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Contents

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James L. Brewbaker

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James L. Brewbaker: Distinguished Geneticist, Tropical Plant Breeder, Inspiring Teacher

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Dr. James L. Brewbaker, "Dr. B" as he is affectionately referred to by students and colleagues, is a plant breeder and geneticist of multiple interests whose nine decades of life on this plant has contributed immensely to the betterment of humankind by increasing the quality and quantity of food, feed, and fuel produced around the world while preserving and protecting the environment. The hundreds of students he had trained over the years, currently some of the most productive geneticists and plant breeders, continue his legacy and contribute to agriculture development across the globe. James Brewbaker is undoubtedly one of our most accomplished geneticists and plant breeders. This chapter is dedicated to his amazing career.

I. EARLY YEARS

James L. Brewbaker was born on October 11, 1926 in St. Paul, Minnesota. Jim was the first child of Illinois farmers Harvey Edgar and Jean Turner Brewbaker, the year his father completed a Ph.D. in Agronomy at the University of Minnesota under Dr. H. K. Hayes. Harvey did his doctoral thesis on "Studies of self-fertilization in Rye," then served as a junior faculty member on the corn breeding program. His father's career would serve as a solid foundation for Jim's life as a tropical plant breeder. Hayes and Harvey's paper on "Double-crossed corn in Minnesota" published in 1930 was considered a landmark paper in the early days of hybrid corn in the United States. Jim's early memories include carrying a box to stand on while putting up shoot bags. The family had expanded with the birth of Jim's sister, Ann, in 1930. Harvey later served with the USDA for 6 years at Fort Collins, Colorado.

In 1936, the family moved to Longmont, Colorado, where Harvey had been invited to direct sugar beet improvement for the Great Western Sugar Co. Jim's early childhood association with field corn and later sugar beet, led to his interest in sweet corn breeding in later years. Jim and his sister Ann were enrolled in the Pleasant View School a mile and a half bicycle ride away. The school had all eight grades, four each in a classroom with one teacher. The entire class for Jim's sixth through eighth grade consisted of three students, Jim, Elmer Rasmussen, and a girl who promptly moved back with her family to Mexico. Jim mused that with parental guidance and help, it was as good or better an education as anyone gets today. The 120 acre family farm had four major sections—sugar beet, alfalfa, corn, and barley—and a large corral where they fed out 100 calves that were bought annually from a ranch in northern Wyoming. Shoveling manure and thinning sugar beet and hoeing weeds were standard summer jobs at 10 cents per hour. It was a splendid introduction to the realism and basic challenges of organic farming. Jim improved on his income by trapping muskrats near Swede Lake, cleaning pelts worth a dollar each, and on one occasion a skunk. The family's larder was always full of fish from the Lake, venison from annual hunts, ducks, and Canada geese, and whatever their Labrador Retriever could fetch when shot and dropped into icy waters.

Teenager Jim attended Longmont High School 1941 to 1944, graduating in a class of about 100 students and gaining one of the four in-state scholarships to college. He had played violin in the orchestra, ran in track and field events, spent his winters skiing in Colorado's hills, performed and starred in some plays, was most inspired by teachers of math and physics. He had been in Boy Scouts and earned Life and Eagle awards, sang in church choir with his mother as organist, spent summers working with his father's sugar beet research team, and hiked Long's Peak and many of Colorado's mountains. The family took summer camping trips to remote montane lakes, and had expeditions to the 1939 World's Fair in San Francisco and a summer trip to Vancouver. As a speaker at his high school graduation, Jim addressed the horrors of WWII and focused on the complicated and tragic lives of Hitler, Mussolini, and Emperor Hirohito. He spent the summer of 1944 as a freshman at the University of Colorado. Turning 18 in the fall, he enlisted in the Navy Air Corps and left for duty as aerial gunner at Memphis, Tennessee. He qualified soon for officers' training and spent one semester at Southern Methodist and two more at the University of Texas before the war ended.

In the summer of 1946 he enrolled at Colorado University as a junior majoring in General Science on the GI Bill. A major inspiration came from a course in Winter Ecology led by Dr. John Marr, with weekends spent at "Science Lodge" high in the Colorado hills. Jim conducted a research project on soil temperatures under snow banks, using a copper pipe he built with inserted thermometer. The small team of largely graduate students joining Marr on these study weekends provided great inspiration for a career in biological research. And the best part was snowshoeing in and skiing out of their research sites, leaving a profound impression of the value of a career that involved healthy outdoor activity. Along the way Jim worked with Professor Bill Weber in cytotaxonomy that led to his first publication on the chromosome numbers of *Physaria*, a local polyploid crucifer genus.

In the summer of 1947 before his senior year Jim got a summer job at the Plant Breeding Department of Cornell University, on advice from his dad. A friend drove him to New York City, then he hitchhiked up to Ithaca. Cornell faculty assigned him to simple field jobs, including a scythe as big as he was for weed control. He was assigned to work 3 weeks each in the department's three major programs—forage crops, vegetable crops, and grain crops. He worked respectively under the inspiring leadership of Drs. Sanford Atwood, Royce Murphy, Henry Munger, and Neil Jensen. This inspiring summer led him to automatically apply for graduate studies at Ithaca in Fall of 1948 and work on forage crop breeding with Dr. Atwood, whom he had first met sitting on a buckrake in an alfalfa field.

After his graduation from the University of Colorado but before returning to Ithaca, Jim spent another summer as field assistant in a remarkable corn research program at the California Institute of Technology in Pasadena. He was hired primarily to pollinate corn alongside graduate students like Ed Coe, Earl Patterson, and Pete Peterson, that he recalls as "simply a thrilling experience." Dr. Beadle's genetics team had arranged for the irradiation of corn seed stocks on U.S. ships deployed around the Bikini and Eniwetok atolls during atomic-bomb exercises. The well-mutated corn was grown under direction of Dr. E.G. Anderson. The summer research team included an array of famous scientist including Charles Burnham from Minnesota, Herschel Roman from the University of Washington, Seattle, and Edgar Anderson from Washington University at St. Louis. Each morning before the smog lifted there was an hour's seminar, and the scientists routinely studied all known genes on the 10 chromosomes, one at a time. It was a veritable graduate education in itself, and clearly inspired Jim for a research career on maize genetics.

In the autumn of 1948, Jim joined the graduate student team of Dr. Sanford Atwood in the Department of Plant Breeding at Cornell and was encouraged to skip the M.S. degree. He served 4 years together with Wayne Keim and Bill Anderson as a Teaching Assistant under Adrian Srb in Genetics, under Royce Murphy and Henry Munger in Plant Breeding, and under Harold Smith in Evolution. Dr. Atwood set Jim down to the analysis of many years' data on self- and cross-fertilization in the polyploid *Trifolium*, and he carried out thousands of crosses in the greenhouse. Many evenings he remembers working over these data around a dining table at the Atwood home. Together they unraveled the complications of the breakdown of self-sterility in polyploids, and integrating it directly into the varietal improvement programs of the pasture research team. Atwood later became Graduate School Dean at Cornell and then became President of Emory University in Atlanta. Cornell's team of faculty and grad students in this post-war era was exceptional in its maturity and dedication to discovery with invigorating seminars and visiting speakers. Faculty and students met twice a month for dinner in the age-old institution of Synapsis, (a Graduate student organization at Cornell), where Jim served as President one year, forging unusual bonds between graduate students and professors. Cornell's beautiful and richly endowed campus provided many other options for learning. Jim played in its fine orchestra, recalling the thrill of concerts with famous musicians like Paul Robeson and Andres Segovia. Jim also spent much time learning about "radar-range" cooking (with free samples) and much about biophysics from three of his roommates. In the summer of 1952, Jim returned to a cabin at Science Lodge in Colorado to type out six copies of his thesis on his trusty Smith-Corona. He returned briefly to Ithaca, handed in his thesis, received his doctorate, and left for Europe, on a National Science Foundation fellowship to work at the Genetics Institute in Lund, Sweden.

II. RESEARCH

The first publication of James Brewbaker came as an undergraduate at the University of Colorado working with taxonomist William A. Weber on the cruciferous genus *Physaria*. He discovered that local Colorado lowland species *Physaria australis* was a diploid (2*n* = 8) but montane *Physaria vitulifera* was polyploid (2*n* = 16).

A. Breeding, Genetics, Irradiation, Virus

1. Clover Self-Incompatibility. At the University of Lund in Sweden, Brewbaker expanded his research on polyploidy and self-incompatibility in clovers under Prof. Arne Muntzing, breeding a series of interspecific hybrids. A large set of publications ensued on the reversal from self-incompatibility at diploid level to self-fertility at tetraploid level resulting from the unique "competition interaction" of *S* alleles in the diploid pollen grains discovered by Brewbaker and Sanford Atwood (Brewbaker 1952, 1953, 1954, 1955b, 1957, 1958; Brewbaker and Atwood 1952; Brewbaker and Keim 1953). These research findings undergird a significant phylogenetic pattern in higher plants, in which high polyploids can afford the luxury of self-pollination. The studies also revealed the multi-allelic inheritance of the V-leaf markings in clovers (Brewbaker 1955c; Brewbaker and Carnahan 1956) and the uniquely cyanidin-red flower based on duplicate recessive genes (Brewbaker 1962). Brewbaker was able to participate in some of the innovative genetic research at Universities of Lund and Svalof involved in breeding of *erectoides* dwarf barleys presaging the Green Revolution with its exploitation of dwarfs and improved harvest indices in rice and wheat.

2. Rice and Corn. Brewbaker joined the University of the Philippines at Los Baños (UPLB) in 1953 as a junior faculty member on the rice and corn (RICO) breeding team of fellow Cornell-graduate Dioscoro L. Umali (later Chancellor) and Dr. H. K. Hayes (his father's major professor). Dr. Hayes made it plain that he had much to learn about the tropics. Brewbaker and students like Ramon Valmayor and David Gorrez studied the genera *Musa* and *Ensete* (bananas, abacá), helping reassemble UPLB's fine pre-war collection of clones. The research (Brewbaker and Umali 1956; Brewbaker et al. 1956; Brewbaker and Gorrez 1956; Umali and Brewbaker 1956) focused on breeding of abacá (Manila hemp) and its hybrids notably to provide virus tolerance. Later in Hawaii he was involved in isozyme studies of *Musa* (Bonner et al. 1974). With Hayes, Brewbaker led the inbreeding of tropical corn populations as basis for the first 4-way hybrids in the Philippines, and helped establish resistance to downy mildew. They identified a major genetic source of DMR in ancient white flints of Mindanao. Many informal publications appeared in the campus' *Philippine Agriculturist*. Brewbaker's fond memories of the Philippines include driving through massive forests, now gone, then covering half of the Philippines' 30 million ha. Today, 5% is left and the human population has increased fivefold to 100 million. Corn breeding also included improvement of *waxy* (*malagkit*) food corns popular in Philippines known as *phil glutinous comps*. Also he helped in the selection of upland rice cultivars, entirely then of the tropical *indica* rice. D. L. Umali was soon to attract the Consultative Group for International Agricultural Research (CGIAR) to bring the International Rice Research Institute (IRRI) in 1960 to Los Baños and initiate introgression of dwarfing genes from the more temperate *japonica* rice, the ultimate basis of the Green Revolution. The RICO team had enlivening discussions at that time on the Swedish experience with *erectoides* (dwarf) barleys with high yield achieved with high N inputs. However, the prevailing attitude was still "taller is better"; Brewbaker recalls that when President Magsaysay visited their rice fields, he was photographed holding the immense cultivar "Peta," taller than he, then a symbol of high yield, but unfortunately, high lodging when N levels increased.

3. Radiation Genetics. Brewbaker's 5-year post-doc (1956–1961) at Brookhaven National Laboratory (USAEC) occurred at a time of incredibly exciting genetic research. In 1953, Watson and Crick had proposed the double-helix structure of DNA as the molecular basis of genes. Later this was linked through messenger RNA to create proteins. In 1966, Dr. Barbara McClintock from the nearby Carnegie Lab lectured with the incredible revelation that genes like *Ds* and *Ac* could act as "mobile elements" and induce apparent mutations through gene suppressions. Also disturbing was the evidence from Jacob and Monod's research that something outside the gene itself could assume a role of epigenetic activity modifying gene action. Brewbaker's research involved studies of the nature of radiation-induced mutations in a team headed by Drs. Arnold Sparrow (cytogenetics) and Harold Smith (evolutionary genetics). It focused on mutations involving the multi-allelic *S* (incompatibility) locus of plants (Brewbaker and Shapiro 1959; Brewbaker and Natarajan 1960; Brewbaker and Swaminathan 1960; Brewbaker 1960; Brewbaker and Emery 1961). Radiation-induced mutations were not intragenic but always involved major chromosome alterations (Brewbaker and Natarajan 1960). Significant related research involved use of the "gamma field" to study effects of extended low-dose irradiation, and Brewbaker raised crops like peppers in these fields. Concurrent research included the identification of cigarette-smoking-induced mutations, and long-term carcinogenic effects from irradiation. His experience led to his appointment to establish and run a Co60 pool-type irradiator with expert M.S. Swaminathan at India's World Agricultural Fair. He directed research use of the facility daily by literally hundreds of Indian scientists with the help of four graduate students from the Indian Agricultural Research Institute (IARI), one of whom, M.D. Upadhya, (Upadhya and Brewbaker 1968, 1971) later joined him as a post-doc in Hawaii.

4. Pollen Biology. The germination and growth of pollen in media (Brewbaker and Majumder 1961a) was shown by Brewbaker and Drs. Beyoung Kwack and Sanat Majumder to rely uniquely on high concentrations of calcium (Brewbaker and Kwack 1963a, 1963b), levels toxic to root hairs or shoot apices. The Brewbaker and Kwack media for pollen tube growth proved to be a standard for pollen studies. Several studies focused on the use of pollen for inducing mutations, including non-ionizing UV irradiation (Brewbaker and Emery 1961; Brewbaker et al. 1965). Dosage responses proved to be linear with ultraviolet 2537 Å but logarithmic with X- or gamma-rays.

A significant publication (Brewbaker 1967a) detailed the results of many years' research on the bi- and trinucleate types of pollen grains in higher plants. Binucleate pollen proved to be the primitive trait of angiosperm families, mutating to trinucleate and largely distinguishing entire families of plants. Binucleate pollen were longer lived, easily germinated in media or in nature, and associated with insect pollination and gametophytic-type self-incompatibility. Trinucleate pollen were shown to typify evolutionarily advanced families (e.g., grasses, composites), wind pollination, inability to germinate in media, and an association with sporophytic-type self-incompatibility. This discovery was recognized as an outstanding contribution to the science of evolution in plants in the 50th anniversary issue of the *American Journal of Botany.*

5. Isozyme Diversity. Brewbaker and colleagues devised an inexpensive method for displaying genetic polymorphism of plant isozymes (Brewbaker et al. 1968), his most-cited publication. His post-docs and students extended this technique profitably to an extremely wide series of genetic inquiries in maize and other crops (Beckman et al. 1964a, 1964b; Makinen and Brewbaker 1967; Hamill and Brewbaker 1969; Brewbaker 1971b; Macdonald and Brewbaker 1972; Peirce and Brewbaker 1973; Brewbaker 1987b), identifying all major peroxidases in maize (Brewbaker and Hasegawa 1974, 1975; Brewbaker 1974) and all esterases (Macdonald and Brewbaker 1974, 1975). Their research underscored the exceptional polymorphism of tropical versus temperate maize, where isozyme polymorphism among temperate inbreds might involve one slow and one fast band but a quick look at any tropical race would reveal multiple isozymes. Subsequent breeding research abundantly verified the narrow genetic base of most temperate corn (Brewbaker 2015a).

6. Food Irradiation. After joining faculty of University of Hawaii (UH) in 1961, he obtained as "Atomic Energy Commission" grant to bring a pool-type 200 cu Co60 irradiator to Honolulu and expand research on radiation biology (Brewbaker et al. 1965) and food pasteurization. Subsequent research with post-doc M.D. Upadhya involved a very wide range of tropical food products including potential commercial applications to papaya and mango (Upadhya and Brewbaker 1966a, 1966b; Upadhya et al. 1967a, 1967b) and pineapple (Brewbaker et al. 1965; Makinen et al. 1967). Pineapple studies also showed their self-incompatibility to be of the *S* allele type (Brewbaker and Gorrez 1967).

7. Resistance to Maize Mosaic Virus (MMV). A major success of Brewbaker and his students (Brewbaker, 1981c) and Ming et al. (1995b) was to conquer a debilitating corn virus called MMV, later mapped on Chromosome 3. The disease thrived in unique tropical environments where maize was present year-round, as both virus and the vector, *Peregrinus* leafhopper, were confined almost exclusively to maize (Brewbaker 2013). Brewbaker and students transferred the virus-resistant gene *Mv* to every field and sweet corn in the expanding University of Hawaii collection (Brewbaker 1997b; Brewbaker and Josue 2007b; Brewbaker 2009a).

8. Maize Virus and Maya Civilization Collapse. Brewbaker and students made five expeditions into Mexico and Central America to collect leucaenas, and the ~220 indigenous races of maize. The lowland civilization of Maya (classic period 300–800 CE) became of major interest, in part as the ecosystem matched that of the Waimanalo station in Hawaii. The MMV virus was seen to be common in modern Maya corn fields. Also, the sole race known to be grown by ancient Maya, called Nal-Tel, was highly susceptible, although otherwise it grew splendidly in Hawaii. Extensive studies and many seminars later, Brewbaker published a manuscript he considers his most significant, "Diseases of maize in the wet lowland tropics and the collapse of the Classic Maya corn" (Brewbaker 1979). The disease most convincingly associated with the collapse proved to be MMV. The thesis has been well received by corn scientists, and time has only reinforced Brewbaker's conviction that many if not most pre-Columbian civilization "rose and fell on their stomachs." It will take a little longer for the anthropologists to admit the power of food or lack thereof. Many seem not to fully recognize the absolute reliance of the Maya (and Teotihuacan, and Zapotec, and Anasazi) civilizations on healthy maize. The same can be inferred for collapses of other cereal-based civilizations, for example, collapse of the Mesopotamian civilization due to four centuries of drought caused by climate change and failure of the wheat crop.

9. Hawaii's Corn Seed Industry. Brewbaker's multi-island breeding of virus-resistant, tropically adapted corns for Hawaii began in 1961 and led him to invite mainland breeders to grow their winter nurseries here (Brewbaker 1965b). Molokai was chosen for the first 5 acres in 1966, and soon breeders settled year-round. By 2012, seed industry, especially corn seed industry became Hawaii's biggest agricultural industry contributing more than $250 million to the local economy. Brewbaker and colleagues founded the Hawaii Crop Improvement Association (HCIA) in 1971 (Brewbaker 1969) and he served many years as its Executive Secretary. His first Ph.D. student, Elizabeth Hamill (Johnson) (Brewbaker et al. 1967; Hamill and Brewbaker 1969) spent her entire career on Molokai directing seed nurseries.

10. Supersweet Corn. With the MMV problem solved, Brewbaker expanded a breeding program of tropically adapted sweet corns (Brewbaker et al. 1966; Brewbaker 1971a), focusing uniquely on the high-sucrose gene *brittle-1*. Long-term evaluations proved this *bt1* gene to be superior to the more common *shrunken-2 (sh2)* for kernel quality and fusarium tolerance in tropical soils (Zan and Brewbaker 1999). The first hybrids were released in 1968 (Brewbaker 1968), then in 1977 the first significant cultivar, "Hawaiian Supersweet #9" (Brewbaker 1977a), was widely grown around the world. Many synthetics and inbreds (Brewbaker 2010b) and new hybrids and cultivars like "Hawaiian Supersweet Silver" and "Kalakoa" (Brewbaker 2011a) have resulted from the breeding, much of it closely integrated with breeding in Thailand. Extensive research involved the genetics of quality in sweet corn, focused on tenderness and the thickness of pericarps. Techniques were refined to quantify tenderness through taste tests, easily planned year-round in Hawaii, and through microscopic measurements (Brewbaker et al. 1996). The broad subject of breeding tropical vegetable corns was thoroughly reviewed for *Plant Breeding Reviews* in 2015 (Brewbaker 2015a).

11. Tropical Virus Resistance. Brewbaker's post-doc year with Rockefeller Foundation breeding corn in Thailand convinced him to expand the Hawaii research on uniquely tropical diseases and insects, notably the ever-present viruses (Brewbaker et al. 1991; Brewbaker 1992). Early studies showed the aphid-transmitted potyviruses to be common on Molokai (e.g., maize dwarf mosaic virus (MCMV) and sugar cane mosaic virus (SCMV). Tolerance to both A and B types proved to be common in Hawaii germplasm and susceptible lines were soon eliminated; this research was only briefly reviewed (Brewbaker 1982a). Genes were identified for resistance to Africa's maize streak virus (Kyetere et al. 1995, 1999; Lu et al. 1999). Following its introduction to Hawaii ca. 2000, MCMV became a significant disease for the corn industry. It was of particular concern as a component of maize lethal necrosis (MLN) involving the co-action of potyviruses. MCMV first appeared in Brewbaker's nurseries on Oahu in 2010 and he initiated resistance breeding employing his system of monthly plantings with susceptible borders and checks. ELISA tests showed the virus to be universally present with no evidence of immunity but abundant sources of high tolerance. Significant tropical inbred sources of MCMV tolerance were identified (Nelson et al. 2011) and provided through Hawaii Foundation Seeds to seedsmen dealing with major crop losses in E. Africa. A major QTL for tolerance was shown to be linked closely to the *brittle-1* locus on which tropical supersweet breeding was based. Several major supersweet inbreds were converted to tolerance for major viruses. No evidence was observed for variations in attractiveness to the thrips vector.

12. Disease-Resistant Corn Breeding. It had been apparent to Brewbaker from his early years in the Philippines that breeding corn in the tropics involved many disease problems unknown or insignificant in temperate regions (Brewbaker 1983a). His sabbatical leaves in Thailand (1967), Philippines (1970), Colombia (1979), Nigeria (1989), and Mexico (1997) all involved collaborative trials of his Hawaii-bred lines, often focused on disease tolerance. Evaluations for diseases unknown in Hawaii such as the downy mildews (DMR) led to identification and release of UH lines to aid breeders abroad. Eleven sets of recombinant inbred lines (RIL) were created, largely through the studies of student H. G. Moon (Moon and Brewbaker 1995; Moon et al. 1999). Each involved a temperate inbred, normally susceptible, and a tropical inbred, where RILs could help identify QTLs for tolerance (Brewbaker and Moon 2000). The Hawaii corn team also assembled an international set of ~50 international trials called "MIR" (maize inbred resistance) with outstanding tropical inbred and temperate checks (Kim et al. 1988; Brewbaker et al. 1989). Genetic studies and associated breeding and selection by Brewbaker and his students included common rust (*Puccinia sorghi*) with extensive research by Dr. Soon Kwon Kim (Kim et al. 1980, 1988; Pataky et al. 2001). They conducted resistance breeding for Southern rust (*Puccinia polysora*) after its appearance in Hawaii ca. 1975, finding absolutely no tolerance in temperate corn (Brewbaker et al. 2011). Major QTLs were identified for polysora resistance and several inbreds were converted to high tolerance. They also discovered QTLs providing tolerance of Stewart's bacterial wilt (Ming et al. 1995a, 1999) and to *Sphacelotheca reiliana* (Lu and Brewbaker 1999b). They also participated in evaluations of corn germplasm for resistance to *Aspergillus flavus* and *Aspergillus parasiticus*-induced aflatoxin (Zuber et al. 1983). Tolerance of *Fusarium verticillioides* was shown to be universally significant in tropical soils and all supersweet breeding required constant selection for seedling mortality and rots of kernels and ears. The unique conditions of Hawaii's breeding in soils growing corn exclusively for 50 years made the genetic improvement so effective that all Hawaii supersweet hybrids survived essentially unaffected. Hosting the National Association of Sweet Corn Breeders in Winter 1987, Brewbaker's display showed that none of the temperate sweet corns could germinate in Hawaii without seed treatment. Evidence for the genetic control, presumably polygenic, was elusive and no significant publications emerged from these many years of observation.

13. Pest-Resistant Corn Breeding. QTLs for insect tolerance were always more elusive than those for tolerance to viruses and other pathogens, reflected in much of the Hawaii research. Tolerance to the pantropical corn earworm was increased by breeding longer husks with tighter husk cover (Brewbaker and Kim 1979). Significantly, 14-row corn ears that tapered through a left-hand spiral came to dominate Brewbaker's sweet corn inbreds and hybrids, ensuring much lower earworm infestation. Hawaii participated in early studies of the earworm-repellent maysin, showing it to be high in the highly colored silks of tropical races like *Zapalote chico* (Widstrom et al. 1982). Tolerance to the corn borers of both temperate and tropical ecosystems was evaluated (Kim et al. 1989) and also summarized (Kim et al. 1988; Brewbaker et al. 1989) from worldwide MIR trials. Discovery of high tolerance to the corn leaf aphid in one of Brewbaker's most-used supersweet inbreds Hi38 (Brewbaker and Chang 1974) led to a scholarly study by Dr. Yoon Sup So that revealed a major recessive allele *aph* that drastically reduced aphid fecundity (Lu and Brewbaker 1999a; Kim et al. 2009).

Since weekly and even daily visits were made to their corn fields, Brewbaker and students assembled a wide array of empirical data on maize developmental genetics and pest relationships. Elusive genes for tolerance were sought for the ubiquitous rose beetle (*Adoretus sinicus*) of the tropics, an insect routinely visiting corn fields in Hawaii after dark and punching holes in leaves. There was no evidence for specific morphological factors affecting damage, but narrow-leaved popcorns proved to be exceptionally susceptible. Some research fields were illuminated daily for four hours after dark in studies of day-length sensitivity, and these showed no rose beetle injury. Feral parrots were present for several years, and their preference for corn clearly focused on sweet corn at 18–22 day harvest maturity, as did damage from feral pigs (present for many years). Seedling loss to Brazilian cardinals was observed to be much more severe on supersweet corn plots than on field corn plots, as the birds were pulling up the week-old seedlings to recover the swollen kernel, and field corns rooted much more aggressively. The tillering of American temperate sweet corns (gene *gt*) predisposed them to much higher populations of insects like aphids, leafhoppers, and thrips.

14. Corn Genetic Studies. Breeding improved field and sweet corns in Hawaii involved many genetic systems in addition to those affecting disease tolerance. Breeding for improved harvest indices in single-cross hybrids had brought great interest in dwarf ideotypes, and inbred conversions (normally six backcrosses) showed the dwarfing locus *br2* (*brachytic-2*) to be an effective option (Djisbar and Brewbaker 1987). Interest in lowered lignin for increased digestibility of silage also made the low-lignin loci of interest, and similar conversions (Lee and Brewbaker 1984) showed *bm3* (*brown midrib 3*) to work well but with yield loss under severe winter conditions. Major tropical field corn populations of enhanced digestibility were bred based on *bm3* and on the double-mutant *bm3* and *grassy tiller* (*gt*). Brewbaker had previously shown, to the surprise of many, that the American sweet corn industry was based on an unusual double mutant of *sugary-1* and *grassy tiller*, leading both to tillering and husk leaves only rarely seen in tropical maize. Among tropically adapted populations released by UH was a composite based on the high-lysine gene *opaque-2* (Brewbaker 2009d). Among unusual genes discovered was one for *double-cob* (Brewbaker 2009b) and one of *floppy tassel* (Brewbaker and Yu 2009), the latter common among the corns with *waxy* locus common as a vegetable in Asia. A major breeding program for waxy vegetable corn for Hawaii, in cooperation with former student M. H. Lee (Lee and Brewbaker 1984) is ongoing. Many morphological traits of tropical corns vary widely, and Brewbaker and students ultimately raised all of the 220 major indigenous races of maize. Among traits widely assessed were tassel branching (Brewbaker 2015a) and husk numbers (Brewbaker and Kim 1979), both significantly higher in lowland than in highland tropical races. A single co-dominant gene *Brta* was discovered that doubled tassel branch numbers (Brewbaker and Yu 2009). Studies were conducted of popcorns and a Hawaiian hybrid released to growers (Larish and Brewbaker 1999). Lime-induced chlorosis was found to be under monogenic control in collaborative studies at a CIMMYT station in Mexico (Nourse et al. 1999). RILs created in Hawaii were used to help identify QTLs for downy mildew resistance in Thailand (unpublished). Hybrids and advanced generations of maize and *Zea diploperennis* were thoroughly evaluated by Srinivasan (Srinivasan and Brewbaker 1999a, 1999b) although the effort to transfer the perennial gene from Z. *diploperennis* to cultivated corn was not successful. However, a highly prolific and high biomass corn composite (Brewbaker 2009b) with one-fourth *Z. diploperennis* was advanced through a dozen recurrent selection cycles. This was later released as HIC#9.

15. Near-Isogenic Lines of Hi27. A long-range project was initiated in 1967 while in Thailand to create a series of near-isogenic lines (NIL) in an adapted tropical inbred. The original intent was to provide genotypes for use in teaching, since available mutants from the Illinois seed stocks were ill-adapted in the tropics and were not NILs. Brewbaker chose a reliable Indian yellow-flint inbred CM104 that traced to Colombian stock, later converting it to MMV resistance and naming it Hi27 (Brewbaker 1995d, 1997b). Over the years ~150 NILs were created through six or more backcrosses (Brewbaker and Josue 2007a). They have proved extremely useful in studies of linkage drag for QTLs of significance, including *Mv* (Ming et al. 1997) and QTLs for tolerance of southern rust (Brewbaker et al. 2011) and MCMV (unpublished). All are duplicated in the Illinois seed stocks.

16. Improved Tropically adapted Corn Inbreds and Populations. A major contribution of the year-round breeding in Hawaii has been to establish field corn inbreds and populations of superior performance and relate them to Hawaii's ecosystem. Brewbaker published the major guide to corn production in Hawaii, *Corn Production in the Tropics: The Hawaii Experience*. A major series of 40 inbreds (Brewbaker 1997b; Brewbaker and Josue 2007b) was bred and released following extensive evaluations that included the worldwide MIR trials. Many originated from other breeders in the tropics, and the inbreds and their performance were fully documented on the HFS website. A series of three composites and six inbred-based synthetics (Brewbaker 2009d) was released and described on this website, several with specific features, for example, disease resistance. These have been carried through almost annual cycles of recurrent selection. All releases have been provided to the USDA Germplasm Resources Center in Fort Collins, CO. Yield trials over 30 years revealed superior hybrids for Hawaii growers that were grown widely in 1980s and 1990s, but have not been grown after transgenic commercial hybrids appeared (with *BT* earworm resistance and glyphosate resistance). Studies were also conducted to define appropriate population densities for Hawaii's growers of silage (Chung et al. 1982).

B. Tropical Legumes Studies

1. Nitrogen-Fixing Tree Association. Brewbaker has carried out extensive studies on tropical legumes and grasses. The legume research focused increasingly on tropical trees (~700 species) that fix nitrogen, in a role vastly more significant than their role in temperate ecosystems (where leguminous herbs dominate). Seed collection expeditions then assembled the world's major provenance collection of the genus Leucaena, noted "multipurpose" tree for forage and fuelwood. With international colleagues, he founded in 1980 the Nitrogen-Fixing Tree Association (NFTA), based in Hawaii, and served as its President more than a dozen years. NFTA identified, assembled seeds, and grew trials of 50 major nitrogen-fixing trees (NFT), publishing documents on each. Brewbaker directed a conference at Bellagio to assemble resource documents on nitrogen-fixing trees in 1982. A follow-up conference in UK, Bellagio II, led to foundation of CIFOR (Center for International Forest Research). NFTA initiated two annual newsletters, one, *Leucaena Research Reports* (LRR) and the other *Nitrogen-Fixing Tree Research Reports* (NFTRR). A worldwide audience of 1500 scientists and growers joined NFTA, and its grant-funding budget approached $250,000 annually. Brewbaker lectured on NFT and Leucaena at international conferences annually for two decades. He organized and helped chair conferences on NFT (Taiwan 1979, Colombia 1982), leucaena (Taiwan

1979, Singapore 1982, Vietnam 1998), the leucaena psyllid (Hawaii 1985; Indonesia 1988, 1989), gliricidia (Costa Rica 1987), sesbania (Kenya 1989), casuarina (Egypt 1990), acacia (Australia 1986), and other subjects.

2. Genetic Improvement of Acacia Koa. Koa is Hawaii's premier timber and a native of highlands in the state. Brewbaker and family initiated seed collections in the 1960s on their family hikes, and incorporated them into early studies of isozyme variations. Mutual interest by State Foresters led to acquisition of a greenhouse at the Waimanalo station at sea level, leading to early definition of koa's cytology (polyploid, $2n = 52$), self-incompatibility, and immense genetic diversity. In 1991, Brewbaker and his new organization, NFTA, organized a conference leading to a publication "Genetic improvement of *Acacia koa*: Resource documents" (Brewbaker et al. 1991). A series of replicated provenance trials was initiated in 1991 at 2200 ft. elevation in the Hamakua Station. Each year for 13 years Brewbaker and students collected and planted ~50 provenances in two-replicated trials of 10-tree plots. Seeds from superior trees entered advanced trials and two major seed orchards, reflecting selection for erect form, lack of fluting and limbiness, and tolerance of fusarium wilt. In 2001 they held a second workshop, Koa: A Decade of Growth (Brewbaker 1997a; Sun et al. 1997). Ultimately 892 provenances were evaluated, of which only 23% of the trees survived. An advanced cycle 3 of recurrent selection was touted as a source of genetically improved forests (Shi and Brewbaker 2006). Initial efforts to clone koa were unsuccessful, but continuing work off-campus (Hawaii Agricultural Research Corporation) showed promise.

3. Genetic Improvement in the Genus Leucaena. The genus *Leucaena* (Shelton and Brewbaker 1994) has been the focus of a major proportion of the productive research of Brewbaker and his students since 1962, when he initiated performance trials. The present world distribution of improved varieties they bred in Hawaii is in the millions of hectares, about equally as forage and for wood (fuel, paper, construction). Five expeditions were conducted throughout their native range from Texas to Colombia. The collection of 1100 provenances represented most of the 22 species in the genus. All accessions were gown at the Waimanalo station in Hawaii, later in replicated trials throughout the islands. Outstanding provenances were advanced through selection and evaluated internationally (Brewbaker 1975a; Pan and Brewbaker 1988). A large series of interspecific hybrids was created and evaluated (Brewbaker