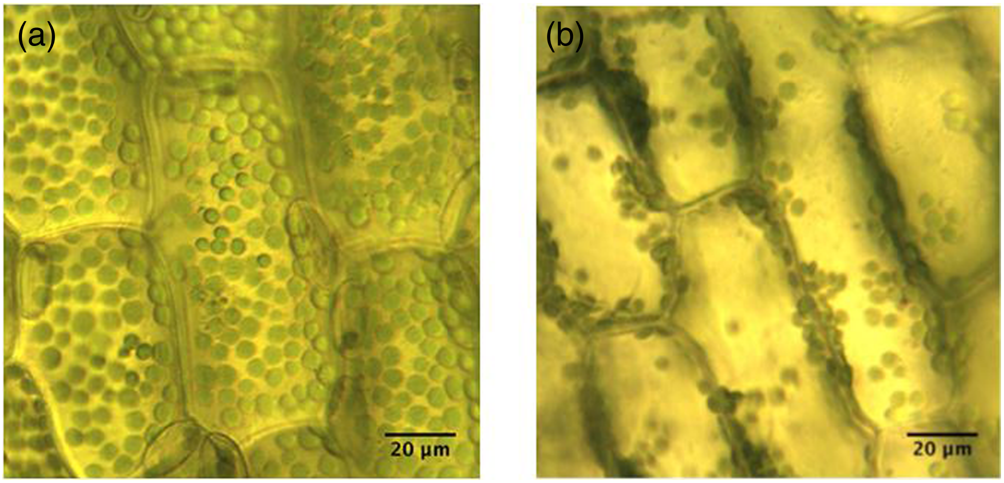

FIG. 8. Widefield image (50×) of chloroplasts in *Elodea*. (a) dark and (b) 10 min of exposure with 488 nm laser at 10^3 W/m^2. Chloroplasts avoid thermal damage and other possible negative side effects due to high light intensity. As chloroplasts aggregate near the membrane wall, the chloroplasts shade each other and reduce dramatically the absorption cross section of the cell.

start moving in arbitrary directions when strong light is present. When they reach the edge, they get stuck there. When the light is removed, diffusion redistributes them uniformly. There is some evidence that at weak illumination, the gradient of light intensity can drive the chloroplasts to bunch up along the cell surface perpendicular to the incidence angle of the sun. In this way, the movement of the chloroplasts, triggered by sunlight, optimizes light absorption depending on the illumination conditions.[36] Coupled with the light driven evaporation for thermal management and the remarkable interplay of optics and fluidics powered by built-in photochemistry, the leaf has the ability to dynamically adapt to make best use of the available solar energy while minimizing harm from overexposure.

Most leaves are highly scattering objects. However, the scattering properties of leaves can be affected by the light illumination.[37] All young leaf buds look the same. Plants on top of the canopy that are directly exposed to light tend to have smooth surfaces whereas shaded leaves develop rough surfaces. Some leaves even form lens arrays on the top surface so that light is focused on the cells below.[38] This is a prudent optical design since leaves on the canopy receive collimated light on sunny days. A smooth top surface maximizes the penetration of light to reach the cells where photosynthesis takes place aided in some cases by optical waveguides that transport the light deeper into the leaf volume.[39] On the other hand, the rough surface of the leaves at the bottom of the tree allows a larger portion of the angular spectrum of the diffuse light illumination to enter the leaf. We suspect that the formation of the texture of the leaf depending on the incident light is an example of the leaf using its microfluidic and biochemical machinery to control its optical properties.

The dramatic movements that the *calathea* plant makes daily are a form of *tropism*.[40] The movements can be actuated through preferential growth driven by light gradients (phototropism)[41] or by optical modulation of the osmotic pressure of *motor cells* (heliotropism)[42] in a mechanism similar to the guard cells of the stomata. These plant movements aim to either increase or reduce the amount of light received by the plant. Phototropism[43] generally occurs at longer time scales, typically over several days. Special light sensitive molecules (other than chlorophyll) signal the production of hormones (called auxins), which diffuse through the nearby portion of the plant and control the growth of the plant, generally towards the direction of the illumination (Figure 9).[44] This process involves, indirectly, the interaction of light and the fluids inside the plant since the release of auxins is optically triggered and their transport is fluidic.[43] A more direct optical-fluidic interaction is employed in heliotropism where the incident light change induce

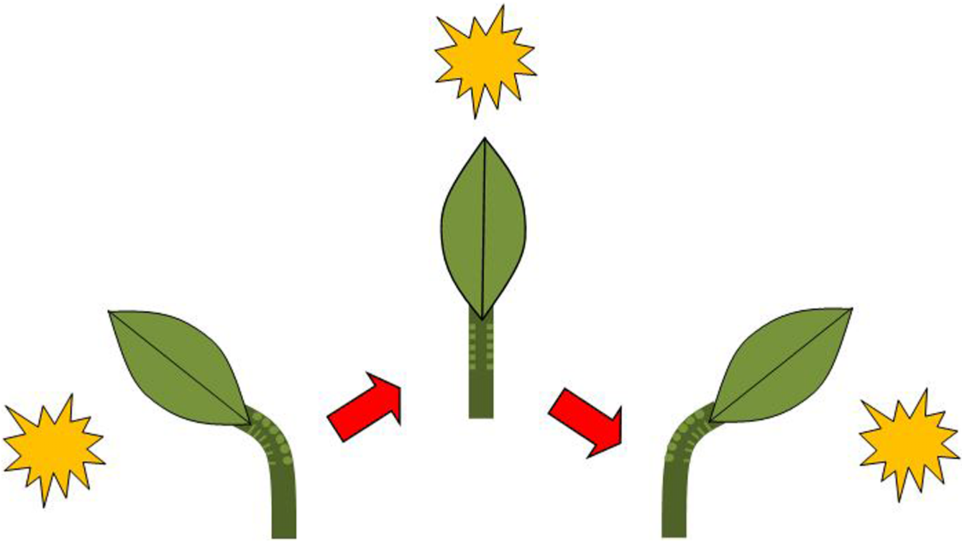

FIG. 9. Diagram of pulvinus in the plant. The cells react to sunlight, changing their turgor. The change in stiffness causes a daily motion of the plants.

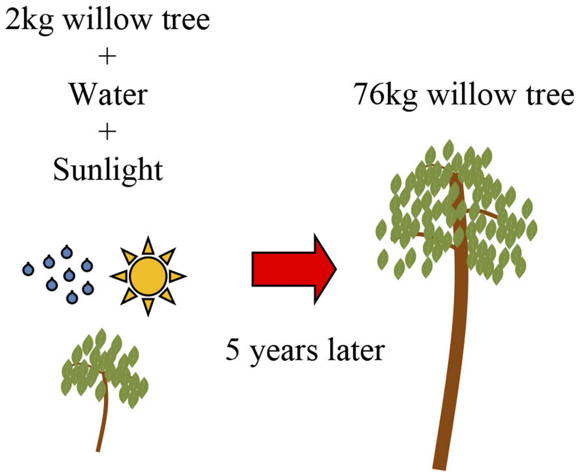

FIG. 10. Jan Baptiste van Helmont experiment.

excess water to flow in motor cells located at the stem of leaves or flowers.[45] The excess water increases the pressure in cells facing the sun, thereby, stiffening the entire stem, causing it to face towards the sun, thereby, increasing its absorption cross section. In this case the fluidic flow in the plant is controlled by light while the fluidic adjustment modifies the plant's optical properties.

In 1649, Jan Baptista van Helmont planted a willow tree seedling in a pot and carefully measured the weight of the plant at the time of the planting and after 5 years growth.[46] The additional weight was 74 kg (Figure 10). He was very careful during the 5 years to make sure that the only substances that entered the pot were distilled water and air. With this experiment he showed for the first time that the mass produced by the growing plant was the result of the interaction of light with two fluids: Water and air from the atmosphere. We now know that photosynthesis is responsible.[47] A plant is also a remarkable water pump drawing water from the soil through its roots and releasing almost all of it as water vapor through the leaves. Most of the solar energy that the plant absorbs is used to help pump the water up and produce water vapor released in the atmosphere. This water transport also brings small amounts of extra nutrients. This water pump is partially driven by the sun while only a few percent of the sunlight energy is trapped in the chemical bonds of the fuels produced by photosynthesis. The dominant portion of the absorbed solar energy is used for thermal control and pumping. The tree lacks a central nervous system (brain), a central temperature control apparatus, a central fluidic pressure management mechanism, or a powered central pump (heart) that controls fluid distribution throughout its body. Instead, it has evolved a remarkable toolkit of distributed mechanisms combining optics, fluidics, and biochemistry to do all these things. The interaction of optics and fluidics (optofluidics) is a key element in all of this.

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