Ralph O. Einchon

Ann. Rev. Plant Physiol. Plant Mol. Biol. 1988. 39:1–22

GROWTH AND DEVELOPMENT OF A BOTANIST

Ralph O. Erickson

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104

FOREWORD

I suppose that my earliest interest in plants stems from my childhood in northern Minnesota and Michigan. Winters there are severe but the long summer days among trees and lakes are delightful. Our family was close to nature in many ways. We often spent days picking wild blueberries and raspberries which my mother canned for desserts through the year. Pin cherries and wild strawberries made excellent jelly. We used our pocket knives to make whistles of poplar twigs, and selected symmetrical maple crotches for sling shots. Later, when my commitment to botany was firm, I was drawn to studies of plant growth and development from a variety of educational and research experiences, but with the strong influence of Edgar Anderson and David R. Goddard. I have had little conventional training in plant physiology, and it may be interesting to try to trace the development of my teaching and research interests from such diverse fields as plant taxonomy, plant anatomy, cytology and cytogenetics, evolutionary theory and ecology, and an interest in statistics and numerical analysis. I can probably be accused of dilettantism.

Discussing this theme in a personal vein, with a bit of apprehension, has resulted in a sort of selective autobiography. One author (24) has written that "autobiography is a most peculiar genre or form....[It] presuppose[s] a particular kind of arrogance, a conviction that one's life is in some serious way exemplary...." However, I may hope that frequent use of the first person pronoun will not be taken as conceit, but as the candor that I intend.

0066-4294/88/0601-0001$02.00

ROOTS

My grandparents were emigrants from Sweden in the 1870s, a decade or so after the Sioux massacre of settlers in the Minnesota River valley in 1862. My mother's parents were from Småland and Västergötland and homesteaded near Bernadotte in southern Minnesota, where they raised ten children. My father's parents came from the Åland Islands and settled near St. Hilaire in northern Minnesota, also as homesteaders. My father, Charles, the second of four children, left the farm at age 19 or 20, against his father's wishes, to attend high school, went on to Gustavus Adolphus College, and graduated in 1913. My mother, Stella Sjostrom, and he were married in 1913, and after two years in Duluth, Minnesota, moved to Rock Island, Illinois, where my father attended Augustana Seminary, graduating in 1918 with a B. D. degree. He was then a Lutheran pastor in Clearbrook, in northern Minnesota. I was born in Duluth, 27 October 1914, the first of six children. When I was five, my mother suffered a severe "nervous breakdown," and the family, then of four children, were dispersed. I was sent to my grandparents Sjostrom, who had retired to St. Peter, Minnesota, and there I attended kindergarten. I have virtually no memory of these years, but I am told that they were unhappy.

My father left the church in Clearbrook for nearby Leonard, a town of 75 people about 15 miles from the Red Lake Indian Reservation (Chippewa). He cleared land beside a small lake and single-handedly built a four-room house for the family, which is still lived in. He was pastor of the church in Leonard, and principal of the three-room school, where I advanced through the first six grades in four years. In sixth grade I heard the seventh and eighth grade recitations, since they were in the same room. At the end of the year I was given, and passed, the State Board examinations for graduation from eighth grade and was then entitled to enter high school when I was not quite eleven.

SI QUAERIS PENINSULAM AMOENAM...

My father was called to a church in Iron River in the upper peninsula of Michigan, which in 1925 was a fairly prosperous iron mining town. The school authorities were dubious about my starting high school, and instead I entered eighth grade. Some of my classmates were the children of the immigrant Italian, Polish, and Finnish miners. It was a rough town. I suppose that my school experience was unusual, since I was two or three years younger than my classmates, and in one's early teens this is important. In high school it meant that I could not join in sports such as football, basketball, or hockey, nor could I join a gang. Also the puritanical character of midwestern Lutheranism at that time meant that, as preacher's kids, we were not allowed to do such "sinful" things as see movies or go to dances.

After classes, piano practice, band rehearsal, and delivering newspapers, I had time to read, and I read widely. In addition to pulps, Jules Verne, and H. G. Wells, I tackled the Bible, and such books as Dostoyevski's *The Brothers Karamazov*. My father's library included, in addition to homiletics and concordances, "Dr. Eliot's Five-foot Shelf of Books" (*The Harvard Classics*), and I believe that I read the entire collection, with or without comprehension. I recall reading Darwin's *Origin of Species* and *Voyage of the Beagle*. I also spent much time with the *Encyclopedia Americana*. At least I learned some words. On entering college, I scored above the median for college graduates on a standardized vocabulary test.

During the summers, we spent much of our time at nearby Fortune Lake where my father organized and built a summer Bible Camp. Having grown up on a farm, he knew carpentry. He also had a woodworking shop at home, which I could sometimes use under strict supervision. At the camp he, my brother and I, and occasionally others cleared brush, built roads and paths, erected buildings, built tables and benches, even rowboats, painted, and installed electric wiring—whatever was required. After a time, I realized that I could cut rafters or hang a door as accurately as a professional carpenter who worked at the camp for a while. We were not paid and so could spend a part of our time at tennis, swimming, diving, and boating. We longed for a canoe. My fond memories of Fortune Lake include recollections of loons, ducks, herons, woodchucks, and deer. I did not care to fish, but heard stories about the bass, trout, and pickerel. Fortune Lake was one of a chain of five or six, and occasionally I would row the whole length to check the beaver lodges or perhaps look for lady's slippers. I remember some irritation that I could not easily learn the trees and other plants. Names people used were contradictory, and I suppose I did not realize then that I needed a manual.

My father also taught us photography, since he had earned a part of his college expenses by photographing barns, livestock, and families and selling the picture postcards he made to the farmers.

GUSTAVUS ADOLPHUS COLLEGE

When the stock market crashed in 1929, the mines closed almost immediately. With widespread unemployment, the church was unable to pay my father's full salary and, when I graduated from high school in 1930, college seemed out of the question. During the next year I had a part-time job and took a course or two at the high school. The following year, my father announced that I could go to Gustavus Adolphus College, St. Peter, Minnesota. As I recall, tuition was about $75 per semester and I lived with relatives for two years, then in a dormitory as a proctor. I worked for meal tickets as an

attendant in the library (more opportunity to read), and as a reader for a blind classmate.

At college I was still two years younger than my classmates and felt exceedingly shy. I was regularly permitted to take one or two courses beyond the required four per term. This entailed some scattering of effort, but I graduated magna cum laude. My major was biology, but I also took most of the math courses offered and not quite enough chemistry for a second major. In addition to zoology, comparative anatomy, human physiology, etc, there was one botany course, taught by a zoologist. One of the assignments was to turn in dried specimens of 10 plants. I did many more. My roommate for two years was a born naturalist, who kept plants and tropical fish in our room. The two of us spent many extra hours in the biology lab and in the field, collected material for use in the biology course, frog eggs in season, and many other things. He became a high school biology teacher in St. Peter and we continued our joint biology ventures for some time.

Music was important at Gustavus; the a capella choir was nearly as important as the football team. I took music seriously. I had voice and piano lessons one year (even played a recital), played clarinet in the band and bassoon in the orchestra, and sang in the choir. I also wanted some music theory. In high school the music teacher, remarkably, gave a course in harmony to a few of us, and in college I was the only person who wanted the course in advanced harmony and counterpoint. One term Dr. Nelson agreed to meet with me once a week at the piano, to play and correct exercises I had written. This was one of my most demanding and satisfying courses. Shortly before the spring choir tour my senior year, Dr. Nelson was ill for about three weeks, and it fell to me to direct the choir in rehearsals and the first concert, which included the Bach motet, *Singet dem Herrn*. This was nearly disastrous, since I felt I had to devote my full time to studying the music, instead of attending classes. In later years my performing skills have atrophied but music continues to be an important part of our family life.

At graduation from college, only two of my classmates had job prospects. I was qualified for certification as a high school teacher, but there were no opportunities. I spent the summer at Fortune Lake wondering what I might do. Late in August a letter arrived from the president of Gustavus offering me the position as assistant (really instructor) in biology, which had just become vacant. The salary was very low even by 1935 standards, but I immediately hitchhiked to St. Peter. The biology faculty consisted of Dr. J. A. Elson and me. I spent four years teaching there, in sole charge of the elementary biology labs and the botany course, 24 contact hours per week. In my fourth year I introduced a course in genetics, using *Drosophila* and segregating ears of corn in the lab.

Funds for lab material were limited; for instance, gophers caught in nearby

fields were dissected in the zoology course, instead of specimens bought from a supply house. The microscope slide collection was inadequate, but the department had a microtome and with an improvised paraffin oven I prepared slides of stem, root, and leaf sections, shoot apices, slides for animal histology, even parasitic flat worms. I converted an ice-box into an incubator, prepared whole mounts of blastoderms and introduced lab exercises on chick embryology. I also made many 2 × 2 inch lantern slides. At times student volunteers helped with this work. I had read Cooper's article on embryo sac development in lilies (7) so I bought some Easter lily plants with flower buds of various ages at a local greenhouse and prepared sections of anthers and ovaries. Since I was into mass production, I could select choice slides for myself of the crucial stages of pollen and embryo sac development, which have continued to be useful in teaching for many years, and I recently learned that some of my slides are still in use at Gustavus.

Something more should be said about Gustavus. The announced mission of the college was, and is, training for Christian leadership. A daily chapel service was compulsory, there were evening prayer meetings, etc. In my third year of teaching, as I recall, a decision was made to ordain the Gustavus professors into the Lutheran ministry. I took little part in the religious life of the college because my interests were elsewhere. The faculty at Gustavus were dedicated teachers, but it occurred to me later that I knew of none who were engaged in scientific research or any other scholarly work. I graduated with only a slight understanding of academe in the wider sense.

SUMMER SCHOOL

After my first year of teaching, I attended a summer session at the Douglas Lake Biological Station of the University of Michigan, taking systematic botany and plant anatomy. The former course was devoted to the local flora and consisted of all-day field trips in which we filled our vasculums, then sat down in some pleasant place to key out our specimens with Gray's *Manual*. It pretty well satisfied my desire to be able to identify plants. C. D. LaRue's plant anatomy was less cut and dried. LaRue was a challenging and entertaining lecturer and he taught us the paraffin technique. I recall some dissatisfaction with the static descriptions in Eames & McDaniels, our text. When I asked how fast the onion root grew and how rapidly cells in the meristem divided, I found no answers. To say that I could not imagine how the root tip could grow so as always to look the same in sections, is perhaps invoking too much hindsight. It was interesting that George Avery shared LaRue's laboratory that summer, working up his sections of *Aesculus* shoots to explore the possible role of auxin in the initiation of cambial activity in the spring (6). This was my first view of research in progress.

The following two summers I had courses at the Lake Itasca Forestry and Biological Station and at the Minneapolis campus of the University of Minnesota. Among them was a field course on the ecology of Itasca Park, a course in genetics, an elementary plant physiology and a seminar course concerned with the structure of chlorophyll and the physiology of photosynthesis, for which I was not prepared. The structure of grana was not then known. This is the extent of my formal training in ecology, genetics, and plant physiology.

SHAW'S GARDEN

Summer experiences and extracurricular fooling around in the laboratory at Gustavus reinforced my desire for graduate study in biology. I had made unsuccessful inquiries about the possibility of doing full-time graduate work in the botany department at Minnesota, and during my fourth year of teaching, I resolved to make a more serious effort to get into graduate school, realizing by that time that my chances of being accepted were slim. My academic record at Gustavus was good, but I was sure that my grades and my recommendations would be discounted. With the advice of people in botany at Minnesota I applied to 12 schools, mainly Ivy League and State Universities, at which work in plant cytology was going on. I got rejections, or no word, from all but one.

Edgar Anderson wrote that he was impressed with my application, that there were no opportunities for support at the time, but that he would "by hook or by crook" see that I could come to Washington University. It is still a mystery to me what merit he could see in my application. Shortly before the start of classes in September 1939, I was awarded a University Fellowship. I hitchhiked to St. Louis, found a boarding house near the Missouri Botanical Garden, and became a graduate student in the Henry Shaw School of Botany. When I had paid tuition, room, and board, I had ten dollars per month. I took Jesse Greenman's course on the flowering plants, which was quite another thing than a local flora. Greenman had studied at Berlin with Adolph Engler and his course was a *grosses Praktikum*, intended to acquaint us with virtually all the plant families, through lectures, and dissection and drawing of boiled-up specimens of dried flowers, fruits, etc., filched from herbarium sheets. I enjoyed it and still value it greatly. During my three years at the Garden, I made a point of walking through the conservatories at least once a week. At the main campus of the University, a course in physical chemistry fulfilled my old intention to major in chemistry, and I had a cytology course, a seminar course in animal embryology, and others.

I chose to do a taxonomic problem for a master's degree, which was narrowed down to a revision of the *Viorna* section of *Clematis*, under Greenman's direction. In retrospect, I can perhaps see Edgar Anderson's hand

in this choice. (By a curious coincidence, I was given a cordial welcome to the Academy of Natural Sciences in Philadelphia and the botany department of the University of Pennsylvania in 1942, when I made a bus trip to Eastern herbaria to study *Clematis* specimens.) My thesis was published (9) as my thickest paper to date, and it earned me several pages of testy criticism from M. L. Fernald in *Rhodora*. However, I am cited in Fernald's *Manual* as author of one variety of *Clematis*, so I can claim to have had a bit of taxonomic competence.

The most valuable part of my experience in St. Louis was association with Edgar Anderson. It was strenuous. From the day I arrived he subjected me to a continual barrage of discussion, wisecracks, pithy anecdotes about other biologists, genetic questions intended to stump me, a continuing contest of wits. I often went with him on field trips, and *Faltboot* trips on Ozark rivers; taught his wife, Dorothy, and him to play recorders; accepted many invitations to the barn at the Gray Summit Arboretum, which he had converted to a summer place; and listened to a certain amount of advice on how I should conduct my life. I also learned a great deal about species of *Iris*, *Tradescantia*, *Acer*, and other genera: their geographical distribution, morphological variation, cytology and, introgressive hybridization. Anderson paid me to help with his study of F2 segregation in a species cross between *Nicotiana alata* and *N. langsdorfii*, photographing and measuring flowers and leaves, and making preliminary extractions of tissue for auxin analysis in F. W. Went's laboratory. Anderson had published (2) on the hindrance to recombination imposed by linkage, and in these studies he wished to document a further hindrance apparently imposed by developmental constraints. I do not believe that this work was published. Anderson was at that time beginning his survey of the indigenous varieties of maize. One summer he paid me to plant, hoe, and self-pollinate a number of strains of maize from the Hopi and other southwest Indians, from Mexico and Guatemala. The latter grew to about 20 feet and pollinating them required a ladder when they tasseled in September, contrasting with an 18-inch Hopi strain. I learned a great deal about the diversity of *Zea*.

Anderson gave a great deal of thought to methods of analyzing and representing variation in natural populations. Although he was far from naive in statistics and mathematics, he preferred graphical methods, such as pictorialized scatter diagrams (3), rather than formal statistical analyses of his data. I was impressed with the outcome of his association with R. A. Fisher, whose discriminant function (23) was worked out using Anderson's data on three species of *Iris* as an example, and has become a useful technique in multivariate analysis. One might argue that Anderson's ideographs (1, Plate 23) visually demonstrate the relationships among the three species as well as Fisher's Figure 1 does. I was also taken with his graphs of internode length vs

number (4) and made similar plots of growing *Clematis* vines. I joked that he had plotted the first derivative of the plants.

My doctoral problem grew out of these discussions, or perhaps it was tactfully assigned to me. The idea of making a thorough field study of the glade leather leaf (*C. fremontii* var. *riehlii*) was roughly formulated in the spring of my first year. I was able to buy a used Model A Ford and a sleeping bag that summer (from hoeing corn), and spent a large part of my time on the Ozark glades (dolomitic barrens with an attractive endemic flora), during all seasons for the next two years, and a lesser part for another two years. At Anderson's urging I took a microscope to the glades and made squash preparations of anthers to look for irregularities in meiosis, which might indicate introgressive hybridization with another *Clematis*. I found none and went on to a study of the ecology, reproduction, and natural variation of the population. This constituted a major in botany and a minor in trespassing. I had found that walking up to the door of a farmhouse to ask the farmer's wife for permission to look at a glade tended to frighten her. A farmer once found some plants with bags over them on his glade and called the State Police, thinking that someone was growing hashish The Police brought one of the bagged plants to the Gray Summit Arboretum and I was called in for an explanation. The specimen, which I had bagged to find out if it would self-pollinate, was then annotated and deposited in the herbarium at Shaw's Garden.

I wrote up my work on the glades as a dissertation and received my Ph.D. degree in 1944. This was well enough regarded to be reprinted (10). In later years, I have had intentions of continuing field work. I made a few collections of two species of *Uvularia* in western New York state, with the idea of studying their relationship, but did nothing with them. Later there were several trips with Robert B. Platt to shale barrens of Virginia and West Virginia, where I learned to know the *Clematis* species, closely related to *C. fremontii*, which are restricted to the barrens. The *Clematis* leaves that I collected have served as samples for the analysis of variance by many biometry classes, but nothing else has come of these efforts. On several occasions I have taken a break from other things and driven to Missouri to revisit the glade *Clematis*, often with one or two students.

WESTERN CARTRIDGE COMPANY

My going to St. Louis in September 1939 nearly coincided with the German invasion of Poland. A year later the Selective Service Act was passed. I was classified 1-A, appealed, and was granted deferment as a student. In the spring of 1942 student deferments were abolished, and through Anderson's acquaintance with the research director at a defense plant, who was an

amateur botanist with a master's degree in botany, I was offered a job as a chemical microscopist. Western Cartridge Co., East Alton, Illinois (later a part of Olin Industries) manufactured small arms ammunition, including smokeless powder. The lab to which I was assigned was mainly concerned with problems of variability of the powder charge in cartridges, and with a polarizing microscope and the guidance of Chamot's & Mason's *Chemical Microscopy*, I was able to learn something about the composition of powder grains (nitrocellulose, nitroglycerin and a plasticizer) from thin sections. I boned up on the processing of wood pulp and on the chemistry of cellulose, nitrocellulose, and polymers generally, all with a crowd of chemical engineers. It seemed to a friend and me that some of the variability of the ballistic tests might arise in the blending of various batches of powder, and we made a statistical test. We had a barrel of marked powder poured through the blending tower with many unmarked barrels, then counted marked grains in samples of the output. Our statistics showed that the blending was very poor, but so far as I know nothing was done about it. After a year I was put in charge of a laboratory to study dry cells (flashlight batteries). So now the topic was electrochemistry, specifically of the Leclanché cell. With a punch press and other equipment, we did not succeed in a year's time in making experimental cells that equalled production cells in their service life. At least I learned some more chemistry, a bit of chemical engineering, and broadened my understanding of microscopy.

ROCHESTER

A position at the University of Rochester became available in the spring of 1944, and Anderson suggested my name to David R. Goddard. He planned to be in Terre Haute, Indiana, on a consulting job and asked if I could meet him there. I played hooky from my job, had the first of countless exhilarating discussions with Goddard and in effect was promised the job then. I now needed approval from the War Manpower Board to change jobs, but that turned out to be a breeze, since I was to be an instructor, teaching in the Navy V-12 program at Rochester. My superiors at Western Cartridge offered me a handsome raise and painted a rosy picture of my future there. When I pointed out that I expected a much lower salary at Rochester, that discussion ended, as did my career in industry.

The biology group at Rochester was largely assembled by Benjamin Willier several years before I came. It was a congenial and exciting group. Curt Stern was a great geneticist who had the collaboration of Ernst Caspari, Warren Spencer, and others on classified work for the Manhattan Project. There were many luncheon discussions of genetics and many other topics, as well as a journal club and "Festschrift." Sherman Bishop, A. W. Küchler, and I organized a memorable seminar on biogeography. I am indebted to Donald R.

Charles for patiently guiding me through an analysis of covariance and the solution of a discriminant function, as well as introducing me to *The Calculus of Observations* (39). I sat in on Dave Goddard's course in plant physiology, and for the first time heard critical lectures on thermodynamics and metabolic cellular physiology. He and I had many free-wheeling discussions of science. I particularly remember that we both felt that the nucleic acids richly deserved study, a few years before Watson & Crick.

I had told Goddard that I wanted to do research in experimental cytology, having only a vague idea of what that meant. Having been fascinated by Darlington's (8) speculations about the evolution of sexuality, and the contrast between mitosis and meiosis, I thought that it would be interesting to try to do something that might illuminate the difference between the latter two processes. This narrowed down to a plan to study the respiration of microsporocytes, microspores, and pollen. Thinking that it would be good to select a plant that had large anthers and was easy to manage, I made a little survey, and concluded that it would be hard to beat the Easter lily, *Lilium longiflorum*. I ordered some bulbs to set out in the greenhouse on a staggered schedule, and Goddard taught me the ins and outs of using the Fenn microrespirometer. This resulted in papers on the respiration of anthers (11), on growth of the flower bud and its parts using log bud length as a developmental index (12), and later, on nucleic acids in the anthers (33). Lilies have now been used by other workers, notably H. Stern (37), in a number of important studies of biosynthetic aspects of microsporogenesis, and Moens (32) for a study of the synaptinemal complex in meiosis.

My wife, Elinor Borgstedt, and I were married after my first year in Rochester. We have two daughters and two granddaughters. Elinor had been a secretary to the research director at Western Cartridge for a year, and was a music student at the University of Illinois at Urbana. She transferred to the Eastman School of Music at Rochester and earned her B. Mus. degree there. She has had a rewarding career as an organist and choir director, and now devotes her efforts to the piano. When long-playing records were announced in 1947, we bought six from the very first list, assembled an amplifier kit from war surplus parts, connected a turntable and speaker, and were both overjoyed with the music. We have been audio fans ever since.

PENN

During my second year at Rochester, Goddard accepted a professorship at the University of Pennsylvania and was succeeded at Rochester by F. C. Steward. With two colleagues at Penn, Goddard obtained research grants from the National Cancer Institute and the American Cancer Society for studies of cell division in plants. After three years at Rochester, I had been promoted to an

assistant professorship, but as it turned out I did not serve in that capacity, since Goddard offered me a position as a research associate in his program. After some soul searching and negotiation, we moved to Philadelphia. Maurice Ogur, a biochemist with particular interests in nucleotides and nucleic acids, joined the group as a research associate, as well as three excellent technicians, Kathie Sax, Gloria Rosen, and Connie Holden.

Goddard and I had reasoned that root meristems, as well as anthers, were favorable for studying cell division, and we began experiments with the primary roots of corn seedlings. They were grown in the presence of certain alkaloids, which were candidates for cancer therapeutic agents. The control and poisoned roots were fixed, sectioned, stained, and examined for mitotic abnormalities. After many weeks of study of the slides, I was frustrated at trying to imagine what had happened, for instance, to nuclei that had surely been in metaphase and after treatment looked something like interphase nuclei. I proposed that we abandon this traditional approach and try first to learn something about how roots and their cells grow. I knew in some detail about the work which Richard H. Goodwin, my predecessor at Rochester, and William Stepka had done in describing the growth pattern of *Phleum roots* (25). (In a footnote they acknowledge the assistance of Don Charles.) Their microscopic method of studying the minute grass roots was not feasible, since we had chosen to work with the much larger roots of *Zea* in anticipation of getting biochemical and metabolic data. At a meeting of our group, I suggested the kinds of data we should try to get and what I had in mind for a growth analysis. I put together a special camera rig to automatically record the displacement of marks placed on the roots, we worked out methods of counting cells, etc. I also supposed that I could handle the math involved in coordinating and interpreting the data. This is the rashest statement I have ever made. It took about 18 months of study to arrive at the analysis presented in the first papers (18, 21, 22), and it is apparent from recent publications by several authors that much remained to be done. In addition to the root work, we made the study of nucleic acids in *Lilium* anthers referred to above (33). The collaboration with Ogur was a great education in biochemical principles and methods of analysis.

After two years Ogur left Penn and a year later I was appointed associate professor. I had participated with John Preer in a biometry course (mostly statistics) for two years, but I now had additional teaching and some administrative duties. Goddard had great talents as an administrator as well as a teacher and researcher, and it was by his efforts that the departments of botany, microbiology, and zoology were merged in 1954 into a greatly strengthened division of biology. In 1961 he became provost of the university and served Penn eminently throughout the turbulent 1960s. Unfortunately, however, the analytical (chemical) work on roots was published only in

summary form (18). The work that had been done on respiratory metabolism of root segments would have yielded estimates of the energetic requirement for growth, but this could not be analyzed or interpreted without Goddard's participation.

With the assistance of Roman Maksymowych, the root studies continued at a reduced scale. We undertook to explore the effects of inhibitors of root growth and cell division, based on the growth analysis that had been worked out on a descriptive basis. However it seemed too laborious to work out elemental growth rates, so we photographed the growing roots with an automatic camera, and on the basis of hourly readings of total root length and measurements of mature cell lengths in sections of roots fixed at the end of each run, were able to calculate average rates of elongation and of cell production. A variety of substances were tried and three distinctive patterns of inhibition were found. Metabolic inhibitors such as cyanide and azide inhibit elongation in a manner suggestive of enzyme inhibition, with no effect on the rate of cell production. Substituted nitrogen bases are potent inhibitors of cell division with no effect on elongation for many hours. Several alkaloids depress both processes. Unfortunately, these results have not been adequately analyzed nor published, since there are certain points that I have not fully understood until recently. Another study was based on data on growth and cell division in *Phleum* roots, which Goodwin kindly provided. Reanalysis of the data for cell division rates showed that all the cells in the apical part of the meristem divide, whereas in the basal part, the proportion of cells that divide falls progressively to zero (13).

The studies of lily anthers and of the corn root were motivated by the idea of doing "experimental cytology." In both cases, however, my interest shifted from the cells per se, to questions of how the organs, the flower and anther, or the root, grow. I was impressed in both cases by the great regularity and coordination of cellular processes into a predictable morphogenesis. If there is a question of whether growth should be modeled as a stochastic process or a deterministic one, I would certainly argue for the latter. While there seemed to be sufficient opportunities to devote a career of research to either anthers or roots, I began to wonder whether the same regularity would be found in other developing systems, such as shoot apical meristems, and set out to obtain growth data.

Zygmunt Hejnowicz joined my lab in 1963–64 and collaborated in root studies. He worked out a method of recording growth using fluorescent marks illuminated with near-UV light, with the idea of applying it to a study of gravitropic curvature of roots, and made a study of the inhibition of root growth by auxin (27). I owe a great deal to him for many animated discussions of growth problems, particularly their mathematical and physical aspects, and we have had the pleasure of visiting him in Poland.

Hejnowicz suggested that we use celery, *Apium graveolens*, for studies of the shoot apex, since it has a large and relatively flat apex. After dissecting out a few young leaves from an otherwise intact potted plant it was possible to focus an Ultropak objective on the apex, and with an automatic camera to obtain photographs with cellular detail. After a great deal of effort we gave this up because of inadequacies in the Ultropak image, based as it is on shifting light reflections from the cell surfaces. We had also attempted to photograph shoot apices of *Xanthium*, chosen because we could assure vegetative growth by keeping these short-day plants on a non-inductive light schedule. This photography was similarly unsuccessful and I began to think of the possibility of an indirect approach, like using log bud length as an index of the development of lily flower buds. Recalling the plots of internode lengths of growing *Clematis* plants which I had made long before, I began daily measurements of internodes of *Xanthium* plants, and saw only that they were quite variable in length and apparently erratic in their growth. There had been some discussion of leaf growth with graduate students, and this led to daily measurements of leaf length in *Xanthium*. One day during a discussion with Mike Michelini of a semilog plot of this data, I found myself writing the formula for the plastochron index on the blackboard, as if by an inspiration (20). The plastochron index has now been used by many authors, including ourselves, in a variety of ways.

Richards & Kavanagh (34) published their analysis of Avery's (5) data on the growth of a tobacco leaf, marked with a grid of points, in 1943. As it happened, I read their paper when that issue of *The American Naturalist* appeared in the current literature box at Western Cartridge. I did not understand it fully then but was convinced that it was important, since it dealt with differentials of spatial dimensions as well as time. Later at Penn, I felt that their analysis could be repeated more satisfactorily with *Xanthium* leaves, and eventually I was able to complete it (14). This two-dimensional analysis of elemental growth rates was then applied to younger *Xanthium* leaves, to a fern prothallus (Mae Chen's Master's thesis), and to the thallus of *Marchantia*. The intention also was to use this analysis for data on shoot apical meristems, but as I indicated, this did not work out. This kind of analysis has scarcely been followed up by other workers but it has been important in our thoughts about the nature of plant growth, and growth analysis, including root growth analysis.

Of the many courses I have taught at Penn, the one I most enjoyed was developmental plant morphology, given occasionally to a class of graduate and undergraduate students, sometimes with the collaboration of a colleague or a visiting botanist. It was a mix of talks by members of the class and myself, with small projects in the lab. The first class, in fall 1952, was a remarkable group, some of whom are now professional botanists. Paul B.

Green took this course as an undergraduate and, in the next term, he enrolled for an independent study course, made a study of the growth of the *Nitella* internode cell, and published it. He went on to graduate school and, a few years later, returned to Penn as a member of the biology department. During his years at Penn, Green was a stimulating colleague. While our formal collaboration (in print) has been minimal, we shared discussions continuously. I trust that I was helpful to Green in some technical matters and his viewpoint has certainly had, and continues to have, a great influence on my thinking.

Wendy K. Silk came to Penn as a graduate student in 1969, with a degree in biomathematics, and for personal reasons stayed only a year. When she had completed her graduate work at the University of California, Berkeley, she came to my lab as a postdoctoral fellow. She had made a compartmental analysis of the uptake and release of gibberellic acid by excised hypocotyl segments of lettuce, *Lactuca*, and wished to analyze growth of the segments in detail. This analysis did not work out well and we began to talk about the curvature of the hypocotyl hook. She set up a time-lapse camera to photograph intact lettuce seedlings and made a thorough analysis of the kinematics of hook maintenance in the growing hypocotyl, which required rather deep study of continuum mechanics. I then suggested that there should be a general article on the kinematics of plant growth (36). In my view, this work has provided a sort of capstone to the growth studies, answering questions that I had only dimly perceived. It has been followed by a number of theoretical papers on plant growth by other authors.

PHYLLOTAXIS AND OTHER THINGS

A topic that I found confusing at first was phyllotaxis, as discussed by taxonomists, morphologists and plant anatomists, and at one point I decided to look into the copious classical literature. I felt that it must somehow be important to understanding plant morphogenesis, implying as it does a very close regulation of the process of leaf initiation at the shoot apex. Aristid Lindenmayer was then a member of the Penn botany department, and in many luncheon discussions, he was very helpful in my early puzzlement about phyllotaxis. (It may be that these discussions played some part in Lindenmayer's later formulation of the cellular automata known as L-systems.) I read Church's 1904 monograph, failing to understand his emphasis on orthogonal parastichies as implying some mysterious physical analogy. I also studied F. J. Richards's papers and quite a few others. Van Iterson's thesis of 1907 was far more difficult since it is in German and bristles with equations, but it impressed me as a much more comprehensive work than Church's. After some time, I came to feel that the supposed conflict between Church's and

van Iterson's models was minor, and could be resolved by rather simple notational changes in the equations used. When I felt that I understood this, a Dutch friend suggested that I write to van Iterson. He responded, generously sending me a copy of his monograph, which I have had bound, and treasure. I have recently completed a review of phyllotaxis (17).

This concern with phyllotaxis has had some unexpected consequences. Maksymowych at Villanova University had described striking changes in the morphology and the growth pattern of vegetatively grown *Xanthium* shoots, as the result of a single application of gibberellic acid. Among other things he made transverse sections of the shoot apex and young leaves of control and treated plants. When I saw them, I exclaimed that the treatment had altered the phyllotaxis. I proposed that we make a careful analysis of the arrangement of leaf primordia at the apex in these plants. We found that the normal pattern had been changed to a stable higher-order pattern (31) and speculated that the effect had some similarity to changes that occur on photoperiodic floral induction. Roger Meicenheimer (19) then induced *Xanthium* plants to flower and found that indeed the shoot apex underwent an identical but transient change in its phyllotaxis. The gibberellic acid effect is one of the few instances of an experimental modification of leaf arrangement in plants.

A second development is at the molecular level. Arthur Veen, a student with Lindenmayer at Utrecht University, had written a computer program to simulate growth of a shoot with the initiation of leaves in phyllotactic patterns (38). Their model was developed on a cylindrical surface, and I was sufficiently interested to write a preliminary program to carry out the simulation in a plane. Veen came to my lab to work with me on it. At that time, Lewis Tilney had developed an elegant technique of high-resolution electron microscopy of negatively stained microtubules. Lewis Routledge, working with Bernard Gerber, was using the technique for studies of bacterial flagella. When Tilney and Routledge showed me their pictures and asked how to analyze the obviously helical arrangement of subunits, my immediate impression was that they resembled certain of van Iterson's models. I suggested measuring distances between the units and certain angles, and constructing cylindrical models. After further discussion, I proposed to do the analysis if they would provide micrographs, references, etc. Veen and I were then deeply involved with computer modeling of phyllotaxis, so that the mathematical work and computations went quickly. In little more than a month the manuscript on tubular packing of spheres was completed (15). I had not been aware of the closely related work on cylindrical crystals by William F. Harris until our manuscript was completed, but I then sent him a copy. This led to voluminous correspondence, a visit by him to my laboratory, a visit to his at the University of the Witwatersrand, and to a far more rigorous analysis of tubular packings, from a crystallographic point of view (26).

The *Science* article on tubular packings (15) attracted the attention of others than biologists. At Penn I was one of the founders of a discussion group of people with varied interests in "form." For about five years this "Form Forum" met monthly, with wine and cheese, for talks and discussions of a remarkably wide range of topics, usually with demonstrations of paintings, sculptures, architectural renderings, tilings, polyhedra, electron micrographs, computer simulations, music, and poetry. I have also participated in two mathematical conferences on polyhedra. It is my hope that this broad approach to the geometry of form may be valuable in biological problems, such as the analysis of cellular patterns.

CALIFORNIA

I have taken three sabbatical leaves from Penn, and in each case have chosen to go to a California institution. In 1954–1955, with the award of a Guggenheim Fellowship, I worked at Frits W. Went's phytotron at the California Institute of Technology where I was incarcerated daily with Lloyd T. Evans, Harry R. Highkin, William S. Hillman, Margaretta G. Mes, Paul E. Pilet, Roy Sachs, and Went, when he was not travelling. There was much discussion of plant physiology, with a slant toward problems of floral induction. My idea was to grow *Xanthium* and perhaps other plants in a range of environmental conditions, using the plastochron index to assess temperature and light effects on the development pattern of the plants. I shared Anton Lang's dissatisfaction with the Cal Tech phytotron (30). My complaint was that growing conditions were not under control! Because carts were moved twice-daily to meet the schedules all of us had requested for our plants, there was no way, short of being an outright stinker, of knowing on a given day whether one's plants would be next to a flat of oat seedlings, or under the shade of a coffee bush. It seemed to me that the temperature coefficients for leaf growth and for the rate of leaf initiation (inverse of the plastochron) were nearly three, implying that the ratio of relative elongation rate to initiation rate (that is, the relative plastochron rate) was nearly constant over a broad range of temperatures. I took this to be an evidence of temperature regulation of morphogenesis, as to leaf initiation and growth, such that plants grown at different temperatures look much the same. Horie et al (29) have since described similar findings with cucumber plants.

But I was unable to get respectable data to support these ideas, and did not publish them. Looking around for other things to do, I set up lights and a 16-mm movie camera, which I had brought from Philadelphia, in a machinery room, which it turned out was air-conditioned. Time-lapse equipment was not then easily available or affordable, but I had brought home-made timers and mechanisms to operate cameras. There was an excellent machinist at the

phytotron who, understandably, did not welcome others to use his shop. But when I had satisfied him that I was not likely to abuse his machines and tools, he gave me nearly free rein, excellent instruction in shop practices, and good advice about getting my gadgets to work. Several striking scenes of *Xanthium* growing from seed to plastochron 15 or so, in continuous light or with a non-inductive dark period, resulted, and some footage on *Coleus*, before the year was out. I also rigged up an automated 35-mm camera, and made the photographs of *Xanthium* leaves, which were analyzed much later (14). Despite my dissatisfaction at the time, it was a profitable year.

Our second California trip was to La Jolla in 1966–1967, where Herbert Stern had welcomed me to his lab at the new campus of the University of California, San Diego. This might have been an opportunity to learn modern biochemical techniques at the bench. However, Stern and I got to talking about some published work on the inhibition of cell division in roots of the broad bean, *Vicia faba*, by a thymine analog, and I decided to resume inhibition experiments with *Zea* roots. I had again brought camera equipment with me, and a student who wanted to learn the paraffin technique assisted. We could find no mitotic figures in sections of roots grown in the presence of purine and pyrimidine analogs, although the overall rate of elongation was normal for as long as 18 hours, during which time the meristem appeared to be "used up." To the question of where these inhibitors were incorporated, Yasuo Hotta suggested the simple expedient of using radioactively labeled inhibitors, putting root segments into the cocktail of scintillation vials and counting them. To our slight surprise, the label appeared not only in the former meristematic region but also in cells quite some distance behind it; but time ran out before this result was reconciled with the growth data. I also set up a time-lapse movie camera to photograph growing thalli of *Marchantia* that a postdoctoral fellow provided, and later analyzed them for the pattern of growth in area. I was enamored of the CDC 6600 computer at UCSD, far more satisfactory than the IBM machine at Penn, and spent a part of my time at the computer center working on problems such as the numerical solution of differential equations.

At Stanford University, in the fall of 1978, we had the pleasure of renewing our long acquaintance with Paul and Margaret Green. Following some discussions with Paul, I began calculations of the effect of growth deformation on the multi-net pattern of cellulose microfibrils in cell walls. This resulted quickly in a geometrical and statistical model of changes in the microfibrillar pattern, which agrees satisfactorily with experimental data on the walls of growing *Nitella* internode cells (16).

In January, we moved to the University of California, Davis, where I had a visiting professorship for the spring term. I collaborated with Wendy Silk in a graduate seminar on plant growth analysis and gave a few other lectures. We

set up an automatic camera to record the growth of marked *Avena* coleoptiles, with the intention of following changes in phototropic curvature (curvature in the mathematical sense.) These preliminary experiments were not entirely satisfactory, but we did get some promising photographs.

One can conclude from these experiences that experiments do not always work out in a new laboratory with a time limitation. By and large, however, the scholarly leave is a valuable institution. The new viewpoints, acquaintances, and intangible benefits that result are ample justification for the inconvenience of moving and the frustrations one encounters. I wish I had taken leaves more often.

COMPUTERS AND CALCULATORS

The history of the computer has been written more than once (28, 35) but there may be some interest in my personal experiences as a user. The situation before the computer revolution is well stated in the preface of Whittaker & Robinson (39), written in 1924 "Each student should have a copy of Barlow's tables of squares, etc...a stock of computing paper (i.e., paper ruled into squares...), and...computing forms for...Fourier analysis... With this modest apparatus nearly all the computations hereafter described may be performed, although time and labour may often be saved by the use of multiplying and adding machines when these are available." As a boy I was impressed by the facility at mental arithmetic of one of my uncles, a bookkeeper, but I was all for machines. In high school I bought a cheap slide rule, possibly the only one in the school, and later I had a simple adding machine with dials to be turned with a stylus, which I could laboriously multiply with. I wore them both out. At Washington University and later, I was usually able to find a mechanical desk calculator of some sort, but when I came to Penn in 1947 there was no calculator in the botany department, only an ancient Monroe in the zoology office. I immediately ordered a Marchant, and soon additional machines were obtained for the biometry course and research. When I could afford it, I bought a Curta hand-held calculator to use at home and was delighted with the watch-like precision of its construction. In the summer of 1951, when the analysis of our root growth data needed to be done, a few of us moved to the Morris Arboretum with Marchant calculators and, on a pleasant terrace, punched the machines every day for about three weeks.

In 1972 Hewlett-Packard announced their first pocket scientific calculator, the HP-35, and I of course bought it for myself and the lab. As improved models appeared, I acquired and used several, including the current HP-28C, which has memory exceeding that of the IBM mainframe computer at which I learned FORTRAN.

By a curious coincidence, at the first scientific meeting I attended, the AAAS Christmas meeting at Richmond in 1938, I saw an exhibit of computing equipment from the Moore School of Electrical Engineering at Penn. It undoubtedly had to do with Weygandt's differential analyzer, an analog computer (35). So I was not as surprised as I might otherwise have been when I learned of the first digital computer, the ENIAC built at the Moore School. Penn had a computer lab when I came, which at one time housed a Univac, and later other machines. Occasionally I visited this lab and found that the staff were friendly enough, but the computers were not. One needed to know a great deal about the machines to use them. In January 1964, Penn acquired an IBM 7040, which was one of the first computers with an operating system designed to accommodate ordinary users. A full-scale computer center was quickly organized and I immediately took the FORTRAN course. At the end of the course each student was to write a program and run it. The instructor suggested a payroll problem, but I wrote my own program to calculate Fibonacci numbers and plastochron ratios. It ran on the first submission. I then proceeded to program the computation of elemental rates of growth in area of the *Xanthium* leaf, and completed the analysis for the 1964 Edinburgh Congress (14). I have now had experience with three or four mainframe computers, as well as two desktop computers.

When microcomputers appeared on the market we were in Silicon Valley, and I spent some time learning about the first Apple and other micros, skeptical at first about their usefulness for serious work. I bought an AIM 65 and set it up in our bedroom in Davis. Soon I had wired up a small speaker and written a program to play tunes through one of the output ports: *Papa Haydn's Dead and Gone*, Brahms's *Lullaby*,... The AIM was perhaps the least expensive, and one of the most educational of the early machines, with provisions for expansion of the hardware and the monitor program. I brought it back to Penn and used it to good effect for about five years. The machine at which I am writing this text is a far more competent personal computer, an MTU-130, which in its turn is about five years old....

LOOKING FORWARD

The years I have written about have of course seen a great revolution in biology, with the development of molecular genetics and many other advances. Reflecting on the state of what might be called the biometry of growth, say in 1936, one realizes that this received very scanty treatment in plant physiology textbooks, and none at all in plant anatomy. One learned of the "grand period of growth," of auxanometers, and of Julius Sachs's root-marking experiments of the 1860s. Plant anatomists wrote of gliding

growth, and used the word plastochron in a purely descriptive sense. In the 1870s Kreusler et al in Germany had studied the growth of *Zea* plants, but in the English-speaking world serious consideration of plant growth seems to have begun with defining of the efficiency index, or relative growth rate, by Blackman and by Briggs, Kidd & West in the early 1920s. Robertson's ideas about a master reaction in control of growth were widely quoted, and Huxley's allometric coefficient was fashionable. Biologists had a definite prejudice against mathematics and statistics and for many years I felt that my work was mostly quietly ignored. At the first presentation of our root work at a meeting, an older botanist took me aside and offered me the fatherly advice to soft-pedal the math.

In the intervening years the analysis of the growth of whole plants and plant organs has advanced considerably, particularly in connection with agricultural research. Statistics such as the absolute and relative growth rates, unit leaf rate, and leaf area ratio in the analysis of growth of individual plants, and related quantities for the growth of crops, appear to be firmly established, with general agreement about how they are to be estimated. Methods for fitting of growth curves, particularly the F. J. Richards function, have been highly developed. There is much activity in mathematical modeling of the growth of plants and crops.

The concept of elemental growth rates was introduced by Richards & Kavanagh in 1943 (34) and much of what I have discussed above, such as root growth analysis and analysis of growth of the *Xanthium* leaf, is related to this idea. This has led to the consideration of the kinematics of plant growth (36) in the context of continuum mechanics. The importance of distinguishing between material and spatial specifications has become clear. Kinematics deals only with motion without consideration of mass and force, but with kinematics as a basis we can look forward to the development of the dynamics of plant growth. Since a large part of plant physiology has to do with growing tissues, it will be important to deal effectively with the kinematics of growth, in order to make valid estimates of biosynthetic rates, for instance. Studies of the role of water and solute transport in tissue growth will have to take account of the kinematics of the growing tissue, as will considerations of the energetics of tissue growth. It is also true that morphogenesis, the development of the form of plant organs from meristematic tissue, is to a large extent a matter of tissue deformation, and it will be necessary to consider the forces that give rise to kinematic displacements and their origin. Work in these directions is under way, and we can look forward to further advances in the empirical analysis of plant growth processes, and in theoretical treatments of plant growth.

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