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Quantifying *green life*: grand challenges in plant biophysics and modeling

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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 CO₂ 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 oxygenduced 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 CO₂ 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 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.
Biomimicking efforts lead to the construc-
tion 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 mainte-
nance of the transport capacity under ten-
sion 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 sys-
tem (Bramley et al., 2009).

Plants stretch their branches and roots
across tens of meters and are often thought
to be systems of modular organisms. Yet, they show
a significant degree of functional and struc-
tural integration. As plants do not have
any designated information distribution
network, the two transport systems that
permeate 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 possi-
ble role to coordinate response at the organ-
ismal 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-architecture.

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 mole-
cule 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 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 subtle-
ties will require a significant amount of
future research.

These are only a few of the vast array
of promising avenues for plant biophys-
ics 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 suc-
cess of the molecular genetics approach
meant that much could be learned about
cell biology, physiology, and development
without resorting to models and mathema-
tical analysis. During the reductionist
era, many students saw in biology a safe
ten away from physics and mathematics,
a paradoxical situation given that molecu-
lar genetics was ushered by two eminently
quantitative sciences, genetics and struc-
tural 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 reduction-
ist 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.

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