NATIONAL ACADEMY OF SCIENCES

KARL SAX

1892—1973

A Biographical Memoir by

CARL P. SWANSON AND NORMAN H. GILES

Biographical Memoir

COPYRIGHT 1987
NATIONAL ACADEMIES PRESS
WASHINGTON D.C.

Karl Sax.

KARL SAX

November 2, 1892–October 8, 1973

BY CARL P. SWANSON AND NORMAN H. GILES

As I view my contribution to the writing of our time, it seems to me to consist of a double affirmative, saying first that an awareness and experience of Nature is necessary to Man if he is to have his humanity, and saying in the second place that that same awareness must have something of a religious quality, the Italian pieta, if you will.

Nature is a part of our humanity, and without some awareness and experience of that divine mystery man ceases to be man. When the Pleiades and the wind in the grass are no longer a part of the human spirit, a part of the very flesh and bone, man becomes, as it were, a kind of cosmic outlaw, having neither the completeness and the integrity of the animal nor the birthright of a true humanity.

THESE WORDS by Henry Beston from his now classic volume, *Outermost House*, strike us as uniquely applicable to Karl Sax. He would not have been found wanting—although he, most certainly, would have raised a quizzical eyebrow unless the term "religious quality" were stripped of any cloying mysticism. He grew up and throughout his life remained close to the soil, and he expressed in words and actions the dignity, integrity, inner strength, and outer optimism that are so often the legacy of such a birthright. He knew the wheatfields of southeastern Washington; he knew how to care for and to harvest that which he had sown; and he knew the wonder of growing things, whether these were plants or hu-

man beings. He acknowledged his birthright and was proud of it, and he shared it with those in both high and low places. His public career was a long and distinguished one, but to those who knew him privately as well, that record was but a partial measure of a great and warm human being.

Karl Sax was born of pioneer parents in Spokane, Washington, on November 2, 1892; he died in Media, Pennsylvania, on October 8, 1973, less than a month shy of his eighty-first birthday. His father, William L. Sax, was, at various times, schoolteacher, county superintendent of schools, farmer, businessman, and mayor of Colville, Washington. His mother, Minnie A. Sax (née Morgan), was an artist and amateur botanist. An exposure to plants and to the natural environment as well as the advantages of higher education were very much a part of his early background. Sax entered Washington State College in 1912 to major in agriculture, and it was here that he met Professor Edward Gaines, a wheat breeder in the Experiment Station. Gaines led him into research and undoubtedly encouraged him to continue his studies at the graduate level. As Sax once wrote, "Here I learned that one could have all of the pleasures of an agricultural career without the financial headaches by going into agricultural research work." This early experience with the problems and techniques of plant breeding expanded into a continuing and absorbing interest that was pursued throughout his life. Other later studies brought him national and international recognition, but they never fully replaced his need to be close to the soil and to growing things.

Sax graduated from Washington State College in 1916, the year in which his first scientific paper appeared. Prior to graduation he had married his cytology teacher, Dr. Hally Jolivette. In the fall of 1916, she accepted an instructorship at Wellesley College, and he entered the Bussey Institution Graduate School of Applied Biology of Harvard University

to work under the direction of Professor E. M. East. He received an M.S. degree in 1917, but his graduate studies were interrupted by World War I. He entered the army as a private and was discharged as a second lieutenant in the Coast Artillery in 1918.

Sax's first academic position was as an instructor in genetics at the University of California, Berkeley, where he also undertook cytological studies in the genus *Crepis* under Professor E. B. Babcock. His stay in Berkeley was brief, however, as was his next move to the private Riverbank Laboratories in Geneva, Illinois, where he initiated his studies on wheat. In 1920 he accepted a position at the Maine Agricultural Experiment Station in Orono; here he completed his doctoral thesis on wheat hybrids, and the D.Sc. was awarded to him in 1922 by the Bussey Institution. One of his colleagues at Orono was John W. Gowen, and they collaborated on a number of occasions: the genetics, productivity, and root and bud selection of apples were their primary concerns. The wheat studies were pursued almost as an avocation, but Sax considered the papers dealing with wheat species and hybrids to be his most important contribution during these early years—in large part because they were among the first of the published works that opened up what was then the new science of cytotaxonomy in this country.

Sax remained at Orono until 1928 when he was appointed associate professor of plant cytology at the Arnold Arboretum and named to the faculty of the Bussey Institution Graduate School of Applied Biology, an affiliate of Harvard University concerned with teaching and research in agriculture and horticulture. Here he joined a faculty of distinguished biologists: W. M. Wheeler and C. T. Brues in entomology, W. E. Castle and E. M. East in genetics, Oakes Ames in economic botany, and I. W. Bailey in wood anatomy. The graduate student body must also have been a stimulating one be-

cause many of those who received their degrees from the Bussey Institution were to become worthy successors to their professors.

Sax was elevated to a full professorship in 1936, the same year in which the dissolution of the Bussey graduate school took place. (In the view of President Lowell, Harvard and applied biology were incompatible.) The dissolution, however, necessitated a move of office, laboratory, and students to the new Biological Laboratories in Cambridge; here he taught courses in cytology and, for a while, genetics—Sax took over teaching the latter on the death of Professor East in 1938. This move, on the other hand, did not terminate his association with the Arboretum and the Bussey. His cytotaxonomy studies continued, and many of his students lived in the Bussey buildings during the summer months of their graduate careers. For many of us this was during the latter years of the Great Depression and under the lengthening shadows of World War II; to make ends meet we were encouraged by him to grow our own vegetables and to raid the Arboretum for appropriate fruits.

With the retirement of E. D. Merrill, Sax was appointed acting director of the Arnold Arboretum in 1946; in 1947 he was named its third director. He held simultaneously the rather empty title of superintendent of the Bussey Institution. But both administrative appointments were abruptly terminated by Harvard University in 1954 as a result of his vigorous but losing opposition to the proposal that the general resources of the Arnold Arboretum—books, herbarium specimens, and funds—be transferred to Cambridge as part of a move for the consolidation of botany. Sax not only believed that the science of botany suffered when instruction at the Bussey was terminated, and that it would deteriorate further when interest in the Arboretum as a living center for horticultural studies was lessened; he also considered the ac-

tion taken by the Harvard Corporation to be an outright breach of trust. To combat the transfer, he enlisted the aid of The Friends of the Arnold Arboretum and cooperated with them when the group filed suit in Massachusetts against the corporation. He contended that he, as director and as a matter of principle, could not be party to the divestiture of the Arboretum's resources without judicial review and legal approval. Sax remained as professor of biology in Cambridge until his retirement in 1959, but the controversy left its mark. The latter years were bitter ones: he was hurt by the alienation of some of his botanical colleagues and by the scientific decline of the Arboretum that had been for so long a significant part of his productive years.

About thirty graduate students took their advanced degrees with Sax, and another fourteen spent their postdoctoral years in his laboratory. He is remembered and revered with unabashed affection by these students; in his gruff but quiet way he embraced them all and brought them into his family. As he said, "My academic children seemed almost as much a part of our family as our three sons."

Karl Sax established a solid and enviable reputation both in this country and abroad. He was as well known to nurserymen as to his fellow cytologists, and this was reflected in his professional affiliations and in the honors bestowed on him. He was a member of the Genetics Society of America, serving as president in 1958; the Botanical Society of America—he received its certificate of merit in 1956; American Society of Horticultural Science; American Genetics Association; Population Association of America; Planned Parenthood League, serving as president of the Massachusetts chapter in 1958; American Academy of Social and Political Sciences; and the Radiation Research Society. He was elected to membership in the American Academy of Arts and Sciences (1941) and the National Academy of Sciences (1941),

to honorary membership in Phi Beta Kappa (1941) and the Japanese Genetics Society (1956), and as foreign correspondent to the French Academy of Agriculture (1946). The Jackson Dawson Memorial Medal of the Massachusetts Horticultural Society was awarded to him in 1959, as was the Norman J. Coleman Award of the American Association of Nurserymen in 1961. He received an honorary doctoral degree from the University of Massachusetts in 1965, from his alma mater Washington State University in 1966, and from the University of Maine in 1971. He was equally pleased, however, to be named "Horticulturist of the Year" (1959) by the Student Horticultural Club of the University of Massachusetts, and to be grouped, by Katherine White in *The New Yorker,* with Charles Sargent and Ernest "Chinese" Wilson as "a distinguished plantsman."

Sax was a national lecturer on the academic circuit for the American Institute of Biological Sciences in 1957 and in 1962 for Sigma Xi. In 1951 he received the signal honor of being asked to deliver the Lowell Lectures in Boston, choosing as his topic world population problems.

The research and publication record of Karl Sax spanned a period of fifty-five years (1916–1971) with but a brief interruption for military service. The publications fall generally into three groups—horticulture, chromosomal studies, and demography—with considerable overlap of the first two areas as much of the cytogenetic and cytotaxonomic work was done on ornamental species in the Arnold Arboretum. The horticultural aspects of Sax's professional career began with his appointment to the Maine Experiment Station, where he was much occupied with improvement of productivity in apples. This interest, which initially involved propagation, crossing, and sterility, was continued at the Arboretum, but the focus of the work was now directed toward an understanding of the origin of the Pomoideae, the production of

desirable ornamental hybrids, and the means for dwarfing well-known and useful varieties of nursery stocks. The dwarfing of fruit trees had been practiced empirically for hundreds of years before being introduced into the Americas but the basis of dwarfing was not understood in a scientific sense. By experimenting with a wide variety of intervarietal, interspecific, and even intergeneric combinations of rootstocks and scions; by the use of different interstocks between root and scion; and by single and double bark inversions to block the flow of nutrients through the phloem, Sax contributed significantly to an understanding of the phenomenon, reduced the variability of graft compatibility and growth, and simplified the techniques to the point where the average nurseryman could readily produce his own dwarfs.

In the area of plant breeding, Sax and his students—in particular George Skirm—were successful in creating a number of excellent hybrids that quickly found their way into the ornamental trade. He was especially proud of the graceful cherry "Hally Jolivette," a hybrid between *Prunus subhirtella* and *P. apetela,* which he named for his wife and frequent collaborator. (The fact that Jolivette could be translated from the French into "pretty little one" added icing to the cake of tribute.) The magnolia "Dr. Merrill" honored his predecessor as director of the Arboretum, while the crabapple hybrids "Henry DuPont" and "Henrietta Crosby" were named after two of the loyal Friends of the Arnold Arboretum, who were also his personal friends and research sponsors. The "Blanche Ames" honored a distinguished botanical artist who was also the wife of Professor Oakes Ames; the hybrid "Mary Potter" was so named because one of the parent species was *Malus sargenti,* named after her father, Charles Sargent.

Sax also produced a number of *Forsythia* hybrids. Beatrix Farrand, a well-known landscape architect, Friend of the Arboretum, and designer of the gardens at Dumbarton Oaks

in Washington, D.C., was recognized by having a triploid hybrid named after her. This turned out to be a lesser improvement than the tetraploid "Arnold Giant," winner of an award of merit by the Royal Horticultural Society of England. The "Arnold Dwarf" proved to be an interesting ground cover but a meager producer of flowers. Still another of his *Forsythia* hybrids, the "Karl Sax," was subsequently named by a nurseryman who was testing it in his trial plots.

The chromosomal studies fell into two subcategories: cytotaxonomy and the effects of radiation and chemicals on chromosome structure. As indicated earlier, his wheat studies provided him with a doctoral thesis as well as helping to establish what was then the developing field of cytotaxonomy in this country. He shared with the Japanese cytologists Kihara and Sakamura the credit for discovering the role of polyploidy and interspecific hybridization in the origin of certain wheat species, a seminal work of great significance in understanding the nature of some of our basic food plants. Comparable studies, in which Hally Jolivette Sax often participated, were carried out on a wide variety of groups growing or being tested in the Arboretum: Pomoideae, Pinaceae, Rosaceae, Cycladales, Hamamalidaceae, Vitis, Yucca and Agave, Rhododendron, Paeonia, Ulmus, and Platanus. The karyotypes of Yucca and Agave were shown to be sufficiently unique to cause them to be removed from the Liliaceae, and to be given familial status in the Agavaceae; moreover, the complete fertility and regular meiotic pairing in the London plane tree, a hybrid between *Platanus occidentalis* and *P. orientalis*, demonstrated that separation by the Atlantic Ocean for millions of years did not necessarily involve chromosomal rearrangements and accompanying sterility.

It was Sax's interest in the American species of *Tradescantia*, sparked no doubt by his collaboration with Edgar Anderson of the Missouri Botanic Garden, that led to the emer-

gence of radiation cytology out of what began as a cytotaxonomic survey of the Commelinaceae. Sax understood that chromosomal rearrangement must play some kind of role in evolution and speciation and that the large size and small number of *Tradescantia* chromosomes in the readily available haploid microspores made them ideal for experimental purposes. Recognizing that X rays not only induced mutations but chromosomal rearrangements as well, he initiated his radiation studies in 1935. The atom bomb and the horrors of radiation exposure were nearly a decade in the future.

Tradescantia paludosa was the species of choice, and the following two decades witnessed an extraordinary outpouring of papers by Sax and his students—papers that provided qualitative and quantitative information on the frequency of both induced and spontaneous aberrations. The implication and transference of these data to problems of radiation therapy, evolution, and speciation were inevitable, as was additional information related to the effects of temperature, cell cycle, dose rate, and dose fractionation on the final frequency of induced change. Sax was the father of radiation cytology, and he spawned a whole generation of "chromosome busters." In his later years, and particularly after retirement, Sax turned to the chromosomal aspects of aging in seeds, and to the radiomimetic effects of caffeine, insecticides, and chemical food additives.

While he vigorously pursued his horticultural and chromosomal investigations, Sax still managed to take an interest in and make a significant contribution to the area of demography. His initial entry into this field undoubtedly stemmed from his close association with his graduate mentor and now colleague, Professor E. M. East; but it was probably fostered as well by the interest of Castle and Brues in applied eugenics. In 1923 East had published *Mankind at the Crossroads,* a Mal-

thusian indictment of the present and future consequences of unchecked human fecundity in a world of limited resources and agricultural productivity. He advocated a conscious and deliberate practice of birth control; in his words, "parentage must not be haphazard." Sax was similarly Malthusian. (Believing that what he advocated publicly should be first practiced at home, he urged all of his graduate students to read the so-called "Bussey Bible," a collection of articles on birth control.) The first of a continuing flow of articles appeared in *The Scientific Monthly* in 1944, but the gist of his thinking was set forth in his Lowell Lectures. The talks were prepared for book form under the title *Malthus and the Modern World;* this was subsequently altered to *Standing Room Only: The Challenge of Over-Population,* which appeared in 1955 and was reissued in paperback in 1960.

Mild-mannered and retiring as he was in his personal relations, Sax was actively aggressive in the Planned Parenthood League and in his demographic speeches and articles. His local target was the restrictive birth control law of Massachusetts. These laws were subsequently changed by a referendum sponsored by the Planned Parenthood League—but not before Sax had invoked the wrath of many religious leaders and particularly those of the Roman Catholic Church of Boston and its suburbs. (The Church proclaimed to its flock that "birth control is against God's Law" and urged all parishioners to vote down the referendum.) He viewed the harassment that resulted as a measure of the effectiveness of his stand, and so he continued his fight on a national scale—believing, as has proven to be the case, that financial aid to the underdeveloped countries without accompanying information and aid regarding birth control was not only politically immoral but, in a human sense, ultimately self-defeating and cruel as well. He considered India a lost cause in this respect, but he held high hopes for the Latin American coun-

tries if aid to them could be tempered with something more than material benefits and weapons.

Sax was a realist and a pragmatist. He was particularly disturbed by demographic and scientific Pollyannas who, through ignorance or design, duped the public with glowing scenes of future happiness and an abundance for all. Consequently Sax reviewed *Enough and to Spare,* a book by Harvard colleague Kirtley Mather, in a tempered but devastating manner to show that both Mather's demography and his biological postulates were utterly without foundation, that his optimism was based largely on pious hopes. Sax himself had a clear vision of the role of science in the betterment of mankind, but he had an equally clear vision of its limitations as well.

In another political direction, Sax took strong exception to the praise that some leading British and American scientists—among them Julian Huxley, J. B. S. Haldane, J. D. Bernal, and L. C. Dunn—accorded Soviet science, particularly genetics. He was too much of a dirt farmer as well as a cytogeneticist to accept Lysenkoism, and he was among the first to call the scientific world's attention to the oppressive treatment given such men as Vavilov, Dubinin, Navaschin, and Timoféeff-Ressovsky.

Retirement in 1959 brought a change of place and of pace. Sax established and maintained an experimental garden on his son's estate in Media, Pennsylvania, but he also traveled and lectured widely. In the years between 1956 and 1966 he held visiting professorships at the Universities of Florida, Tennessee, Georgia, and California at Davis; at Yale University; and at North Carolina State University. For a brief period in 1962, he was resident collaborator at the Brookhaven National Laboratory. In 1961, at the age of sixty-nine, he was a Guggenheim fellow at Oxford University where C. D. Darlington, the dean of British cytologists, held sway.

Darlington and Sax were sharply contrasting scientists. As Sax once wrote, paraphrasing Francis Bacon, he was the ant, the gatherer of quantitative data from which his ideas emerged; Darlington was the spider, the gifted spinner of theories in which facts were often of secondary importance. Both had published on chromosome structure, the mechanisms of crossing over, and the origin of chiasmata, with the Darlingtonian views the more nearly correct. Both were also interested in demography—Sax again the pragmatist, Darlington the theorist, as he wove genetics, race, IQs, mating patterns, and the improvement of mankind into his mental cobwebs. It is regrettable that their conversations were not recorded, for Sax, in his own way, had great respect for Darlington's facile mind—even though he referred to Darlington's *Recent Advances in Cytology* as "a masterpiece of mythogenesis."

In his later years, Professor and Mrs. Sax spent each winter at the University of Georgia. He published regularly during these years, and his papers continued to reflect the breadth of his interests. Fittingly, one of his last journal papers was in response to a request from the Genetics Society of Japan, of which he was an honorary member. Perhaps even more fittingly, it was coauthored by Mrs. Sax, his companion, colleague, and gentle critic for fifty-eight years.

Comparisons are more likely to be invidious than they are to illuminate, but Professor Sax's secure place in his several fields of interest was earned and not thrust upon him: he was an imaginative and dedicated scientist, a plant breeder of note, and a citizen who had a clear vision of the place of science in human affairs. His greatness as a human being, however, was innate. To those of us who gained our scientific stripes under his tutelage, and who came to know him privately as well, he was a father figure: a quiet, decent man who at times was reserved, gruff, even unapproachable; at other

times, warmly human and humorous. He treated us all alike, encouraging everyone, but infinitely patient if we could only plod. He was not an eloquent speaker. He let his published papers speak for themselves, or he deferred to his students and colleagues at national and international meetings. But when his deeply held and cherished principles were challenged or misrepresented, he never hesitated to enter the lists. Supported always by Mrs. Sax, he was never an unprepared or unworthy opponent. He rarely dealt in personalities when the subject was controversial, for he could respect another's position or belief even when he disagreed with it; but he was not a compromiser of principles even though, as in the Arnold Arboretum controversy, it might cause him anguish and cost him position and friends.

Karl Sax was survived by his wife, Hally Jolivette, who passed away on March 20, 1979; three sons—Dr. Karl J., an industrial organic chemist, Dr. W. Peter, a psychiatrist, and Edward D., an industrial engineer; nine grandchildren; eight great-grandchildren; and those who, like ourselves, remember him with deep and sincere affection.

BIBLIOGRAPHY

1916

Fertilization in *Fritillaria pudica.* Bull. Torrey Bot. Club, 43:505–22.

1918

The inheritance of doubleness in *Chelidonium majus, L.* Genetics, 3:300–307.

The behavior of the chromosomes in fertilization. Genetics, 3:309–27.

1921

Sterility in wheat hybrids. I. Sterility relationships and endosperm development. Genetics, 6:399–416.

A simple device for weighing seeds. Bot. Gaz., 71:399.

With J. W. Gowen. Productive and unproductive types of apple trees. J. Hered., 12:291–300.

Studies in orchard management. II. Factors influencing fruit development of the apple. Bull. Maine Agric. Exp. Stn., 298:53–84.

Chromosome relationships in wheat. Science, 54:413–15.

1922

With J. W. Gowen. The relation of tree type to productivity in the apple. Bull. Maine Agric. Exp. Stn., 305:1–20.

Sterility relationships in Maine apple varieties. Bull. Maine Agric. Exp. Stn., 307:61–76.

Sterility in wheat hybrids. II. Chromosome behavior in partially sterile hybrids. Genetics, 7:513–52.

Sterility in wheat hybrids. III. Endosperm development and F_2 sterility. Genetics, 553–58.

1923

With H. C. McPhee. Color factors in bean hybrids. J. Hered., 14:205–8.

NOTE: The authors would like to thank Professor William Provine of Cornell University for checking the bibliography.

With J. W. Gowen. The cause and permanence of size differences in apple trees. Bull. Maine Agric. Exp. Stn., 310:1–8.
With J. W. Gowen. Permanence of tree performance in a clonal variety and a critique of the theory of bud mutation. Genetics, 8:179–211.
The association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris*. Genetics, 8:552–60.
Bud and root selection in the propagation of the apple. Proc. Am. Soc. Hortic. Sci., 20:244–50.
With J. W. Gowen. The place of stocks in the propagation of clonal varieties of apples. Genetics, 8:458–65.
The relation between chromosome number, morphological characters and rust resistance in segregates of partially sterile wheat hybrids. Genetics, 8:301–21.

1924

The nature of size inheritance. Proc. Natl. Acad. Sci. USA, 10:224–27.
With E. F. Gaines. A genetic and cytological study of certain hybrids of wheat species. J. Agric. Res., 28:1017–32.
With Hally Jolivette Sax. Chromosome behavior in a genus cross. Genetics, 9:454–64.
The "probable error" in horticultural experiments. Proc. Am. Soc. Hortic. Sci., 21:252–56.
Nursery stock investigations. Proc. Am. Soc. Hortic. Sci., 21:310–12.

1925

Fertilization of apple orchards in Maine. Bull. Maine Agric. Exp. Stn., 322:1–8.

1926

With Iva M. Burgess. Varieties of ensilage corn for Maine. Bull. Maine Agric. Exp. Stn., 330:49–56.
Sweet-corn breeding experiments. Bull. Maine Agric. Exp. Stn., 332:113–44.
Quantitative inheritance in *Phaseolus*. J. Agric. Res., 33:349–54.
A genetical interpretation of ecological adaptation. Bot. Gaz., 82:223–27.

Statistical methods in horticulture. Proc. Am. Soc. Hortic. Sci., 23:141–49.

1928

Bud and root selection in the apple. Bull. Maine Agric. Exp. Stn., 344:21–32.

Chromosome behavior in *Triticum* hybrids. (Verhandl. V. Internat. Kongresses Vererbungs-wissenschaft, Berlin, 1927.) Z. Indukt. Abstamm. Vererbungsl., suppl. 2:1267–84.

1929

Chromosome counts in *Vitis* and related genera. Proc. Am. Soc. Hortic. Sci., 26:32, 33.

Chromosome behavior in *Sorbopyrus* and *Sorbaronia*. Proc. Natl. Acad. Sci. USA, 15:844, 845.

1930

Chromosome number and behavior in the genus *Syringa*. J. Arnold Arbor., 11:7–14.

With D. A. Kribs. Chromosomes and phylogeny in the Caprifoliaceae. J. Arnold Arbor., 11:147–53.

Chromosome structure and the mechanism of crossing over. J. Arnold Arbor., 11:193–220.

Arnold Arboretum cytological laboratory report, 1929–1930. J. Arnold Arbor., 11:237, 238.

Chromosome stability in the genus *Rhododendron*. Am. J. Bot., 17:247–51.

1931

The origin and relationships of the Pomoideae. J. Arnold Arbor., 12:3–22.

Chromosome numbers in the ligneous Saxifragaceae. J. Arnold Arbor., 12:198–206.

Arnold Arboretum cytology laboratory report, 1930–1931. J. Arnold Arbor., 12:299.

The smear technique in plant cytology. Stain Technol., 6:117–22.

Chromosome ring formation in *Rhoeo discolor*. Cytologia, 3:36–53.

Crossing over and mutation. Proc. Natl. Acad. Sci. USA, 17:601–3.

Plant hybrids. Arnold Arbor. Bull. Popul. Inf., 5:17–20.

1932

With E. C. Abbe. Chromosome numbers and the anatomy of the secondary xylem in the Oleaceae. J. Arnold Arbor., 13:37–48.

The cytological mechanism of crossing over. J. Arnold Arbor., 13:180–212.

Chromosome relationships in the Pomoideae. J. Arnold Arbor., 13:363–67.

Arnold Arboretum cytological laboratory report, 1931–1932. J. Arnold Arbor., 13:450, 451.

Meiosis and chiasma formation in *Paeonia suffruticosa.* J. Arnold Arbor., 13:375–84.

The cytological mechanism for crossing over. In: *Proceedings of the Sixth International Genetics Congress,* vol. 1, pp. 256–73. Brooklyn: Brooklyn Botanic Gardens.

Flowering habits of trees and shrubs. Arnold Arbor. Bull. Popul. Inf., 6:14–16.

Review of *Recent Advances in Cytology,* by C. D. Darlington. Collecting Net, 7:201–3.

1933

With Edgar Anderson. Segmental interchange in chromosomes of *Tradescantia.* Genetics, 18:53–67.

With Hally Jolivette Sax. Chromosome number and morphology in the Conifers. J. Arnold Arbor., 14:356–75.

With H. W. Edmonds. Development of the male gametophyte in *Tradescantia.* Bot. Gaz., 95:156–63.

Species hybrids in *Platanus* and *Campsis.* J. Arnold Arbor., 14:274–78.

Chromosome behavior in *Calycanthus.* J. Arnold Arbor., 14:279–81.

The origin of the Pomoideae. Proc. Am. Soc. Hortic. Sci., 30:147–50.

Chromosome numbers in *Ulmus* and related genera. J. Arnold Arbor., 14:82–84.

With Susan Delano McKelvey. Taxonomic and cytological relationships of *Yucca* and *Agave.* J. Arnold Arbor., 14:76–81.

1934

Interlocking as a "demonstration" of the occurrence of crossing over. Am. Nat., 68:95, 96.

With Edgar Anderson. A cytological analysis of self-sterility in *Tradescantia.* Bot. Gaz., 95:609–21.

With J. M. Beal. Chromosomes of the Cycadales. J. Arnold Arbor., 15:255–58.

With Edgar Anderson. Interlocking of bivalent chromosomes in *Tradescantia.* Genetics, 19:157–66.

With L. M. Humphrey. Structure of meiotic chromosomes in microsporogenesis of *Tradescantia.* Bot. Gaz., 96:353–62.

Cytology for students. (Review of *Introduction to Cytology,* by L. W. Sharp.) Science, 80:407.

1935

With Edgar Anderson. Chromosome numbers in the Hamamelidaceae and their phylogenetic significance. J. Arnold Arbor., 16:210–15.

Chromosome structure in the meiotic chromosomes of *Rhoeo discolor* Hance. J. Arnold. Arbor., 16:216–24.

The cytological analysis of species-hybrids. Bot. Rev., 1:100–17.

Variation in chiasma frequencies in *Secale, Vicia* and *Tradescantia.* Cytologia, 6:289–93.

The effect of temperature on nuclear differentiation in microspore development. J. Arnold Arbor., 16:301–10.

With Hally Jolivette Sax. Chromosome structure and behavior in mitosis and meiosis. J. Arnold Arbor., 16:423–39.

1936

The experimental production of polyploidy. J. Arnold Arbor., 17:153–59.

With Ladley Husted. Polarity and differentiation in microspore development. Am. J. Bot., 23:606–9.

Polyploidy and geographic distribution in *Spiraea.* J. Arnold Arbor., 17:352–56.

Chromosome coiling in relation to meiosis and crossing over. Genetics, 21:324–38.

With Edgar Anderson. A cytological monograph of the American species of *Tradescantia.* Bot. Gaz., 97:433-76.

1937

Effect of variations in temperature on nuclear and cell division in *Tradescantia.* Am. J. Bot., 24:218–25.

Chromosome inversions in *Paeonia suffruticosa.* Cytologia, Fujii Jubilee Volume:108–14.

With Hally Jolivette Sax. Stomata size and distribution in diploid and polyploid plants. J. Arnold Arbor., 18:164–72.

Chromosome behavior and nuclear development in *Tradescantia.* Genetics, 22:523–33.

Review of *Recent Advances in Cytology,* by C. D. Darlington. J. Hered., 28:217–19.

1938

The relation between stomata counts and chromosome number. J. Arnold Arbor., 19:437–41.

Chromosome aberrations induced by X-rays. Genetics, 23:494–516.

1939

The time factor in X-ray production of chromosome aberrations. Proc. Natl. Acad. Sci. USA, 25:225–33.

With K. Mather. An X-ray analysis of progressive chromosome splitting. J. Genet., 37:483–90.

With E. V. Enzmann. The effect of temperature on X-ray induced chromosome aberrations. Proc. Natl. Acad. Sci. USA, 25:397–405.

1940

An analysis of X-ray induced chromosomal aberrations in *Tradescantia.* Genetics, 25:41–68.

The effect of radiation on chromosome structure. Am. Philos. Soc. Yearb., 1940:240, 241.

1941

With J. G. O'Mara. Mechanism of mitosis in pollen tubes. Bot. Gaz., 102:629–36.

With C. P. Swanson. Differential sensitivity of cells to X-rays. Am. J. Bot., 28:52–59.

The behavior of X-ray induced chromosomal aberrations in *Allium* root tip cells. Genetics, 26:418–25.
Types and frequencies of chromosomal aberrations induced by X-rays. Cold Spring Harbor Symp. Quant. Biol., 9:93–101.

1942

The distribution of X-ray induced chromosomal aberrations. Proc. Natl. Acad. Sci. USA, 28:229–33.
The mechanisms of X-ray effects on cells. J. Gen. Physiol., 25:533–37.
Diffusion of gene products. Proc. Natl. Acad. Sci. USA, 28:303–6.

1943

The effect of centrifuging upon the production of X-ray induced chromosomal aberrations. Proc. Natl. Acad. Sci. USA, 29:18–21.
With Robert T. Brumfield. The relation between X-ray dosage and the frequency of chromosomal aberrations. Am. J. Bot., 30:564–70.

1944

Population problems of a new world order. Sci. Mon., 58:66–71.
Soviet biology. Science, 99:298–99.

1945

The demographic dilemma. Science, 101:325–26.
Lilac species hybrids. J. Arnold Arbor., 26:79–84.
Population problems. In: *The Science of Man in the World Crisis,* ed. Ralph Linton, pp. 258–81. New York: Columbia University Press.

1947

How new plants are made. Horticulture, 25(n.s.):127, 128.
Mechanism of heredity. Am. Fruit Grow., 67:16, 28, 29.
Plant breeding at the Arnold Arboretum. Arnoldia, 7:9–12.
Temperature effects on X-ray induced chromosome aberrations. Genetics, 32:75–78.
Soviet science and political philosophy. Sci. Mon., 65:43–47.

The Arnold Arboretum during the fiscal year ended June 30, 1947. J. Arnold Arbor., 28:447–52.

The Arnold Arboretum of Harvard University. Arnold Arbor. Bull., 10(3):9, 10, 24.

The Bussey Institution. Arnoldia, 7:13–16.

With Hally Jolivette Sax. The cytogenetics of generic hybrids of *Sorbus*. J. Arnold Arbor., 28:137–40.

1948

The Arnold Arboretum during the fiscal year ended June 30, 1948. J. Arnold Arbor., 29:422–28.

1949

The Arnold Arboretum during the fiscal year ended June 30, 1949. J. Arnold Arbor., 30:450–55.

John George Jack, 1861–1949. J. Arnold Arbor., 30:345–47.

The use of *Malus* species for apple rootstocks. Proc. Am. Soc. Hortic. Sci., 53:219–20.

1950

Rootstocks for lilacs. Arnoldia, 10:57–60.

The cytological effects of low intensity radiation. Science, 112:332–33.

Dwarf trees. Arnoldia, 10:73–79.

Oakes Ames, 1874–1950. J. Arnold Arbor., 31:335–49.

The effect of X-rays on chromosome structure. J. Cell Comp. Physiol., 35 (suppl. 1):71–81.

The Arnold Arboretum during the fiscal year ended June 30, 1950. J. Arnold Arbor., 31:430–34.

The effect of the rootstock on the growth of seedling trees & shrubs. Proc. Am. Soc. Hortic. Sci., 56:166–68.

Population and agriculture. In: *Twentieth Century Economic Thought,* ed. Glen Hoover, pp. 647–68. New York: Philosophical Library.

1951

Biological resources as a factor in international understanding. Sci. Mon., 72:300–305.

Can the earth feed its millions? UN World, 5:22–25.

Photosynthetic energy via agriculture. Proc. Am. Acad. Arts Sci., 79:205–11.
The Arnold Arboretum during the fiscal year ended June 30, 1951. J. Arnold Arbor., 32:412–16.
Food resources and population growth. Bull. At. Sci., 7:105–7.
Population problems in world development. In: *Social Progress Through Technology: The Human Conditions of Economic Growth,* pp. 4–6. (A week-end conference in four panels.) MIT Foreign Student Summer Project. Cambridge, Mass.: MIT Press.

1952

With Henry Luippold. The effect of fractional X-ray dosage on the frequency of chromosome aberrations. Heredity, 6:127–31.
With E. D. King and H. A. Schneiderman. The effects of CO and O on the frequency of X-ray induced chromosome aberrations in *Tradescantia.* Proc. Natl. Acad. Sci. USA, 38:34–43.
The Arnold Arboretum during the fiscal year ended June 30, 1952. J. Arnold Arbor., 33:403–9.

1953

Interstock effects in dwarfing fruit trees. Proc. Am. Soc. Hortic. Sci., 62:201–4.
Enough for all? (Review of *The Road to Abundance,* by J. Rosin and M. Eastman.) J. Hered., 44:203, 204.
The Arnold Arboretum during the fiscal year ended June 30, 1953. J. Arnold Arbor., 34:412–16.
Review: Symposium on chromosome breakage. Science, 118:658, 659.
With H. Kihara. Genetics in the U.S.S.R. J. Hered., 49(4):132, 158.

1954

The control of tree growth by phloem blocks. J. Arnold Arbor., 35:251–58.
Here's an easy way to dwarf trees. Better Fruit, 49:9, 10.
Population problems of Central America. Ceiba, 4:153–64.
Stock and scion relationship in graft incompatibility. Proc. Am. Soc. Hortic. Sci., 64:156–58.

1955

With E. D. King. An X-ray analysis of chromosome duplication. Proc. Natl. Acad. Sci. USA, 41:150–55.

The effect of ionizing radiation on plant growth. Am. J. Bot., 42:360–64.

With E. D. King and H. Luippold. The effect of fractionated X-ray dosage on the frequency of chromatid and chromosome aberrations. Radiat. Res., 2:171–79.

Evaluation of the recombination theory. J. Cell. Comp. Physiol., 45(suppl. 2):243–47.

Plant breeding at the Arnold Arboretum. Arnoldia, 15:5–12.

With A. G. Johnson. Induction of early flowering of ornamental apple trees. J. Arnold Arbor., 36:110–14.

Dwarf trees with bark inversion. Am. Fruit Grow., 75(3):38, 39.

Standing Room Only: The Challenge of Overpopulation. Boston: Beacon Press.

Pflanzenzuchtung im Arnold Arboretum. Dtsch. Baumsch., 7:177–83.

1956

What's new in plant propagation? Natl. Hortic. Mag., 35:116–18.

With Alan Q. Dickson. Phloem polarity in bark regeneration. J. Arnold Arbor., 37:173–79.

Paste the poison ivy. Arnoldia, 16:5–8.

The story behind dwarf fruits. Horticulture, 34(n.s.):203, 233.

The population explosion, pp. 3–61. Headline Series, Foreign Policy Association no. 120.

Review of *Chromosome Botany,* by C. D. Darlington. Science, 124:688.

1957

The control of vegetative growth and the induction of early fruiting of apple trees. Proc. Am. Soc. Hortic. Sci., 69:68–74.

The effect of ionizing radiation on chromosomes. Q. Rev. Biol., 32:15–26.

Dwarf ornamental and fruit trees. Proc. Plant Propagators Soc., 7:146–55.

1958

The juvenile characters of trees and shrubs. Arnoldia, 18:1–6.

The genetic future of man. In: *The Population Ahead,* ed. Roy G. Francis, pp.87–97. Minneapolis: University of Minnesota Press.

Experimental control of tree growth and reproduction. In: *The Physiology of Forest Trees,* ed. K. Thimann, pp. 601–10. New York: Ronald Press.

Forsythia "Beatrix Ferrand." Natl. Hortic. Mag., 37:112, 113.

Breeding ornamental trees and shrubs. Proc. Plant Propagators Soc., 8:120–26.

1959

The cytogenetics of facultative apomixis in *Malus* species. J. Arnold Arbor., 40:289–97.

1960

Meiosis in interspecific pine hybrids. For. Sci., 6:135–38.

Standing Room Only: The World's Exploding Population, rev. ed. (paper). Boston: Beacon Press.

1961

With Hally Jolivette Sax. The effect of age of seed on the frequency of spontaneous and gamma ray induced chromosome aberrations. Radiat. Bot., 1:80–83.

Radiation sensitivity of *Tradescantia* microspore chromosomes to a second exposure of X-rays. Radiat. Res., 14:667–73.

1962

With Hally Jolivette Sax. The effect of X-rays on the aging of seeds. Nature, 194:459, 460.

Aspects of aging in plants. Annu. Rev. Plant Physiol., 13:489–506.

1963

The stimulation of plant growth by ionizing radiation. Radiat. Bot., 3:179–86.

With Lloyd A. Schairer. The effect of chronic gamma irradiation on apical dominance of trees. Radiat. Bot., 3:283–85.

With Hally Jolivette Sax. The effect of chronological and physiological aging of onion seeds on the frequency of spontaneous

and X-ray induced chromosome aberrations. Radiat. Bot., 4:37–41.

1964

The world's exploding population. Perspect. Biol. Med., 7:321–30.
Population problems. Topic, 8:5–19.

1965

With H. J. Teas and Hally Jolivette Sax. Cycasin: Radiomimetic effects. Science, 149:541, 542.

1966

Biological problems of the age of science. Wash. State Rev., 10:5–9.
The Bussey Institution: Harvard University's Graduate School of Applied Biology. J. Hered., 57:175–78.
With Hally Jolivette Sax. Radiomimetic beverages, drugs and mutagens. Proc. Natl. Acad. Sci. USA, 55:1431–35.
Radiomimetic effects of beverages, drugs and insecticides. Cranbrook Inst. Sci. Newsl., 36:46–49.
The world population explosion. Medicine Today, 1:8–14.

1968

With Hally Jolivette Sax. Possible mutagenic hazards of some food additives, beverages and insecticides. Jpn. J. Genet., 43:89–94.
With Hally Jolivette Sax and Wayne Binns. Radiomimetic effects of veratrum. Toxicon, 6:69–70.

1969

Ethical aspects of the population crisis. BioScience, 19:303.

1970

With Hally Jolivette Sax and W. B. Itturian. Effects of sonic energy on chromosomes. Environ. Mut. Soc. Newsl., 5:24, 25.