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Over 40 years of Contributions to Genetic Concepts: Genetics from A to Zea in Three Score and Ten*

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This issue of MAYDICA honors John R. Laughnan, a teacher who has brought the pleasure and stimulation of genetics to large numbers of students in the classroom, laboratory and field, and a scientist whose elegant research style has influenced lifetime students of the discipline of genetics, teaching them how to define and attack problems, and how to analyze and assess the resulting data.

When speaking of a scientist like John Laughnan, too serious a tone may be inappropriate. As the first syllable of our subject's last name is often mispronounced, we believe an audacious "laughdation" better suited to John Laughnan's wit, whimsy, and hyperbole than a lofty laudation enumerating his many scientific contributions and praising his undeniable virtues of dogged curiosity and creativity.

First, a bit of data would be desirable before any conclusions can be drawn. Our subject was born on a farm in a Wyoming township near Spring Green, Wisconsin, on Sept. 27, 1919. The family moved to Sauk City,

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Wisconsin, where schooling years were completed. His B.S. (1942) was in Plant Sciences at the University of Wisconsin, where he became acquainted with R. A. Brink and was advised to pursue a graduate career in maize genetics with L. J. Stadler at the University of Missouri. The research for his Ph.D. (1946) focused on the structure and function of the *A1* locus of maize and involved chemical and histological studies of pigments associated with a series of alleles and dosages. A post-doctoral NRC fellowship at Iowa State with G. F. Sprague was followed by two years as Assistant Professor at Princeton and a Gosney Fellowship at California Institute of Technology with E. G. Anderson. In 1948, he was offered an Assistant Professorship by the University of Illinois Botany Department at the request of a new staff member, Professor M. M. Rhoades, who was seeking a congenial and able associate. Following the death of L. J. Stadler in 1954, John was called to Missouri as Stadler's replacement, but after one year was called irresistibly back to Illinois to chair the Department of Botany. From 1955-59, and again from 1963–65, he headed that Department. Teaching and research have been his delight throughout.

Genetics from A to Zea (recollected by E.H.C. and S.G.-L., with stimulation from other lettered colleagues): After exhaustive analysis of the *A1* locus, John's research emphasis underwent an alphabetical transition, subtly and perniciously accompanied by an organismal diversion. In retrospect, it is clear that the transition to the next letter was signaled by detailed studies of the allele then called "A super B" (now known as *A-b* or *a-b*). In that now-gone era, presentation of a model called for construction of contradicting arguments to be shot down, and his arguments were sometimes all too effective. Having argued effectively (1949) that certain *A* alleles in maize were not simple but were part of compound tandem repeats that underwent unequal recombination between duplicated components, he faced a new problem. A number of events persistently occurred in the absence of recombination, which appeared to be due to gene conversion. This too-simple answer called forth from him an alternative model ("intrachromosomal exchange"). Evidence by which one might rule out the exchange model could be sought from the other mecca of genetic and cytological analysis, *Drosophila melanogaster*, where a compound tandem-repeat locus, Bar (*B*), was ready for exploitation. To the surprise of all, this effort happily failed to contradict the model. Despite his commendable attempts to eliminate the model, this study serves as a precedent for a new kind of chromosomal behavior (curiously, occasional reports can be

seen still, even in maize or *Drosophila* literature, that attribute non-recombinant events to gene conversion or mutation). In future studies with loci affecting disease resistance and the many functions involved in quantitative traits, these analyses of the genetic behavior of duplicated segments may occasionally be remembered. Incidentally, B of maize was graciously passed over and left for a former student to examine; so was C (that is, the nuclear gene, not the cytoplasm, cms-C, to which he did in fact make his own way). So much for an undeviating path.

Duplication in alphabets: Not confined to one path, our subject at one and the same time has advanced in the Greek alphabet as well as the Roman alphabet, some of which is known only to intimate insiders. Pressing forward with alpha and beta but foregoing gamma, he soon employed delta as a marker in chromosome 3 (delta: an arcane symbol for translocations learned from E. G. Anderson while waiting for smog to clear for Caltech pollinations). Another segment, on chromosome 10, was marked with E, but that gene and those experiments are known only to a discreetly limited audience. Yet another controversial marker, nonetheless, is etched in the memory of a large audience. Study of F, H, or I is unrecorded, but g and j took extended roles with E. Because others used K as a marker on chromosome 10, little reason was left to hob-knob with K except to argue its validity. Then there was *lg2*, which results in ligulelessness. But enough guilelessness; the reader at this point in the alphabet must be tolerant, as the trail only rises to general consciousness again at S (about which more later) and at *sh2* (next).

A gustatory digression: According to historical sources [E.H.C.], serendipity played a part in a practical discovery (1953) from which many sweet corn worshipers now benefit. Soaking and chewing upon a corn seed to aid in concentration is a pervasive but minor indiscretion in the profession, generally conducted surreptitiously and especially embraced when seeking rare mutations or recombinants. Muttering, so it is said, "that's shrunken, too," then "super, it's sweet!" our subject came upon the now popular and widely grown, high-sugar Super Sweet type. When next the reader has a table ear with butter (or better, corn oil margarine) and salt, it might be gratefully remembered that the *sh2* factor is so close to *A1* that it was originally attractive as a marker in intensive genetic analyses—else it might yet be only a phenotypic curiosity. The gene of importance is now reversed, but a is still present in Super Sweet strains despite crosses and crosses. If this obscure

recessive has any influence on flavor, our subject has never defined this by taste tests on recombinants, though he did propose that the A gene did not do what it is now known it does. But this was in the era when speculations on gene functions were permitted by reviewers; so much for consistent serendipity.

On clairvoyance (or, being on the bandwagon before there is one): By the time of the 1970 epidemic of *Helminthosporium maydis* race T, our maize geneticist already had set out to identify and to characterize mutations in cytoplasmic male sterility traits, and was doing so. To the extent that organelle-inheritance research in higher plants was popular at the time, it consisted of conceptual black boxes whose dissection, in the absence of molecular tools, was conducted only in the realm of "operational thinking."

If black boxes were too simple and one wished to undertake study of a system whose biology interferes with analysis, then as challenging as any would be mutation studies involving a maternally transmitted character expressed only in the male inflorescence (so much for a quick and easy route to fame). The analysis entailed finding fertile exceptions in cms-S strains that had occurred at a time such that the male and female inflorescences would both carry the genetic change. The cases were followed up by reciprocal progeny analysis sufficient to establish whether the mutation was nuclear or cytoplasmic. Teachers of genetic reasoning and design take note: a student who can follow such reasoning should be warned that a career may be looming on the horizon, and that many, but by no means all, colleagues in the profession will follow the reasoning. A student in whom this tendency is recognized might well be given this further problem: construct experiments that will establish whether nuclear constitution (1) influences the frequency of fertile exceptions, and (2) influences the relative frequencies of cytoplasmic vs. nuclear events. After the student has figured out how to do this, the publications and data of our subject should be casually made available. Given the mutation data, if the student dares to suggest that an episome might be involved, and offers experiments to challenge the idea, release the student upon the genetic world. Today efforts are proceeding to catch up on all the molecular basis of what has been found; tomorrow there will be more genetic designing required, and our subject is each summer and winter up to his ears doing that.

A teacher's cunning: Effective teachers often set out mazes for the student to explore, and then stay available to help when they miss a corner. "I [Ellen Dempsey] remember Jerry Kermicle's story of how he became fascinated

with genetics after John Laughnan, who taught the class for undergraduates, took the time to help him untangle his neglected *Drosophila* cultures. John set a good example for worthwhile teaching...."

About true grits: "Some twenty years ago, there were a number of successive years in which I [E.B.P.] accompanied John Laughnan to pollinate winter plantings of maize in south Florida. One trip stands out in my memory because it involved breakfast menus and the fact that John was on a diet. He usually ordered eggs for breakfast and invariably was given the accompanying choice of hash browns or grits. Actually, he wanted to avoid both. Declining the potatoes was no problem, but he was concerned that if he declined the grits he might hurt the feelings of the waitress. So he conceived the idea of ordering grits enthusiastically, but leaving them on his plate. This spotlighting of grits, however, led to a lengthy discussion of their popularity and the immense logistical problem of delivering them to all the vast number of restaurants and lunch counters throughout the South. We could only shake our heads in wonder. Then one day John whooped in exultation as he hit upon an explanation that cleared everything up for him. As soon as he shared his speculation, I had to admit that it appeared to offer a satisfactory solution. Proceeding down the highway were two cement mixer trucks, their barrels turning busily in hominy."

More alphabet: In 1970, John was on leave from U of I, serving a sojourn with AEC (now DOE). This period may aptly be referred to as a rare instance in which he took time to go fission.

About being organized: "I [E.B.P.] have never known anyone who would become immersed so completely and so tirelessly in painstaking field research during the long days of summer for a period that regularly extends to some fifty consecutive days. During these times of unrelenting daily work schedules, any interruptions or distractions easily evoke feelings of frustration. And yet these interruptions are inevitable: short-deadline reports, visitors to be met, committee meetings, phone calls to be returned, messages to be relayed, information to be provided, essential errands, unpredictable minor crises.

"Just to keep track of all these items requires a bewildering array of reminders detailing time, place, subject, information to be assembled, etc. During the period when the field nursery is the constant base of operation, these reminders frequently take the form of notes or messages hastily scrawled on whatever writing surfaces are immediately at hand, and then the notes may be

thrust into any one of several pockets, tucked into pollinating aprons or stashed in momentarily plausible locations in field vehicles.

"John Laughnan has wryly and unerringly recognized a central truth. Before we can address any task, we must first be reminded of it. Recently he was asked how things were going. He glanced around cautiously, then sidled up with an air of great confidentiality and affirmed reassuringly, 'I have it all written down.'"

Organizational activities (source a "ditto" letter found while screening colleagues' files and minds for suitable material): "An informal discussion... led to the suggestion that we consider an annual, informal get-together of maize geneticists... The purpose of this letter is to indicate that we would be happy to sponsor such a meeting at Illinois and would suggest that January 8 and 9, 1959, might be satisfactory dates. We think there should be maximum opportunity for participation by graduate students... May we have your comments at your earliest opportunity?" John R. Laughnan, November 26, 1958). The Annual Maize Genetics Conference began that January and has grown from a cozy group of two dozen to a cozy group of over 300, including students, post-docs, technicians, long-timers and worldwide participants. There is still no formal process for the get-together, no fixed mailing list, no "leader" but plenty of "helpers." Our subject may be seen standing out of the crowd in the accompanying 1960 photograph (Part A, Fig. 23). So much for grand contributions to organizational structures.

Lest we may have strayed too far, we return to this central point: This issue huskily honors John R. Laughnan, teacher and scientist, cooperator in maize genetics, colleague and friend, whose enthusiasm for science is an inspiration.