



Paul B. Green 1931–1998.

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A Tribute to Paul Green

In July of 1998 Peter Ray, Karl Niklas, Nancy Dengler, and I wrote a brief citation for the Merit Award to be presented to Paul Green at the annual meeting of the Botanical Society of America. The citation read, “To Paul Green for innovative, technically brilliant, and analytically fundamental work on biophysics of plant morphogenesis; for the first direct measurements of cell turgor pressure and the quantitative description of the importance of wall rheology in governing growth rates in *Nitella*; for microscopic studies of the initiation and early growth of leaves and flowers; for elucidating the biomechanical principles underlying phyllotactic pattern; for his eloquent, good-humored, inspired and inspiring presentations that have linked the communities interested in developmental and theoretical biology.” Sadly, Paul was too ill to attend the meeting, although colleagues and friends were able to tell him of the award at a symposium held at Stanford in his honor.

The citation gives only a hint of the influential nature of Paul Green’s work in plant science. Bota-

nists, developmental biologists, mathematicians, engineers, and physicists have had their ideas shaped by his publications and presentations. From the many people influenced by his work there must be many views of the relative importance of his contributions in different areas. The following appreciation is one attempt to acknowledge the power of his work.

I first met Paul in 1969, when I began graduate work in biology at the University of Pennsylvania. For my first term at Penn I was awarded a research assistantship in Paul’s laboratory. He was then finishing the experiments that would be published with Erickson and Richmond (1970) as “Metabolic and physical control of cell elongation rate. *In vivo* studies in *Nitella*.” Although I had not read much in the literature of plant physiology, I knew enough to be deeply impressed by the power of Paul’s experimental work. His elegant micromanometer (the first pressure probe) allowed Paul to measure the intracellular pressure by compression of an air bubble in a capillary tube impaled in the *Nitella* cell. He had

also built a movie setup to follow the growth of the algal cell, and he was resolving the spatial pattern of the growth rate by observing the separation of anion exchange resin beads that adhered tightly to the *Nitella* cell wall. Cell turgor was modulated by a rapid, automated change to a bathing solution of desired osmotic potential. With this well designed and carefully built apparatus, Paul was able to analyze the importance of cellular water relations and wall rheology in regulating the cell growth rate. He provided the first empirical evidence for Lockhart's postulated relationships among growth rate, turgor pressure, and wall yield point. His thoughtful mathematical treatment of the results indicated that the plant quickly modified mechanical properties of the wall to restore growth rate over a range of turgor pressures. This work has stood for more than two decades as the definitive analysis of biophysics of cellular growth.

The *Nitella* work epitomizes Paul's approach to science in several ways. He brought tools from physics and mathematics to solve problems in biology. His experimental design was profoundly original. And his conclusions often provided major insight into mechanism.

Although his training was in laboratory science, he made several important contributions to theory. For instance, his critique of cell division theory (1976) was a courageous stand against the physically untenable models popular among botanists at the time. Green always insisted on the impossibility of "growth by cell division," and urged his colleagues to speak in physically meaningful terms of "growth with or without cell division." In addition, his work with Colin Goodall (1986) provided a statistically sound method to analyze two-dimensional expansion patterns from photographic records of marked surfaces. And in his most recent work he collaborated with engineers to solve a mathematically daunting problem: to find the minimum energy configurations during apical morphogenesis (Green, Steele, and Rennich 1996).

From his earliest professional papers, his work was also characterized by the design of ingenious experimental techniques. For instance, he has taken advantage of the surface properties of different organs to mark plants for growth analysis. Anion exchange resin beads were used to cling to negative charges on cell walls and small droplets of heavy teflon oil to cling to lipophilic fern walls. He has used optical tools to particularly good advantage. He was a pioneer in the use of differential interference microscopy to find the mass density during growth. His use of polarizing microscopy revealed a great deal about wall structure. In particular his early work (1960) offers the best empirical support for the

multi-net growth hypothesis, and he predicted the existence of microtubules as organizing structures long before they were discovered by ultrastructuralists.

In the 1980's Green turned his attention from axial extension to problems of axis initiation and phyllotaxis. His work explored the hypothesis that microtubule organization controls cellulose deposition and thereby the anisotropy required to produce a new organ (Hardham, Lang, and Green 1980; Green and Lang 1981; Lang, Eisenger and Green 1982; Selker and Green 1984; Sylvester, Williams, and Green 1989). In this period the use of birefringence microscopy revealed the organization of the wall and allowed testing of models of stress-strain relationships during morphogenesis.

In the last decade of his life Paul Green worked with both biologists and engineers to develop an integrated theory of phyllotaxis. He sought empirical evidence that growth parallel to the surface of the apical dome produces a gradient of shear stress, with high shear but low tension at the site of the future leaf primordium. An existing primordium exerts a tensile force tangent to its base and a compressive force perpendicular to its base. Thus growth of the existing form creates a stress field that leads to primordium initiation to maintain the phyllotactic pattern (Selker, Steucek, and Green 1992). He sought a thermodynamic basis to this model in terms of minimum energy configurations (Green, Steele, and Rennich 1996). He argued persuasively that genetic, hormonal, and environmental effects are best seen as inputs to the basic physical process causing the famous, mathematically regular patterns of leaf initiation. His last paper (1999, published posthumously with help from Jacques Dumais) was a review of his ideas, emphasizing interactions between cell-scale and tissue-scale processes and the differential-integral relationships in morphogenesis.

Over the years I was delighted by Paul's offbeat teaching efforts. He gloried in the use of metaphor. I love his description of the Menten-Michaelis model as "the approximation of the well-stirred beaker." In this one pithy metaphor Prof. Green described the famous time-dependent, spatially uniform model that, as he gleefully pointed out, is exactly the wrong pair of assumptions for the plant axis. His lectures were studded with brilliant puns and startling physical images, such as the hoop-reinforced water tower, used to represent an anisotropic plant cell, and the potato chip, used to represent a surface of minimum surface energy. Paul even provided metaphors for my work. He was interested in my use of continuity equations to calculate rates of change in growing tissue and thought of the maintenance of sand piles on a moving conveyer belt as a way to visualize the formalism. The dry

mathematical expressions immediately took on a lively physical form.

I am grateful to Paul Green for his a tireless advocacy for physical approaches to solve biological problems. He insisted with unquenchable enthusiasm that developmental biology must be understandable in terms of physics and describable in the language of mathematics. In his own work he did a tremendous amount to elucidate morphogenesis in physical terms.

In this issue of the *Journal of Plant Growth Regulation* we feature problems and themes that were interesting to Paul Green. Several of the articles discuss the mechanics of tissue morphogenesis. Dumais and Steele show that fields of tension and compression exist in the plant apical meristem and correlate with patterns of primordium initiation. Moulia presents the basic concepts of shell theory that must be used to understand how mechanics and botanical structure work to produce leaf rolling. Both of these articles provide powerful evidence for Green's contention that tissue-scale processes interact with those at the cellular level to produce coherence across spatial scales. In another biomechanics paper, Hejnowicz and colleagues also emphasize that within a tissue different walls are under different types of stress. Compressive and tensile stresses coexist as a result of the different wall extensibilities. The organizational importance of the microtubular arrangements become clear when these underlying mechanical fields are recognized. This paper supports the multinet hypothesis of growth that was explained and defended by Paul Green early in his research papers.

The relationship of cell division to tissue expansion, a favorite theme of Paul Green, is addressed in two of the papers. Granier and others synthesize their earlier work to show that in dicot leaves, rate of growth in area is proportional to cell number. The linkage can be produced by kinematically different temporal sequences and so need not be causal. Zagorska-Marek and Turzanska have analyzed fixed and cleared apices of many spruce and magnolia stems to identify cell packets. From these observations they have deduced the growth trajectories and cell divisions of initials and derivatives initially at the apex, and they conclude that initial cells change their position within the apex as it grows. In particular, they show impermanent initials arise even when the morphology of the apex is steady.

The relevance of growth analysis to plant physiology is evident in the paper by Walter and colleagues in which we use a continuity equation with data on the axial distributions of growth velocity and mineral element content to calculate mineral deposition rates in roots growing at different soil pH.

The spatial patterns are correlated to axial patterns of wall chemistry and cell function to infer mechanisms for the pH effects on nutrition of the growth zone. Another growth analysis is provided by Groot and Meicenheimer, who have explored the use of the plastochron index to characterize the morphogenesis of leaf teeth in the *se* mutant of *Arabidopsis*. With the developmental index (but not with the more conventional allometric analysis), the authors were able to show that the mutant initiates teeth much earlier in development and has a more complex, biphasic growth rate pattern than the wild type controls.

Paul Green's innovative use of microscopes and construction of novel laboratory devices are in a tradition continued in two of the papers of this memorial issue. Lintilhac and others, in their article on ball tonometry, describe a rapid non-destructive method for measuring cell turgor pressure in thin-walled plant cells. Particular cells can be measured repeatedly over time to reveal pressures associated with growth of surface cells. Taking another direction, Ogata describes a double-water-film electrode with which he measures resistance and capacitance of the junction between the node and internode in a single celled organism, *Chara*.

In the symposium held at Stanford in his honor, and in this issue of *Journal of Plant Growth Regulation*, it is clear that Paul Green's colleagues will carry his scientific vision into the future.

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