e-ISSN:2582-7219

INTERNATIONAL JOURNAL OF MULTIDISCIPLINARY RESEARCH IN SCIENCE, ENGINEERING AND TECHNOLOGY

Volume 5, Issue 6, June 2022

INTERNATIONAL STANDARD SERIAL NUMBER INDIA

Impact Factor: 7.54

International Journal Of Multidisciplinary Research In Science, Engineering and Technology (IJMRSET)

| ISSN: 2582-7219 | www.ijmrset.com | Impact Factor: 7.54||Monthly, Peer Reviewed & Referred Journal |

| Volume 5, Issue 6, June 2022 |

| DOI:10.15680/IJMRSET.2022.0506095 |

Plant Biophysics and Modeling

Ms. Shubhra Chaturvedi

Assistant Professor, Botany, Govt. College, Malpura, Tonk, Rajasthan, India

ABSTRACT: Plant biophysics and modeling is diverse, ranging from the molecular to the organismic level. It covers the areas of molecular and cell biophysics, physiology, bionics, computational cell biology, structural protein analyses, synthetic biology, quantitative plant development, and biomechanics. Biophysics is best defined as a mindset than as a specific subject matter (Nobel, 1974; Phillips et al., 2008). The biophysicist strives to quantify biological processes and to analyze them in terms of universal physico-chemical principles such as mass conservation, force balance, and thermodynamic equilibrium. Biophysics has played an important role in the growth of biology, especially in elucidating how the folded structure of proteins determines their function (Anfinsen, 1973; Dobson, 2003), but also in providing a solid foundation for electro-physiology, photosynthesis, respiration, and many other basic biological functions. The lasting contributions of physicists-turned-biologists such as Max Delbrück (Luria and Delbrück, 1943; Delbrück, 1970) and Francis Crick (Watson and Crick, 1953; Crick, 1970) illustrate the power of the physical perspective in biology.

The scope of biophysical investigations in plants is vast. Photosynthesis makes plants both unique in their biology and indispensable for life on Earth. Most of the processes taking place within plants support, directly or indirectly, the central photosynthetic function of the chloroplasts. Plant biophysics can thus be thought of as a rigorous quantification of the processes associated with green life. The 400 million years elapsed since the movement of plants onto land have yielded a tremendous diversity of structures capable of lifting chlorophyll-bearing cells to more than 100 m into the air (Holbrook and Zwieniecki, 2008), of accessing water in arid conditions (Mooney et al., 1980), and even endowing plants with the ability to move with sufficient swiftness to catch insects (Forterre et al., 2005). Many of the problems that had to be solved to accomplish these feats are physical in nature. It is therefore to be expected that plant biophysics has had a long and illustrious history that dates back to the publication of Stephen Hales' "Vegetable Staticks" in 1727. To these days, the steady publication of monographs on various aspects of plant biophysics is a testimony of the sustained appeal the field has had on quantitatively minded people (Clayton, 1965; Briggs, 1967; Slatyer, 1967; Nobel, 1974, 2005; Preston, 1974).

Several broad areas of research are likely to be the cornerstones of plant biophysics in the coming decade:
The problem of the structure–function relationship of proteins occupies a central place in biophysics. In and of itself, it reflects many of the subtleties involved in understanding how the information encoded in the genes contributes to the functions that support life at the cell level and above. Although the amino acid sequence, hence the primary structure, of a protein is plainly specified by the codon sequence of the gene, the detailed function of many proteins is not clearly seen until the tertiary structure of the polypeptide has been computed. This requires understanding in quantitative terms the electrostatic and steric interactions between different protein subdomains. Therefore, biophysics shows its importance from the very first step of the long causal sequence between the genes and plant functions. Yet, five decades after the formulation of the central dogma of molecular biology outlining the flow of information from the genes to proteins (Crick, 1958), computation of protein structures from first principles remains a daunting problem. The development of tools and new approaches to solve the structure–function relationship of proteins will undoubtedly continue to be an active area of research in coming years. Of particular interest for plants are the structure of photosystems I and II (Liu et al., 2004; Loll et al., 2005), of the various proteins involved in the assembly and modification of the cellulosic cell wall (Hrmova et al., 2002; Burton et al., 2006), and of cellulose itself (Nishiyama et al., 2002).

The use of light energy for the reduction of CO_2 and, ultimately, its incorporation into organic molecules, i.e., photosynthesis, is the best recognized biophysical problem in plant biology; and for good reason since the conversion of light into chemical energy is one of the most striking feats achieved by living organisms. In particular, the oxygenic photosynthesis performed by plants has led to the most drastic atmospheric change that the planet has seen (Canfield, 2005; Knauth and Kennedy, 2009) and presents itself again as a central player to counter the warming effect of rising CO_2 levels (Cox et al., 2000). Research efforts to understand photosynthesis resulted in several Nobel prices; yet we are just starting to comprehend this process well enough to tackle the fundamental trade-offs that have held photosynthetic efficiency to less than 5% of intercepted light energy for millions of years. Studies of carbon dioxide transport, membrane properties, light

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focusing, and protein interaction are just a few examples of biophysical research that could provide us with the tools to improve photosynthetic efficiency.

Another active area of biophysical research is the mechanism of plant cell expansion or plant growth in general. Some of the greatest challenges are to explain: (i) the dual role of the cellulosic wall in supporting the internal turgor pressure of the cell while, at the same time, allowing cell expansion (Geitmann and Ortega, 2009; Szymanski and Cosgrove, 2009); (ii) the feedback between growth and the flow of water across tissues to maintain osmotic equilibrium (Boyer and Silk, 2004); and (iii) the control of the direction of expansion in cells and plant organs (Baskin, 2005). Most plant cells grow in a highly anisotropic fashion, i.e., growth favors one direction over all others. The role of cellulose microfibrils in controlling the mechanical anisotropy of the wall was demonstrated many decades ago (Roelofsen, 1950; Green, 1962) although quantitative models are still few and not yet well established (Dumais et al., 2006; Dyson and Jensen, 2010). On the other hand, our understanding of the molecular basis of wall assembly, in particular the involvement of cortical microtubules, has developed tremendously in the last decade; in part because of the development of techniques to track microtubules and cellulose synthase complexes in vivo (Gutierrez et al., 2009; Chen et al., 2010; Nakamura et al., 2010; Chan et al., 2011). These breakthroughs, combined with robust protocols to track wall expansion at the subcellular level (Dumais and Kwiatkowska, 2002; Dumais et al., 2004), have opened the door for bottom-up models of wall assembly and cell expansion. This body of work offers the first glimpse of how gene products can specify cell shape.
The maintenance of life requires homeostatic control over the physico-chemical processes of the cell in the face of an ever changing environment. Thus perception, transduction, and response to environmental cues across organizational scales are at the basis of organismal life. We know that cells can sense general properties of their environment such as gravity (Leitz et al., 2009), light (Babourina et al., 2002), temperature, and of their immediate surroundings such as humidity, concentration of chemicals, and mechanical stress (Hamant et al., 2008; Uyttewaal et al., 2010). However, much has yet to be learned about the physical interactions, the integration of potentially opposing cues, and the link to molecular and genetic activity that allow cells to perform their functions.

The gross morphology of plants, as well as their internal organization, all speak to the fact that plants are transport systems whose function is to bring water and nutrients from the soil to the photosynthetic cells in the leaves and then distribute back photosynthates across the plant dendritic body. Unlike the vascular system of animals, the xylem and phloem of plants are open transport systems and operate without the need for moving parts. The stability of water in the xylem is remarkable as tension can exceed 10 MPa dwarfing the range of negative pressure that can be supported by most man-made devices. Only recently did biomimicking efforts lead to the construction of evaporation-driven devices capable of transporting water under conditions similar to those found in nature (Wheeler and Stroock, 2008). The role of structure and material properties in the maintenance of the transport capacity under tension remains an active area of biophysical research (Zwieniecki and Holbrook, 2000, 2009; Zwieniecki et al., 2001). Another important axis of research focuses on the exquisite control of the transpiration stream exerted by stomata (Blatt and Thiel, 1994; Blatt, 2000; Franks, 2004) and the root system (Bramley et al., 2009).

Plants stretch their branches and roots across tens of meters and are often thought of as modular organisms. Yet, they show a significant degree of functional and structural integration. As plants do not have any designated information distribution network, the two transport systems that pervade the plant body must act in lieu of a nervous system. The biophysical principles behind the use of the vascular network as “information superhighway” and its possible role to coordinate response at the organismal level is still an open and fascinating area of research (Frommer, 2010). Chemical transport, changes in tension and pressure, the sensing of pathogen attacks, and many other plant interactions with the external and internal environments result in systemic responses that use transport systems as the primary signal carrier with speeds often exceeding mass flow rates (Thompson and Holbrook, 2003; Thompson, 2006; Gorska et al., 2008a,b). To fully understand the informational role of transport systems we need to learn more about the link between material properties of the network and its micro-rheology.

It could be argued that the pace of progress in biology is in large part set by technological advances. The great improvements in magnification made to the microscope in the seventeenth century and the development of powerful molecular tools in the second half of the twentieth century have transformed completely how biologists approach the subject matter. We may therefore ask what technologies are likely to support the progress in plant biophysics in the coming decades. The probes and optical techniques for single molecule measurements are among the most exciting new developments (Weiss, 1999; Grier, 2003). For example, the atomic force microscope and optical traps have allowed the first measurements of the forces exerted by molecular motors (Funatsu et al., 1995; Mehta et al., 1999) and the force required to

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stretch macromolecules (Rief et al., 1997; Wang et al., 1997). The experimental effort within biophysics to understand green life is also supported by advances in biomimetics. Although the application of biomimetics to plants is relatively new, it has already transformed our understanding of the constraints acting on plant structures. For example, analysis of fluxes in artificial leaves made out of polyacrylamide provided the basis for scaling laws of leaf venation placement (Noblin et al., 2008), while microfluidic reconstruction of phloem revealed scaling laws linking the size of plant to phloem dimensions (Jensen et al., 2011). Other works have focused on the self-actuation and deployment of structures such as fruits pods and pollen grains (Burgert and Fratzl, 2009; Katifori et al., 2010) with an eye toward applying these in technology. While these examples are exciting, the big challenge of biomimicking photosynthesis or tension driven flow in all their subtleties will require a significant amount of future research.
These are only a few of the vast array of promising avenues for plant biophysics in the coming years. It is revealing that biophysics has remained an active area of research despite shifting attitudes toward physics and mathematics within the biological community at large. The success of the molecular genetics approach meant that much could be learned about cell biology, physiology, and development without resorting to models and mathematical analysis. During the reductionist era, many students saw in biology a safe haven away from physics and mathematics, a paradoxical situation given that molecular genetics was ushered by two eminently quantitative sciences, genetics and structural biology (Keller, 1990; Holliday, 2006). The purely reductionist era is now coming to an end. The rapid growth of systems biology and biophysics marks a return to a more healthy coexistence of reductionist approaches with integrative approaches that often rely on quantitative models and analyses (Bray, 2001). As we look toward the future of biophysics, the first grand challenge for the field will be to lead the way in promoting quantitative approaches in biology and quantitative skills among biologists. Schrödinger's (1962) excitement that the study of life would yield new physical principles not yet explored in physics laboratories lives on within the field of biophysics.

KEYWORDS: plant,biophysics,modeling,paradoxical,technology,photosynthesis,research

I.INTRODUCTION

A mechanical effect is one of the important reasons for plant diversity, whose phenotype is crooked branch. Parametric curve equation, or skeleton extraction from image or video, or interactive design is often used to simulate branch bending. These methods generally could not dynamically demonstrate the process of deformation caused by stress. Moreover, they seldom consider biophysical behaviors. In this paper, we integrated Bio-mechanical Model with Functional Structural Plant Model (FSPM), specifically GreenLab model, both of which are biologically-based methods. The combined model is able to simulate the morphological changes of dynamically developing plants constrained by external loads, such as gravity and wind. It could also mimic tropism, which is associated with maturation strains of reaction wood. Feedback between FSPM and Bio-mechanical Model is constructed by linking the bud break strategy to the architecture. Using the models based on the botanical and biological knowledge, we could generate plausible plants in accordance with reality. Meanwhile this study lays a good foundation for studying the optimization of plant's growth behaviors when considering biomechanics.[1,2,3]
Spontaneous formation of a lipid bilayer at the interface of the cytosol of a living cell and its environment is a prerequisite for the cell survival and function. In more complex eukaryotic cells (such as in plants) there is a broad range of intracellular membranes surrounding various cellular compartments and organelles. As the lipid bilayer is not permeable to small inorganic ions, ion transport and communication between cell compartments and between the cell and its environment is mediated by membrane-bound ion-permeable transporters. This issue of AIMS Biophysics explores the mechanisms of how these transporters operate and co-operate in plants.

The range of topics covered involves but is not restricted to
• Structure-function relations in ion channels, transporters and pumps
• Kinetic modeling of the transporter function and its regulation
• Nutrition and long-distance transport, ion compartmentalization
• Excitability
• Calcium signaling
• Operation of energy-coupling membranes (mitochondria and chloroplasts)
• Vacuole as a dynamic store

It is fascinating to observe an organism grow and acquire its shape–a process known as morphogenesis. Plants are particularly suited to investigate morphogenesis since cells are glued together, easing the tracking of specific cells. They pro-

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duce new organs (leaves, flowers...) throughout their life, enabling the investigation of multiple occurrences of the same morphogenetic process. Plants are sessile and need to grow in order to 'move' and respond to external cues like light. Finally, the mechanics of plant tissues is relatively simple because it is dominated by cell walls (extracellular matrix) and inner hydrostatic pressure. These features have attracted scientists from various backgrounds, who are tackling the mathematical description of morphogenesis, the measurement of physical properties of tissues, the links between biological regulation and physical properties, or how plants respond to external cues

Despite the diversity of living systems, they all possess the following specific features that must be taken into account in constructing the models.[5,7,8]

1. Complex systems. All biological systems are complex, multicomponent, spatially structured, and their elements possess individuality. Two approaches are feasible in modeling such systems. The first one is aggregated and phenomenological. According to this approach, the determining system characteristics are singled out (for example, the total number of classes) and qualitative properties of the behavior of these quantities in time are considered (stability of a stationary state, presence of oscillations, existence of spatial nonhomogeneity). Such an approach is historical the most ancient and is inherent in the dynamic theory of populations. Another approach implies the detailed consideration of the system's elements and their interactions, the construction of an imitation model, whose parameters have clear physical and biological sense. Such a model does not permit an analytical examination but, if the fragments of a system are sufficiently examined experimentally, can yield a quantitative forecast of the system's behavior under various exterior impacts.

2. Proliferating systems (capable of self-reproduction). This most important feature of living systems determines their ability to reprocess inorganic and organic matter for the biosynthesis of biologicalmacromolecules, cells, and organisms. In phenomenological models, this property is expressed by the autocatalytic terms in equations, which determines the possibility of growth (exponential under unlimited conditions), of the instability of a stationary state in local systems (the necessary condition for the appearance of oscillatory and quasistochastic regimes), and of the instability of homogeneous stationary state in spatially distributed systems (the condition of spatially inhomogeneous distributions and autowave regimes). An important role in the development of complex spatio–temporal regimes belongs to the processes of interaction between the components (biochemical reactions) and to the transfer processes both chaotic (diffusion) and associated with the direction of exterior forces (gravity, electromagnetic fields) or with adaptive functions of living organisms (for example, the motion of cytoplasm in cells under the action of microphylaments).

3. Open systems, steadily passing through themselves the flows of matter and energy. Biological systems are far from thermodynamic equilibrium and, therefore, are described by nonlinear equations. The linear Onzager relations that relate the forces and flows are valid only near the thermodynamic equilibrium. [9,10,11]

4. Biological objects possess a complex multilevel regulation system. In biochemical kinetics, this is expressed by the presence of feedback loops, both positive and negative, in systems. In equations of local interactions, the feedbacks are described by nonlinear equations; their character determines the possibility of the appearance and properties of complex kinetic regimes, including oscillatory and quasistochastic ones. Such types of nonlinearity, in describing the spatial distribution and transfer processes, stipulate the patterns of stationary structures (spots of various forms, periodic dissipative structures) and types of the autowave behavior (moving fronts, traveling waves, leading centers, spiral waves, etc.).

5. Living systems have a complex spatial structure. A living cell and the organelles in it have membranes, and any living organism contains enormous number of membranes, whose total area reaches tens of hectares. It is natural that the medium inside living systems cannot be regarded as a homogeneous one. The emergence of such a spatial structure and the laws of its formation represent one of the problems in theoretical biology. Mathematical theory of morphogenesis is one of approaches to the solution of this problem . The membranes not only single out various reaction volumes of living cells, but also separate the biotic and abiotic (medium). They play a key role in the metabolism selectively, passing through themselves the flows of inorganic ions and organic molecules. In the membranes of chloroplasts, the primary photosynthesis processes occur:[9,10,11] the accumulation of the light energy in the form of the energy of highly energetic chemical compounds; they are used for the synthesis of organic matter and in other intracellular processes. The key stages of the breathing process are concentrated in the membranes of mitochondria, the membranes of nerve cells determine their capability to the nerve conductivity. Mathematical models of the processes in biological membranes comprise a significant portion of mathematical biophysics. Existing models are mostly presented by the systems of differential equations. However, it is obvious that continuous models cannot describe in detail the processes that occur in such individual and structured systems as living systems. As computational, graphical, and intellectual facilities of computers develop, the imitation models, based on the discrete mathematics, play ever increasing role in mathematical biophysics.

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6. Imitation models of concrete complex living systems, as a rule, take into account all available information about given object. The imitation models are employed to describe the objects of different organization levels of live matter: from biomacromolecules to biogeocenoses. In the latter case, the models must include the blocks describing both living and «inert» components . Models of molecular dynamics are a classic example of imitation models, in which the coordinates and impulses of all atoms that compose a biomacromolecule and the laws of their interactions are prescribed. A pattern of «life» of a system, simulated by computer allows one to follow the manifestation of physical laws in the functioning of the simplest biological objects – biomacromolecules and their environment. Similar models, in which the elements (bricks) are not atoms but groups of atoms, are employed in modern technique of the computer construction of biotechnological catalysts and therapeutics that act on certain active groups of membranes of microorganisms and viruses or perform some other directed actions. The imitation models were created for describing the physiological processes that occur in vitally important organs: nerve tissue, heart, brain, digestive tract, and blood vessels [12,13,15]These models are used to simulate the «scenarios» of processes that occur normally and in various pathologies, to examine the influence of various exterior impacts to these processes, including the therapeutics. The imitation models are widely used for describing the productio n process in plants and are applied to the development of optimal regime of growing plants aimed at obtaining the maximal harvest or the ripening of fruits uniformly distributed in time. Such projects are especially important for expansive and energy consuming greenhouse farming.[17]

II.DISCUSSION

We took a modeling approach to generate tools to dissect better membrane network transition during cell plate maturation. Due to the complexity of cell plate development, we decided to look for energy minima within a parameterized restrictive geometry basis set, thereby adopting a restricted variational approach within testable approximated structures. We found that existing general adaptive mesh approaches, such as Surface Evolver, while in principle more accurate, were not amenable for application in our study, due to their inability to incorporate the spreading/stabilizing force into such a large-scale system . There are several potential contributing factors during cell plate maturation including cell wall polysaccharides. Given that the model examines the specific transition between TN to a fenestrated sheet and a mature cell plate, the timing of the contributing sources at the lagging zone is critical. Among the different polysaccharides we first examined callose.

To circumvent these hurdles and to better dissect cell plate maturation, we used biophysical modeling. [15]We developed a model based on the Helfrich free energy for the cell plate surface with the incorporation of a spreading/stabilizing force as an “areal pressure” (force per unit distance). [1,17,18]From an energy minimization analysis, we have shown that a planar spreading/stabilizing force is vital for cell plate to transition from vesicle membrane network to a fenestrated sheet and late stage/mature cell plate. We also show that in the absence of a spreading/stabilizing force, the addition of membrane material yields stable TN structures, but that those structures are unable to mature beyond this stage. As shown by different simulations, the need for this spreading/stabilizing force is magnified when we compare a single mature cell plate to multiple smaller vesicle network structures of the same total area. We do not have the detailed molecular scale mechanisms behind the spreading/stabilizing force, but we show that a simple model based upon the expansion of a quasi-two-dimensional self-avoiding polymer captures the correct form. To reach a mature cell plate, our model requires the late-stage onset of the spreading force coupled with a concurrent loss of spontaneous curvature. This raises the intriguing possibility of a common origin to the decrease in spontaneous curvature and onset of a spreading/stabilizing force. In the model, the spreading force is relevant when there is sufficient connection of individual oblate spheroidal vesicles, and it is at this stage that we shut off the spontaneous curvature. The nanoscale surface topography can potentially serve as a direct biochemical signal to activate this process (Lou et al., 2019). The possible tethering of polysaccharides or glycoproteins to the membrane could concomitantly induce spreading and reduce spontaneous curvature by modifying the membrane mechanics. Notably, inhibition of long chain fatty acid affects cell plate maturation (Bach et al., 2011). It is plausible that membrane microdomains control both spontaneous curvature and the onset of a spreading force at the cell plate.[17,18]

Curvature-stabilizing proteins are active at the cross-sections of tubules and sheet edges of endoplasmic reticulum (Shemesh et al., 2014; Schweitzer et al., 2015). While force generating proteins are involved in the tubulation and membrane material recycling processes (Otegui et al., 2001; Ahn et al., 2017), no proteins have been identified with properties of membrane expansion at the cell plate.

The phragmoplast-driven vesicle delivery is a dynamic and complex process (Buschmann and Müller, 2019) that with the aid of motor proteins can be considered as a spreading/stabilizing force during cell plate maturation. For example, Myo-

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sin VIII plays a role in guiding phragmoplast expansion (Wu and Bezanilla, 2014), while several kinesins are involved in the functional organization of the phragmoplast (Buschmann and Müller, 2019). Microtubule directed vesicle delivery occurs at the leading edge; however, it is followed by microtubule depolymerization at the lagging zone, which is the transitional stage that the model describes (Lee and Liu, 2013). Furthermore, inhibition of myosin causes a broader effect on cell plate expansion, as it is involved in general vesicle delivery (Figure 5). Therefore, it is challenging to assign a specific function of motor proteins to cell plate maturation at the lagging zone. Time-lapse experiments directed at the role of motor proteins at the lagging zone will shed light on their contribution to the stabilizing and spreading force that the model predicts.[20,21]

It is plausible that polysaccharide deposition serves as this stabilizing and spreading role. The matrix polysaccharides hemicellulose and pectin are synthesized in the Golgi apparatus and delivered via vesicles from the beginning of cytokinesis (Moore and Staehelin, 1988; Toyooka et al., 2009; Rybak et al., 2014). Thus, these classes of polysaccharides are unlikely the major players as they do not overlap with the predicted onset of the spreading/stabilizing force, although experimental verification awaits. Callose and cellulose are synthesized directly at the plasma membrane and are excellent candidates for exploration. Our data showed that pharmacological inhibition of cellulose at the root tip inhibited cell elongation in general, while inhibition of callose deposition led to cytokinesis defects consistent with the conformations predicted by the model in the absence of a spreading force. Callose accumulation peaks at the intermediate TN stage, a transitional stage that coincides with loss of membrane volume (Samuels et al., 1995; Segui-Simarro et al., 2004). The timing of callose deposition in late stages when the overall cell plate membrane network “flattens” (Samuels et al., 1995; Segui-Simarro et al., 2004) is consistent with the need of callose in providing a lateral spreading/stabilizing force. Furthermore, the predicted required values of callose deposition[19,20,21] are within biological thresholds (Him et al., 2001; Pelosi et al., 2003). Notably, a study by Thiele et al. (2009) indicates that callose is required to establish the connection between the nascent cross-wall and the parental cell wall, rather than stabilizing the young cell plate (Thiele et al., 2009), so that further analysis on the role of callose in the proposed model awaits verification. It is plausible that callose could serve as a scaffold into which other more permanent polysaccharides and proteins are later deposited (Stone and Clarke, 1992; Him et al., 2001). Potential transient interaction with cellulose or other glucans (Miart et al., 2014; Gu et al., 2016; Abou-Saleh et al., 2018) can contribute to a composite that supports the stability of the cell plate and helps the attachment to the parental cell wall. Structural glycoproteins such as extensins (Cannon et al., 2008) can provide a scaffold for polysaccharide deposition, and these altogether can generate the desired spreading/stabilizing force proposed by the model. [18,19,20]Further (challenging) experiments are necessary to determine how the possible conformations of different polysaccharides and proteins or their combinations, synthesized in vitro in an artificial membrane setup, can contribute to different magnitudes of spreading/stabilizing force in lipid vesicle networks.

A unique element in the study was the approximation of cellular compartments with testable shapes such as vesicles and complete cell plates with oblate spheroids, fused vesicles and tubular structures with elliptical hyberboloids and their combination in a network. Approximating vesicles, tubulations and their networks in the current model has the potential of a wider application and can be adopted during quantitative assessment of membrane dynamics. It can be used as a basis for addressing the equilibrium of vesiculation (oblate spheroids) and tubulation (elliptic hyperboloids) and applied to ER-intermediate compartments, Golgi, and endosomes in all eukaryotic cells.

Schematic representation of cell plate development stages and the potential role of a spreading force in cell plate maturation. A–D, Cell plate development occurs centrifugally in multiple stages. A, During the first stage (I), cytokinetic vesicles guided by the phragmoplast accumulate at the center of the dividing cells, at the cell plate assembly matrix. B, Vesicles undergo fusion and fission and conformational changes resulting in TVN (Stage II). C, Interconnected membrane structures transition to a TN. At this stage high callose deposition occurs (Stage III). D, The membrane network further expands to an almost continuous fenestrated membrane sheet (PFS) (Stage IV). Deposition of additional polysaccharides helps transition to a new cell wall, separating the two daughter cells. Note that different stages can occur simultaneously, images are not to scale. This simplified representation emphasizes on cell plate membranes (Samuels et al., 1995; Segui-Simarro et al., 2004). E–H, Schematic representation of cell plate development describing the role of a spreading force. E, Early stages of vesicle accumulation and fusion and F, TVN and TN structures are shown. Two different possibilities are projected for stage transition (1) Incomplete/arrested cell plate G. In the absence of a spreading force G, tubular and fenestrated structures accumulate, and there is a lack of maturation towards a single, complete cell plate structure. (2) Normal cell plate transition H. In our calculations, we discover that for expansion/maturation to occur as in D, the presence of a spreading force is required, along with the decrease of spontaneous curvature to a threshold value. This allows for a sheet-like cell plate (SCP) structure to form. The structures in this schematic description are adapted from data collected from EM tomography (Segui-Simarro et al., 2004) with bars in E–G = 50 nm, H = 0.25 µm. Dark blue vesicles

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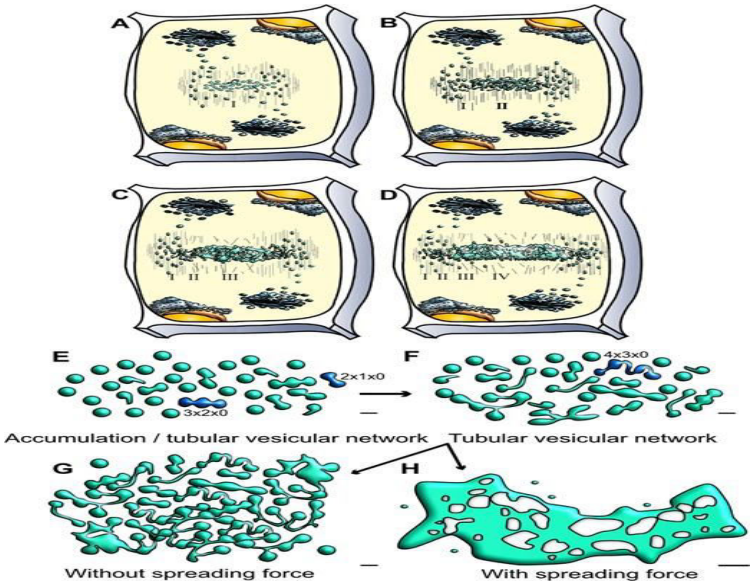
denote those labeled by the mathematical naming schema as described in Figure 2. Whereas in E, 2 × 1 × 0 denotes two oblate spheroids, one tubular connection, and zero holes.



III.RESULTS

Current concepts of growth hydraulics in higher plants are critically revisited, and it is concluded that they partly fail to interpret the experimental data adequately, particularly in the case of hydroponics-grown roots. Theoretical considerations indicate that the growth rate in roots is controlled by the extensibility of the cell wall, excluding water availability (i.e. hydraulic conductance) as a major constraint. This is supported by the findings that the growth rate does not scale with turgor, and that no radial nor axial water potential gradients have been observed in the root elongation zone. Nevertheless, a water potential deficit ranging from –0.2 to –0.6 MPa has repeatedly been reported for growing cells that by far exceeds the shallow trans-membrane water potential difference required for the uptake of growth water. Unexpectedly, growth was also shown to depend on the hydraulic conductance (LP) of the plasma membrane of root cells, even though LP should generally be too large to have an impact on growth. For leaves, similar observations have been reported, but the interpretation of the data is less straightforward. Inconsistencies associated with the current model of growth hydraulics prompt the author to suggest a revised model that comprises, in addition to a passive mechanism of water transport across the plasma membrane of growing cells mediated by aquaporins (‘leak’) a secondary active water transport (‘pump’), in analogy to a mechanism previously demonstrated for mammalian epithelia and postulated for xylem parenchyma cells in roots. Water is hypothesised to be secreted against a trans-membrane water potential difference by cotransport with solutes (salts, sugars, and/or amino acids), taking advantage of the free energy released by this transport step.[20,21,22] The solute concentration gradient is supposed to be maintained by a subsequent retrieval of the solutes from the apoplast and back-transport at the expense of metabolic energy. Water secretion tends to reduce the turgor pressure and retards growth, but turgor and, in turn, growth can be upregulated very rapidly independent from any adjustment in the osmolyte deposition rate by increasing LP and/or reducing secondary active water transport, e.g. when the root is exposed to mild osmotic stress, as confirmed by experimental studies.

IV.CONCLUSIONS

Due to osmosis, when there is a difference in gradient the water and nutrients flow from the root to the highest point of the plant where there will always be the lowest concentration of solutes. Due to the gradient, the plant will have moments of imbalance so through physiological mechanisms of the plant; roots adapt to rebalance the natural state of the plant.[23] At microscopic scales, the vibrations emitted by electrons make it possible to recognize any substance. These vibrations are fingerprints and are thus a highly reliable factor in scientific and industrial matters. Kyminasi Plant Booster recognizes each frequency emitted by the plants and intervenes resonance reaching the optimal frequency thus giving biological balance.

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| Volume 5, Issue 6, June 2022 |

| DOI:10.15680/IJMRSET.2022.0506095 |

Biological balance allows plants to develop in a healthy way, without stress and with better results in quality and quantity, all this in an organic and sustainable way. Plants are complex organisms that adapt to changes in their environment using an array of regulatory mechanisms that span across multiple levels of biological organization. Due to this complexity, it is difficult to predict emergent properties using conventional approaches that focus on single levels of biology such as the genome, transcriptome, or metabolome. Mathematical models of biological systems have emerged as useful tools for exploring pathways and identifying gaps in our current knowledge of biological processes. Identification of emergent properties, however, requires their vertical integration across biological scales through multiscale modeling. Multiscale models that capture and predict these emergent properties will allow us to predict how plants will respond to a changing climate and explore strategies for plant engineering. In this review, we (1) summarize the recent developments in plant multiscale modeling; (2) examine multiscale models of microbial systems that offer insight to potential future directions for the modeling of plant systems; (3) discuss computational tools and resources for developing multiscale models; and (4) examine future directions of the field.[25]

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| ISSN: 2582-7219 | www.ijmrset.com | Impact Factor: 7.54||Monthly, Peer Reviewed & Referred Journal |

| Volume 5, Issue 6, June 2022 |

| DOI:10.15680/IJMRSET.2022.0506095 |

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