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9 Mendel in America: Theory and Practice, 1900-1919

In September 1903, Williel Hays addressed the first meeting of the American Breeders Association (ABA). A founding member and guiding spirit of the association, Hays was then professor of agriculture at the University of Minnesota and director of the state experiment station; two years later he would be appointed Assistant Secretary of Agriculture. In his opening remarks, he lamented:

Science has been content to remain at the task of proving for the ten thousandth time that Darwin's main contention is true but has allowed the great economic problems of evolution guided by man to remain almost a virgin field. Only recently have such men as Galton, Mendel, de Vries, Bateson and a few others, entered upon comprehensive lines of research and many of these have hardly grasped the vast economic interests which are at stake, nor have they seen the open doors of opportunity which might be entered by cooperation with the men who control the breeding herds and the plant-breeding nurseries.'

Hays's opinions were widely shared. Excited by developments in what would soon be called "genetics," most ABA members agreed with William Bateson that: "At this time we need no more *general* ideas about evolution. We need *particular* knowledge of the evolution of *particular* forms." Francis Galton's law of ancestral heredity, Gregor Mendel's laws of dominance, segregation and independent assortment, and Hugo de Vries' mutation theory were all greeted enthusiastically. Because the ABA had a varied membership, there was more than one source of interest in the new discoveries. The chief factor, however, was a belief that these laws could readily be used to improve artificial selection. Some association members were particularly concerned

with selection in humans. A greater emphasis on eugenics was promoted by Charles Davenport, who argued that "society must protect itself; as it claims the right to deprive the murderer of his life so also it may annihilate the hideous serpent of hopelessly vicious protoplasm."¹¹ The majority, however, were less concerned to improve humans than grapes, hogs, beans, or, especially, corn. Their primary concern, in Deborah Fitzgerald's phrase, was with "the business of breeding."¹²

Who were these early enthusiasts for Mendel? Why did they accord his work such a warm reception? How did their response compare with that of biologists whose interests were principally descriptive or theoretical, rather than applied? And how did their concerns with agricultural practice inform their program of research?

We find that particular economic pressures and practical demands on agricultural breeders, within the context of late nineteenth-century agricultural reform, encouraged actively interventionist, experimental techniques. These included hybridization and the crossbreeding of varieties.¹³ In particular, a perceived crisis of wheat overproduction in the 1870s prompted the United States Department of Agriculture (USDA) to elaborate a policy of diversifying agricultural products. USDA officials saw creation of novelty as crucial to this program. More specifically, they aimed to increase variation and produce stable hybrids. In the 1880s and 1890s, the department expanded its own experimental breeding work along these lines and, significantly, promoted such work at state agricultural colleges and experiment stations.

Focusing on experimental creation of variation and the inheritance of particular characters, the work of scientists at agricultural institutions converged with that of an international group of botanists and hybridists interested in evolutionary problems (including de Vries and Bateson). After 1900, these contacts provided American agriculturalists with ready access to Mendel's work, while their technical and intellectual background prepared them to receive it enthusiastically. The strength of breeding and genetics programs at agricultural colleges and experiment stations in the decades that followed insured the pursuit of genetics at publicly supported institutions characterized by simultaneous commitments to the ideal of basic research and the practical demands of economic agriculture. The early work on hybrid corn, presented here as a case study, illustrates the importance of this context for the direction of genetics research.

Who Were the "Breeders"?

From 30 August to 2 September 1902, the International Conference on Plant Breeding and Hybridization met in New York City. Reviewing the conference for *Torrey*, Walter Cannon noted that, "generally speaking, the plant breed-

ers had not taken advantage of the Mendelian theory in their work, and some of them did not know of Mendel or of his experiments before the Conference."¹⁴ But they left it as converts to the new genetics. C. W. Ward, a carnation grower, was one of the commercial breeders in attendance. His remarks attest both to the degree and source of the excitement with which such breeders greeted Mendel's work: "I have known nothing of Mendel's theory or law until the day before yesterday," he said, "but what I have heard here regarding Mendel has awakened an increasing interest in the work of hybridizing and I shall secure his books and read them with the greatest interest, for if there is a fixed rule by which I can produce six inch carnations on four foot stems I certainly wish to learn that rule."¹⁵

One of the foreign visitors, speaking on "Practical Aspects of the New Discoveries in Heredity," was William Bateson.¹⁶ Following the talk, Liberty Hyde Bailey of the state agricultural college at Cornell recommended Bateson's just-published book, *Mendel's Principles of Heredity: A Defence*. "If you wish to follow this [the Mendelian hypothesis] with the greatest degree of accuracy, you should get Mr. Bateson's recent book," he urged, adding that: "I expect to use this book as a basis for all our work in plant breeding."¹⁷ His advice was apparently heeded. On 3 October, Bateson wrote excitedly to his wife: "At the train yesterday, many of the party arrived with their 'Mendel's Principles' in their hands! It has been 'Mendel, Mendel all the way,' and I think a boom is beginning at last. There is talk of an International Assn. of Breeders of Plants and Animals and I am glad to be right in the swim."¹⁸

Commenting on this letter, Garland Allen suggests that: "It may perhaps seem curious that plant and animal breeders, with their primary concern for practical results, would have taken more readily as a group to Mendel's theoretical presentation than many of the more academic biologists."¹⁹ He is certainly right to note that Mendelism made sense of breeders' results—both their successes and failures—and was thus greeted as a means to improve the efficiency of breeding practice.²⁰ The distinction between breeders and academic biologists is, however, somewhat misleading if the former are equated with farmers or "seedsmen."²¹ To be sure, some "practical breeders" such as L. H. Kerrick and Eugene Funk were founding members of the ABA. This group also played an important role in garnering political support for the work of agriculturalists at state institutions, which was crucial to the establishment of genetics as an academic discipline.²² But the enthusiasts referred to by Bateson were mostly scientists, not seedsmen. Of course they were scientists of a particular kind, both institutionally and in respect to their aims. Employed at agricultural colleges and agricultural experiment stations, rather than at arts and sciences institutions, they were concerned with the implications of Mendelism for practice as well as theory.

The dominant force at the 1902 New York Conference was Bateson; his

lead paper combined a straightforward account of Mendel's laws with a discussion of their applied, and especially commercial, importance. To the breeders he argued:

Now when we come to the question of the significance of these things to the breeder and to the hybridist, it will be found that the significance is exceedingly great. I am afraid of saying that we have reached a point when the practical man who is doing these things with a definite, economic object or commercial object in view can take the facts and use them for his definite advantage. But we do for the first time get a clear sight of some of the fundamentals on which he will in future work, and it cannot be now very many years, if the investigations go on at the present rate, before the breeder will be in a position not so very different from that in which the chemist is:—when he will be able to do what he wants to do, instead of merely what happens to turn up.¹⁶

The following two papers, by C. C. Hurst (Bateson's close friend and colleague) and Hugo de Vries, focused on Mendel as well.¹⁷ In all, ten participants either presented papers or made extended remarks promoting Mendelism. Seven were Americans: Willet Hays of the Minnesota Agricultural Experiment Station, Liberty Hyde Bailey of Cornell, S. A. Beach of the New York State Experiment Station, Walter Austin Cannon of Columbia and the New York Botanical Garden, and O. F. Cook and W. J. Spillman, both of the USDA. If members of this group are to be characterized as "breeders," it follows that many breeders active in promoting Mendelism were academic biologists. Of course, they were academic biologists of a particular kind, both institutionally and in respect to their goals. These biologists were generally affiliated with the USDA or state agricultural colleges and experiment stations and they aimed to combine practical public interests with theoretical science.

Our paper details the crucial, yet historically neglected, role of this group in introducing and popularizing Mendel's work. But we should note that biologists with a primarily theoretical orientation were also generally receptive to Mendelism (in sharp contrast with naturalists, who were decidedly cool).¹⁸ T. H. Morgan was a severe critic, but his views on Mendel were atypical. While some biologists who employed the method of experimental breeding (either to improve selection or to answer questions regarding the physical basis of heredity or its relation to evolution) were indifferent to the new genetics, few were actively hostile. Indeed, most were enthusiastic, irrespective of whether they were employed at state agricultural institutions or elite colleges and laboratories. Walter Sutton, Nettie Stevens, E. B. Wilson, E. M. East, William E. Castle, Charles Davenport, and George H. Shull, for example, were all avid Mendelians, whose principal concerns were theoretical. The last four also belonged to the ABA.

If Allen asserts too sharp a separation between breeders and academic biologists, Jan Sapp rejects the distinction altogether. In his view, "breeder" is practically synonymous with "geneticist" until at least 1915, because in the early years "Mendelian investigators recognized no distinction between pure science and applied science."¹⁹ But although many academic biologists, particularly those employed at state agricultural institutions, pursued both pure and applied research, they certainly recognized "pure" and "applied" as categories; indeed, the proper balance between them was a matter of intense concern. Moreover, as we have seen, there were breeders whose interests were purely applied and geneticists whose interests were largely (in a few cases, entirely) theoretical. Eugene Funk was not a "geneticist," nor George Shull a "breeder." The relationship between practical breeders and geneticists was addressed by Hays in his opening speech at the first meeting of the ABA:

The producers of new values through breeding are brought together as an appreciative constituency of their servants, the scientists. They are ready to aid in securing all needed means for scientific research in problems relating to heredity, provided the scientists can develop methods of research which will aid the breeders in more rapidly improving the plants and animals. The scientists, on the other hand, are ready to emerge from the cloister of species and genus grinding in the study of historic evolution, and cooperate with practical breeders in the study of breed and variety formation and improvement. . . . No less of an incentive, at least to the scientists, is the possible solution of some of the intricate problems of development in plants, in the lower animals, and in man.²⁰

What united virtually all ABA members—whether commercial seedsmen, editors of farm journals, USDA officials, or researchers at state agricultural colleges or elite arts and sciences institutions—was their enthusiasm for the technique of experimental breeding. Some hoped to answer theoretical questions, others to improve agricultural practice; many aimed to do both. But however disparate their motivations, those who used experimental methods generally expressed a keen interest in Mendel's work.

The USDA and the Reception of Mendelism

No organization played a more important role in the dissemination of Mendelism than the USDA. At the 1902 New York Conference, eleven of the seventy-five participants were employed directly by the USDA; many more were affiliated with state agricultural colleges and experiment stations. At the first two meetings of the ABA (1903 and 1905), seventeen of forty-five papers were presented by USDA officials; these included the majority of

papers dealing primarily with Mendelism, such as Spillman's "Mendel's Law in Relation to Animal Breeding" and Webber's "Explanation of Mendel's Law of Hybrids."²¹

As early as 1901, the USDA's *Experiment Station Record*, which functioned as an information clearinghouse for the experiment stations, published a detailed synopsis of Mendel's work based on Bateson's communication to the Royal Horticultural Society, "G. Mendel, Experiments in Plant Hybridization."²² The *Record* summarized Mendel's concepts of dominance and independent assortment of different pairs of characters, and discussed the significance of his statistical ratios. It also quoted Bateson's claim that Mendel's laws were "worthy to rank with those that laid the foundation of the atomic laws of chemistry."²³

An abstract of Tschermak's article on the inheritance of characters when crossing peas and beans immediately followed this report. According to the *Record*, Tschermak's work tested Mendel's predictions and, while losing something of the generality of his results, nevertheless underscored its "importance for theoretical and plant breeding purposes."²⁴ A few issues later, the *Record* provided a synopsis of Bateson's earlier communication to the Royal Horticultural Society on "Problems of heredity as a subject for horticultural investigation," which was "largely a review of the work of Mendel and de Vries."²⁵

By choosing to abstract this work in detail, and through its editorial remarks, the *Experiment Station Record* conveyed to its readers a profound appreciation of the scientific value of Mendelism and its implications for horticultural investigation. In the years immediately following, the *Record* reported both American and European work, noting obvious limitations as well as evidence of its potential applicability to practical problems.²⁶ Thus, news of Mendel's work and the experiments and controversies it prompted was available to experiment-station personnel in every state.

The USDA also helped popularize Mendelism through its Graduate School of Agriculture, inaugurated in July 1902 (only two months before the New York Conference). Seventy-five students attended, of whom twenty-seven were faculty at agricultural colleges and thirty-one assistants in the agricultural colleges and experiment stations. According to Liberty Hyde Bailey: "Perhaps the two agencies most responsible for the dissemination of the Mendelian ideas in America were the instruction given by Webber and others in the Graduate School of Agriculture at Columbus last summer, and the prolonged discussion before the International Conference on Plant-Breeding at New York last September."²⁷

The USDA was founded in 1862, the same year as passage of the Morrill Land-Grant Act, which established most of the country's agricultural colleges. In the 1870s and 1880s, the federal government began to increase markedly its commitment to agricultural research. As Margaret Rossiter has noted,

the degree of federal support is striking, given the depressed condition of contemporary agricultural science: there had been no intellectual successes since the development of agricultural chemistry in the 1840s and 1850s and low enrollments in agricultural subjects persisted at state colleges.²⁸ Nevertheless, the Hatch Act, funding the experiment stations, was passed in 1887 and the Morrill Act, primarily for establishing black colleges of agriculture, in 1890. During the same period, appropriations for the USDA itself increased dramatically, as did the number of its employees.

These agricultural appropriation acts, reflecting greater federal intervention in agriculture, were contemporaneous with others that signaled an end to the laissez-faire ideology characteristic of nineteenth-century America. Both the Interstate Commerce Act and Hatch Act were passed in the same year; so were the Sherman Anti-Trust Act and the second Morrill law. As the United States entered international commerce following the Civil War, both industrial and agricultural production were thought too important to be left to chance. The government, with the aid of various interest groups, was now prepared to intervene in the interest of the national economy.²⁹

In response to the social and economic crises that marked this period, federal administrators and researchers advanced the cause of science-based agriculture. They held that agricultural problems could be addressed most effectively through the application of work in the natural and social sciences, pursued by experts at centralized institutions and disseminated to farmers. Their program was a response, and potential antidote, to the campaign for structural changes advocated by populists. It also helped decide a long-standing debate among agricultural educators in favor of those who believed that state colleges and research institutions should pursue basic research (not just vocational training). The expansion of science-based agricultural curricula, the federal funding of state experiment stations, and the development of extension services were thus elements in a linked program of scientific, social, and professional reform. In this context, manipulative experimental techniques such as hybridization and crossbreeding served a dual role. They helped define agricultural expertise in terms of schooled scientific skill rather than day-to-day practice; and they promoted active intervention to achieve practical goals.

These techniques were central to the USDA's response to a crisis resulting from the overproduction of wheat, with the consequent glutting of world markets and decline in the value of wheat and wheatstuffs. The great expansion of productivity in American agriculture that created this surplus preceded by more than a decade the official promotion of hybridization by the USDA. The purpose of intensive and specialized hybridization work was therefore not a generalized increase in productivity, which had been achieved by other means. It was part of the refinement of the system—a means to cope with a specific crisis of agricultural production.

The massive increase in U.S. production of wheat in the 1870s, according to USDA statistician J. R. Dodge, was attributable to three factors: the ready availability of fresh agricultural land; the penetration of the railroads into areas previously inaccessible to markets; and, most important, an extraordinarily inflated demand resulting from several years of European crop failures.²⁰ The problem, apparent by 1880, had intensified by the middle of the decade. With the wheat crop of 1884 five times the size of the 1830 crop, and with prices falling in the world market as European production recovered, the problem of American overproduction began to concern USDA officials.²¹

In 1885, Dodge suggested a solution ultimately adopted by the department. He directly linked the overproduction of wheat to the underproduction of other valuable commodities that the nation now imported.²² The solution required that farmers decrease the acreage devoted to wheat production and extend cultivation of other crops.²³

With this goal, the USDA developed a three-part corrective program aimed at diversification of the nation's agricultural products: decreasing the acreage of wheat in the production; decreasing U.S. reliance on particular import items; and increasing exports of specialty items of high quality, for which there was strong market demand.²⁴ Generally, this solution involved an intensification of economic and scientific research, centrally directed by the USDA, and expert analysis of the general problems of national agricultural production. In 1887, Commissioner of Agriculture Norman J. Colman explicitly linked efforts to diversify with the search for new products:

It is an important question, in view of the rapid increase of available rural labor, tending to overproduction of the fruits of the soil and the cheapening of their value, what can be done to give greater variety to the products of agriculture? What can this Department do towards the introduction of new plants and development of new rural industries?²⁵

In his statistician's report for 1889, Dodge stressed that solving the problem of overproduction "required the fullest and promptest information concerning new fruits, fibers, or products of economic plants."²⁶ Rather than depressing production, it should be encouraged in new directions, particularly toward the cultivation of products hitherto imported.²⁷ Throughout the 1890s, the secretaries of agriculture echoed these sentiments; the American farmers should pursue a favorable balance of trade through the "substitution in our own markets of home-grown for foreign-grown products."²⁸

As diversification, quality improvement, and increased self-sufficiency became central to the USDA's response, various branches of economic botany assumed greater importance within the department. Seed introduction, plant exploration, botany, and horticulture gained in status and acquired new institutional structures. Botanical specialties such as plant pathology, pomology, and

agrostology achieved independent divisional status for the first time.²⁹ Scientists working in these divisions found hybridization and cross-fertilization valuable for both theoretical and practical purposes.

In 1885, William M. King, chief of the Seed Division, drew an explicit connection between crop improvement, hybridization, and reformist conceptions of social and scientific progress. In pursuit of the division's purpose, to "promote the interests of all classes, in whatever industrial pursuits . . . by an increased improvement in both quantity and quality of agricultural products," it should strengthen ties with foreign governments that would promote the exchange of plants and seeds.³⁰ King also had specific ideas concerning the fate of these imports: Hybridization was the chief means to seed improvement, according to King, and he provided a two-page summary of hybridization techniques, citing no less an authority than Charles Darwin in support of the contention that cross-fertilization was generally beneficial and self-fertilization injurious.³¹ His discussion placed in the fore the improvement of wheat and creation of new varieties, not surprising given the specter of overproduction and the importance of grain for the export market. King reproduced a letter from A. E. Blount, of the State Agricultural College of Colorado, whose hybridization work in wheat involved "over 300 varieties of seed obtained from almost every wheat-producing country in the world."³²

In 1886, the report of H. E. Van Deman of the new Division of Pomology directly addressed a crucial aspect of the department's diversification program—namely, the production of fruits for export. The apple and citrus fruits were seen as particularly significant; Van Deman's staff was seeking unusual varieties, both domestic and foreign, of these and other fruits.³³ The following year, as the acquisition of plants and seeds from foreign countries continued, the pomologist emphasized the importance of the "science of breeding" in the creation of artificial hybrids of economic importance.³⁴

Hybridization was thought to apply to "all cultivated plants," thus cutting across boundaries traditional in agricultural and horticultural research.³⁵ This aspect of hybridization was of immense practical and institutional significance. Numerous specialty divisions of the USDA (as well as other agricultural research organizations) could offer support. Furthermore, its universality implied that the technique was based on fundamental natural laws. Hybridization thus validated agriculture as a biological science, a feature of special importance to agricultural scientists working in an academic context. Experiment station researchers and academic reformers ultimately capitalized on both the technical and institutional implications of hybridization in their promotion of experimental breeding techniques.

Within the USDA, the laboratories of the Division of Vegetable Pathology became the locus of hybridization and breeding investigations. Division chief Beverly T. Galloway insisted on the crucial relationship between vegetable pathology and vegetable physiology, pointing to the "urgent necessity of a

thorough study of the normal physiology of a plant, as a groundwork for pathological investigations."⁴⁰ Scientific practice within this conception of the study of plant diseases required "the aid of many branches of science."⁴¹ plant breeding among them. Indeed, Galloway argued that the problems of plant breeding were inseparable from work in plant pathology and physiology, because the conditions of development dictated by the inheritance of the organism were as crucial to a successful crop as were the conditions of the environment in which the crop was grown. The goal was to uncover principles that "will enable the grower to not only modify his conditions to suit the plants, but to modify the plants to suit the conditions."⁴²

By the close of the century, studies of inheritance in plants and experimental improvement through breeding and selection were secure elements in the research of the division, which had been appropriately renamed the Division of Vegetable Physiology and Pathology. Division researchers had undertaken crossbreeding with grapes, oranges, pineapples, pears, and wheat and were soon to work with cotton, in all cases seeking to combine excellent quality of the fruit or grain with hardiness in the face of climatic severities or with resistance to specific plant diseases. Discussing the work of the division in 1898, A. F. Woods reported more than 20,000 crosses of raisin grapes, 116 crosses of pear varieties, the production and propagation of hundreds of hybrid pineapples, oranges, and other citrus fruits, and the breeding of wheat for disease resistance and yield.⁴³ Several important plant breeders began their professional careers within this division, including Herbert J. Webber, who would be an important advocate of Mendelism within agricultural institutions.⁴⁴

During the 1880s and 1890s, then, efforts of USDA administrators and scientists to generate new products promoted hybridization and varietal crossing. The cultivation of specialty items to replace some imports and provide new products for export was central to their program of economic reform. Moreover, the use of hybridization, presented as a technique demanding specialized skills, also played an important role in scientific reform, which penetrated not only the USDA but the nation's agricultural colleges and experiment stations.

Research and Reform: The Place of Hybridization

By the 1880s, USDA officials had developed a strong research orientation. The scientific work conducted under their auspices was accompanied by a marked appreciation for the power of science.⁴⁵ At the same time, with passage of the Hatch Act ensuring that agricultural experimentation would receive significant public support, USDA administrators were determined to exert more control over the state experiment stations.⁴⁶ The scientific research

ethos permeating the department inevitably played a role in management of the stations, as shown by the annual reports filed by the secretary of agriculture. Each year the secretary complained that farmers and state legislators who demanded practical help misunderstood the purpose of the experiment stations, whose mission was original investigation. James Wilson's report for 1898 is typical. After noting that experiment stations were not the only means for educating the farmer (who could make use of agricultural colleges, farmers' institutes, and boards of agriculture), he argued:

It is the business of the experiment station, on the other hand, to advance knowledge of the facts and principles underlying successful agriculture and to teach the farmer new truths made known by their investigations. The act of Congress creating the Stations clearly defines their functions to be the making and publishing of original investigations. Whenever a station has neglected this and merely endeavored to educate the farmer, we find a weak station, and whenever a station has earnestly devoted itself to original investigations, we find a strong station.⁴⁷

The Office of Experiment Stations (OES) was created by the commissioner of agriculture, under the authority of the Hatch Act, to oversee the work of the stations and provide a central clearinghouse for station research.⁴⁸ Its commitment to station research increased under Alfred C. True, who became director in 1893.⁴⁹ At the same time, a number of botanists and horticulturalists at the agricultural colleges and stations, some with training or research experience at elite American and European institutions, were happy to comply. In fact, they had pioneered experimental work at their home institutions and introduced it in their teaching.⁵⁰ Plant breeding, already recognized as an important experimental technique with agricultural applications, assumed its place in the armamentarium of reform. Scientific reformers like True, endeavoring to achieve their goals while maintaining a commitment to practical applications, promoted breeding work as part of the movement to transform the agricultural experiment stations into scientifically oriented research centers.

The leadership of the OES at this time was important because, despite the enthusiasm of like-minded investigators at some institutions, horticultural work at most stations consisted chiefly of variety testing, some plant pathology, and experimentation with culture methods.⁵¹ The horticultural work of many stations was weakly developed, and in 1889 four stations specified that no varietal improvement would be attempted in vegetable crops.⁵² But the same economic forces that prompted development of the USDA's diversification and crop improvement program operated in the states with even greater immediacy, and in the years following passage of the Hatch Act, many stations adopted programs of variety improvement, to proceed chiefly by selection techniques. By 1889, twenty-three stations reported active or planned

programs of variety improvement, and eight specified that hybridization would be part of these efforts.⁵⁰

True and his staff were not content merely to document a growing interest in hybridization. In 1890, the OES published results of a questionnaire that it had presented to the stations, probing the nature and extent of botanical work by station researchers. Most questions pertained exclusively to applied research. Two questions, however, specified research areas with no explicit mention of practical applications. One concerned plant physiology. The other asked pointedly: "Are you experimenting in cross-fertilization and hybridization in the hope of obtaining better knowledge of the laws that underlie these processes?"⁵¹

The research areas singled out were unambiguously stamped with OES approval, and the questionnaire therefore served a propagandistic, as well as informational, purpose. The responses from station botanists reveal that they were prepared to be encouraged. Of thirty-eight stations responding, twenty indicated that they were already engaged in cross-fertilization and hybridization work. Seven of the twenty specified that their work in this area was limited, but six indicated that crossbreeding work was expected to be a major aspect, in some cases a specialty, of their research. Three others that had not yet begun such work reported plans to initiate it in the near future.⁵²

As important as the actual extent of hybridization work is the evidence of growing interest in the subject among station researchers. Since the 1888 station reports to the OES, the number of institutions undertaking crop improvement through hybridization as well as selection had increased from seven to twenty. The particular economic pressures within the various states ensured the application of the technique to virtually all horticultural and field crops. At the Florida station, investigators hybridized peaches and oranges; at Arkansas, strawberries; at Michigan, wheat; at Massachusetts and Indiana, fruit trees; and at Iowa, corn. Other stations quickly followed suit.⁵³

Significantly, this late nineteenth-century work in hybridization and crossbreeding was undertaken by personnel at publicly supported research and teaching institutions, unlike such work earlier in the century, which was pursued chiefly by private individuals or commercial concerns. The public institutions, numerous and geographically dispersed, were charged with education and technical training; researchers, and more importantly students, gained experience in growing, propagating, manipulating, and hybridizing plant materials—skills crucial for research in plant inheritance. The public institutions thus provided a new context for hybridization studies, a formally structured academic context, where workers undertook research beneath a standard proclaiming commitment to science as the basis for practical advancement. Although improved varieties of agricultural crops were undoubtedly the ultimate goal of the USDA or station-sponsored work, the wording of the OES's 1890 questionnaire explicitly presented the aim of such work as

"better knowledge of the laws that underlie these processes." At the stations, as at the USDA, the significance and institutional success of crossbreeding lay in its dual implications for practical applications and scientific theory. The technique was particularly appropriate for the agricultural institutions, struggling to combine their economic and social service role with allegiance to the values of academic science.

The rediscovery of Mendel's work in 1900 thus occurred at a time when hybridization was of unprecedented importance in American agricultural research. The scientific reform of agricultural research and education ensured that many breeders would be college professors or college-trained researchers. For these men, breeding work had a scientific goal, the investigation of universal laws of inheritance, as well as a practical one. Station investigators were thus sensitive to problems uniting intellectual and commercial concerns—and hence particularly concerned with the nature of variation—before 1900. Station botanists sought to understand the relationship between certain types of crosses and the appearance of sterility in offspring, a result obviously to be avoided in efforts to produce self-sustaining lines of improved varieties. Several researchers studied the influence of crossbreeding and hybridization on the expression of heritable characteristics in search of regularities in their transmission.⁵⁴ Workers with corn at the Illinois station considered commercial features such as size of the ear as well as patterns in the inheritance of kernel color, and then examined the greater or lesser stability (or constancy) of hybrid effects in subsequent generations.⁵⁵ In short, at many of the agricultural experiment stations researchers were engaged in the study of variation—its appearance, alteration, and constancy through several generations.

Mendel, Bateson, and American Agriculturists

In this same period, variation also assumed a central place in biological investigations. Darwinian evolutionary theory, whether accepted or rejected, defined the problems of biological research in the second half of the nineteenth century. Chief among the serious objections to Darwin's theory were perceived inadequacies in his treatment of the origin and transmission of variation. For scientists concerned with evolutionary issues, the production of new varieties through cross-fertilization and hybridization represented a valuable experimental method for investigating these problems. William Bateson published his *Materials for the Study of Variation* in 1894, providing scientists with a handbook of "experimental evolution," and Hugo de Vries's concern for both hybrid constancy and spontaneous appearances of salutory variation.⁵⁶ The conjunction of research interests among students of evolutionary

theory and practical breeders proved crucial for the rapid success of Mendelism in the United States. The 1899 Conference on Hybridization and Crossbreeding, convened in London by the Royal Horticultural Society, brought these groups together. In attendance were British, American, and continental scientists with wide-ranging theoretical, practical, and commercial interests in botanical hybrids.

The participants included William Bateson, Hugo de Vries, and C. C. Hurst. Also present, by invitation, were American agricultural scientists Herbert J. Webber, David Fairchild, and Walter Swingle of the USDA and Willet M. Hays of the Minnesota experiment station. Liberty Hyde Bailey also invited but unable to attend, sent a paper.⁶⁹ The conference proceedings reveal that theoretical investigators, practical agriculturalists, and commercial breeders had common interests in hybridization.

William Bateson was a masterful presence; his conference paper, focused on transmission of discrete characters in hybrid crosses between closely related individuals, emphasized the value of experimental hybridization for evolutionary theory. He also discussed the problem of swamping, raised regularly in critiques of Darwinism.⁶⁹ De Vries explained his most recent breeding experiments, interpreting the creation of apparently stable hybrid crosses as a possibly crucial mechanism of evolution.⁷⁰ Hurst discussed his crossbreeding experiments at length, and elaborated a law of "partial prepotency."⁷¹ When both Bateson and de Vries addressed problems of concern to practical investigators, Hurst was the most thorough and explicit in linking the work of practical breeders and students of evolution. He insisted that the results of crossbreeding experiments seemed to "bear directly upon the problems of inheritance and variation," and pointed to the problem of hybrid constancy as central to breeding practice.⁷² He thus provided a powerful justification for pursuing basic research on hybridity as the basis for further practical achievements.

The Americans spoke and wrote almost exclusively of practical advances in plant breeding in the United States. Thus Webber lauded the successes of the USDA's hybridization work in oranges, pineapples, pears, apples, wheat, corn, and cotton.⁷³ Hays's contribution indicates that, in general, the American focus was on broad characteristics of economic significance, such as vigor, hardness, and size.⁷⁴ But despite some differences in orientation, the American agricultural scientists were obviously excited by the spirit of scientific cooperation, and seemed impressed by the British and European studies. They also made a strong impression on their British audience, some of whom expressed envy of the institutional support available for hybridization work in the United States.⁷⁵

Between the 1899 conference in London and the 1902 conference in New York, Mendel's work had been rediscovered, and Bateson had embarked on a campaign to promote it. Because American agriculturalists were already fa-

miliar with Bateson's views and because the American agricultural research apparatus was attuned to the relevant issues, Bateson's success at the 1902 conference is understandable. The editorialist for the *Experiment Station Record* crowed that "there was an almost universal acceptance of Mendel's law regarding the appearance of dominant and recessive hybrids."⁷⁶ Although not every participant was persuaded either of the generality of Mendel's laws or their practical importance, the enthusiasm was widespread—among seedsmen as well as scientists. We have tried to explain Mendel's appeal to agricultural scientists. But what was his appeal to seedsmen?

Marketing Mendel

The answer is partly that Mendelism offered a plausible explanation for the extreme difficulty in obtaining varieties that would "breed true." Specific results that had long puzzled practical breeders included the "reversions on crossing" discussed by Darwin, the greater variability of new types, and the problem of fixing hybrids. It was doubtless interesting to know why some varieties could apparently not be fixed, despite repeated selection, and why success was so long in coming with others. However, these breeders were also practical, interested in knowledge as a means to power, and power as a means to profit, not as an end in itself. The laws of heredity were sold to breeders as a set of rules for efficient selection, worth "a total of hundreds of millions of dollars' worth of added annual income with but little added expenditure."⁷⁷ The laws of dominance and segregation were unabashedly advertised as a means to make money; Spillman could assert that "If Mendel's law is true, it means to millions of dollars to the breeders of plants in this country."⁷⁸

Among the scientists, only Liberty Hyde Bailey was publicly doubtful. "The wildest prophecies have been made in respect to the application of Mendel's law to the practice of plant breeding," he wrote in 1903.⁷⁹ Bailey's caution reflected his doubt about the generality of Mendel's results. But it also reflected his realization that even if Mendel's laws were both true and universal, they would have no immediate dramatic effect on the practice of plant breeding. Before Mendel, breeders selected, after Mendel, they would do the same. They might be moved to keep better records, select individuals, and select from a larger number of plants. The main difference, however, was that they could now provide plausible explanations for their successes and failures. They would learn that the "rogue characters" they each year hoed out resulted from "the fortuitous union of recessive germs."⁸⁰ But they could not eliminate these rogues except by the methods they always used. Their traditional maxims had been: "Avoid breeding for antagonistic characters." "Breed for one thing at a time." "Know what you want." "Have a definite ideal," and "Keep the variety up to standard."⁸¹ They now knew that these maxims made

sense. But Mendelism did not, could not (indeed, cannot) offer a fixed rule by which to "produce six inch carnations on four foot stems." It could not, at this point, do much for commercial breeders at all. That situation would change dramatically with two linked developments: a Mendelian interpretation of the effects of inbreeding (and crossbreeding) and invention of the double-cross method of breeding—work that made possible the development of hybrid corn.

The Invention of Hybrid Corn

Hybrid corn has been repeatedly characterized as "the greatest success story of genetics."¹⁰ The belief that hybrids are responsible for vast increases in yield has, however, recently been challenged by Jean-Pierre Berlan and Richard Lewontin.¹¹ In their view, the story of hybrid corn illustrates the success of seed companies, not science. Traditionally, farmers harvested their next year's seed from their own plants. But one cannot use seed obtained from hybrids without suffering substantial declines in yield. Thus farmers must buy their seed anew each year. This feature of hybrids—and not any intrinsic superiority in respect to yield, disease resistance, or other important traits—explains seed companies' huge investment in their development. Conventional comparisons of hybrids with open-pollinated varieties are therefore beside the point. Hybrids, of course, do better. They have been intensively improved for the last sixty years. Had mass selection of open-pollinated been pursued with equal zeal, they should now out-perform hybrids.¹² But seed companies have no incentive to improve a product that anyone can reproduce.

However, hybrid corn was initially developed by scientists, not seedsmen. Why should they have cared if breeders were commercially successful? To answer this question, it is necessary to sketch briefly some developments in maize genetics between 1905 and 1919.

Hybrid corn developed out of the work of three geneticists: George H. Shull, then at the Carnegie Station at Cold Spring Harbor, Edward M. East, then at the Connecticut Agricultural Experiment Station, and East's student, Donald F. Jones, also at Connecticut. East and Shull were particularly concerned with the analysis of quantitative characters. All worked with corn, an ideal subject for such study. Naturally open-pollinated, each kernel may be fertilized with pollen from a different plant. In a single ear of corn, therefore, the researcher can obtain a large and highly variable population. Moreover, that variability is reflected in such easily measurable characteristics as the size, shape, number, and color of different kernels. It was also a crop of great, and steadily increasing, economic importance. Between 1866 and 1900 the total corn acreage tripled while production quadrupled; by the turn of the century, twice as much corn was produced as wheat, the second most valuable crop.

Thus theoretical and practical interests combined, in the early years of American genetics, to focus attention on corn. The careers of East and Shull nicely illustrate this point. East began as a chemist at Illinois, working with C. G. Hopkins to develop strains of corn with high oil and low protein, and low oil and high protein content (to improve its value as livestock feed). In 1905, he began experiments to examine the effects of inbreeding, work he expanded after moving to Connecticut later that year. Shull, on the other hand, initially used corn to test a criticism of de Vries's *Oenothera* studies (that his mutations were artifacts of selfing a species that was naturally cross-fertilizing). This work spurred an interest in testing the effects of selfing and crossing on the expression of a purely quantitative character.¹³ Because it was such an easy trait to measure, Shull chose the number of kernel rows in an ear of corn.

Using hand pollination, Shull inbred a number of lines (thereby reducing their variability). As inbreeding progressed, the plants declined in respect to such desirable traits as size and strength of the stalks, number of ears, and resistance to disease; the decline in "vigor" corresponded with the increase in homozygosity and ultimately leveled off.¹⁴ Shull assumed that his inbreeding had resulted in the isolation of "pure lines" or "biotypes" similar to those described by Wilhelm Johannsen in beans. When he then crossed these lines, the offspring were not only superior to their parents in size and general vigor; they sometimes surpassed the original open-pollinated corn plants. (Working independently, East had observed similar effects of inbreeding and crossing, but did not connect them to Johannsen's pure lines.)

East and Shull were hardly the first to note that deterioration often accompanies inbreeding, and an increase in general luxuriance or vigor the crossing of closely related strains. However, the cause of "inbreeding depression" remained obscure, as did its relation to hybrid vigor. The former was generally assumed to result from an accumulation of injurious individual variations, which in turn produced "unbalanced constitutions." Inbreeding was thus viewed as a process of continual degeneration.¹⁵ Shull argued that deterioration did not result from self-fertilization per se. In his view, it was an indirect effect of the isolation of distinct biotypes (or pure lines). Hybrid vigor resulted from their mixture, and was therefore simply the converse of inbreeding depression.

Shull also recognized that it was almost impossible for a corn plant to self-fertilize, given the lightness of the pollen shed by the male flowers and the location of the female flowers halfway down the stem. He therefore concluded that virtually every plant in a field of corn is naturally a hybrid—although one resulting from a "promiscuous" process of fertilization. To exploit fully the benefits of hybrid vigor, he proposed to substitute a process that was completely controlled. His "pure line method of corn breeding" would maintain otherwise useless inbred lines of corn solely for the purpose of utilizing the vigor obtained from their crossing. Shull argued that a policy of simple selec-

tion for the best individuals would not be effective, because the value of the resulting strains differed not only in their pure state but also in their various hybrid combinations. Ordinary methods of selection could take only the former into account. However, it was not possible to predict the relative vigor of hybrids simply from the value of the pure lines that produced them. "The object of the corn-breeder" Shull wrote, "should not be to find the best pure-line, but to find and maintain the best hybrid combination."⁵⁶ But the technique he suggested produced seed corn too expensive for commercial use.

The ultimate source of hybrid vigor is moreover as obscure in Shull's account as it was in pre-Mendelian works, such as Darwin's.⁵⁷ According to Shull, vigor results from crossing because crossing greatly increases the mixture of biotypes in the new hybrid strains. But why should mixing biotypes be beneficial? On this point, Shull is silent. In early 1909 however, he read a paper by East, also opposing the view that inbreeding per se was deleterious, in which East did advance an explanation of inbreeding depression and hybrid vigor.⁵⁸ More accurately, he proposed two.

Following Davenport, East first considered a simple Mendelian account of the effects of inbreeding—that it uncovers deleterious recessives (whose effects are masked by crossing). However, he believed this hypothesis inadequate for it failed to account for both developmental and genetic effects. East assumed that sexual reproduction has two functions: to recombine hereditary characters and to stimulate development. He suggested that this beneficial stimulation would be increased by the crossing of "two strains differing in gametic structure."⁵⁹ (That fertilization serves to "rejuvenate the egg" as well as create new genetic combinations was then a common belief.⁶⁰) Hybrid vigor is thus largely attributable to "the physiological stimulation of heterozygosis," a phrase that Shull shortened to "heterosis" in 1914.⁶¹

From this standpoint, hybrid vigor results from the beneficial effects of hybridity per se. "In other words," Shull wrote, "hybridity itself,—the union of unlike elements, the state of being heterozygous,—has, according to my view, a stimulating effect upon the physiological activities of the organism."⁶² As a corollary, it was not possible to produce pure lines as productive as hybrids; and because the quality of hybrids deteriorates after the first generation, the only way to obtain maximum yields was to return each year to the original combination.⁶³ Farmers could not effectively reuse their seed. "Like the mule, crossed corn has the advantage of hybrid vigor," asserted an early advertisement, like the mule, it is also (effectively) sterile. As Shull approvingly noted: "When the farmer wants to duplicate the splendid results he has had one year with hybrid corn, his only recourse is to return to the same hybridizer from whom he secured his seed the previous year and obtain again the same hybrid combination."⁶⁴

If vigor is a function of the degree of heterozygosis, hybrids are grounded in an unfortunate (from the farmers' perspective) fact of nature. However, the

view that heterozygotes were inherently superior had become a minority position long before the commercial development of hybrids. From the beginning, it had a rival—a truly Mendelian interpretation of inbreeding. Even in the nineteenth century, a few breeders held that in crosses parents usually possess different defects that tend to cancel out in their progeny.⁶⁵ After 1900, this insight was easily rephrased in Mendelian terms—that is, in the course of selection for various traits, breeders create strains that are homozygous for deleterious genes elsewhere in the genome. A hybrid formed between two inbred strains would acquire normal, dominant alleles at most of these loci.

The dominance interpretation of hybrid vigor was not immediately compelling because it predicted results that did not completely accord with observation (such as a skew distribution in the second generation). These anomalies disappeared, however, when linkage or the involvement of at least twenty genes was assumed. Moreover, the concept of physiological stimulation arising in some unknown way from heterozygosity was both distressingly vague and unsupported by any evidence.⁶⁶ Even East was later to admit that it was "an assumption for which there was no proof, and which was not illuminating as a dynamic interpretation."⁶⁷

By 1919, when East and his student Jones published their influential book *Inbreeding and Outbreeding*, the "heterosis concept" was already in retreat.⁶⁸ Jones invented the double-cross method of breeding, which made the production of hybrid seed commercially viable.⁶⁹ They themselves concluded that the dominance interpretation of hybrid vigor was correct—hence, that pure lines were in theory more desirable than hybrids.⁷⁰

In the 1920s and 1930s, the dominance explanation was generally accepted. In the 1940s, it would be challenged by Fred Hull, who argued that intrinsic heterozygote superiority (which he termed "overdominance") provided a partial explanation of hybrid vigor in corn.⁷¹ This view was popularized by Jay Lush, author of the leading text on animal breeding.⁷² Thus the East/Shull thesis of vigor resulting from the physiological stimulation produced by unlike gametes would eventually reappear in new, Mendelian garb. By then, however, virtually the entire corn belt had been planted in hybrids.⁷³ If the dominance explanation was widely accepted in the 1930s, how were hybrids justified? In part, as an expedient.

East and Jones believed that mass selection of open-pollinated varieties would ultimately produce lines as good or better than hybrids. In *Inbreeding and Outbreeding*, the success of the dominance interpretation of hybrid vigor is characterized as a "happy result." Why? Because the physiological stimulation hypothesis "locked the door on any hope of originating pure strains having as much vigor as first generation hybrids."⁷⁴ Hybrids produced a uniform field and (under some circumstances) a rapid boost in yield.⁷⁵ But selection could ultimately do the same, and more. For East and Jones understood that dominance was rarely complete. "Perfect dominance, except in more or

less superficial characters, rarely occurs, and even when it does occur, it may be merely an appearance rather than a reality," they wrote. The consensus was "that there is no such thing as perfect dominance, that the heterozygote merely approaches the condition of one or the other parent more closely."¹⁰⁶

The conclusion is obvious. If dominant genes do not completely mask the effects of deleterious recessives, selection should eventually produce pure lines superior to hybrids. In their words: "if dominance is but partial, this [homozygous] individual, through the very fact of its homozygous condition, will be even more vigorous than those of the first hybrid generation."¹⁰⁷ Thus, they predicted that hybrids would ultimately be replaced by pure lines.¹⁰⁸ Yet when they considered the mechanics of plant and animal improvement, the only method described was hybridization, and hybrids, in fact, remained the only approach to improvement of corn. By the 1930s, mass selection of open-pollinated varieties was no longer discussed.

East and Jones also provide a clue to the reason why. After explaining that Jones's double-cross method might appear complex, they write:

It is not a method that will interest most farmers, but it is something that may easily be taken up by seedsmen; in fact, it is the first time in agricultural history that a seedsman is enabled to gain the full benefit from a desirable origination of his own or something that he has purchased. The man who originates devices to open our boxes of shoe polish or to autograph our camera negatives, is able to patent his product and gain the full reward for his inventiveness. The man who originates a new plant which may be of incalculable benefit to the whole country gets nothing—not even fame—for his pains, as the plants can be propagated by anyone. There is correspondingly less incentive for the production of improved types. The utilization of first generation hybrids enables the originator to keep the parental types and give out only the crossed seeds, which are less valuable for continued propagation.¹⁰⁹

East and Jones believed that commercial breeders would not have sufficient incentive to improve plants until they could prevent farmers from using their own crops to propagate the next generation. Hybrids in effect conferred the equivalent of a patent right on new varieties of seed. East and Jones knew that, in theory, hybrids were not the only, or even best route, to improvement of corn. They themselves identified the alternative: "But that method, as a breeder associated with Jones wrote, would probably "spoil the prospects of any one thinking of producing the seed commercially."¹¹⁰ Without the commercial incentive provided by hybrids, they believed that corn would not be improved. With the breeders, East and Jones also thought it fundamentally unjust that the creators of new plants and animals should fail to profit by their inventions.¹¹¹

They thus faced a dilemma. East and Jones held a scientific theory accord-

ing to which pure lines should produce maximum increases in yield. But they also held a social theory (reflecting the facts of their actual world), according to which improvement of corn required an incentive for commercial producers that only hybrids could offer. Their prediction that pure lines would one day replace hybrids was therefore naive. Who would improve the open-pollinated varieties? The answer might seem obvious: state universities and their affiliated experiment stations. After all, a commitment to the welfare of the farmer and the general public was at the heart of experiment station ideology. However, public institutions proved unable to resist the clamor for hybrids, on the part of both farmers (excited by seed company advertising and focused on short-term gains) and large seed producers (whose representatives dominated university crop advisory committees).¹¹² Thus the interests of those who aimed to make seed a commodity ultimately prevailed over those who opposed it. But that is another story.¹¹³

Conclusion

The development of hybrid corn was no simple matter of the transfer of theoretical science from an elite academic to an applied commercial context. Much of the theoretical work that made hybrids possible was pursued at institutions concerned with improving the efficiency and productivity of agriculture. In the 1880s, agricultural administrators began to promote hybridization as part of an effort to produce commercially viable new varieties. Ongoing interest in hybridization, in turn, underlay an enthusiastic response to Mendelism among researchers at the USDA and at agricultural colleges and experiment stations. However, agricultural leaders and researchers were also committed to basic research and scientific reform. The agricultural disciplines and institutions were themselves flourishing hybrids.

Mendelism between 1900 and 1910 was thus an applied science, in the literal sense of both; it was surely applied, and it was certainly science. The rapid development of genetics within an agricultural context, where breeding, selection techniques, hybridization, and even evolutionary issues had been addressed in the late nineteenth century, endowed Mendelism in the United States with a strongly practical and popular aspect. It also ensured that fundamental problems in genetics would be addressed within institutions oriented to practical ends—and that the subsequent development of genetic research would often reflect dominant social and economic interests in American agriculture.

The case study of hybrid corn illustrates these points. George Shull was not trained at an agricultural institution nor did he ever work at one; but his early experience of Mendelism brought him close to horticultural and agricultural researchers and to involvement with practical issues. Edward East was

trained and did his early work at agricultural colleges and experiment stations before moving to Harvard's Bussey Institution, and Donald Jones worked at the Connecticut station throughout his career. That their research ultimately provided an important breakthrough for commercial agriculture is comprehensible within the complex constraints and constituencies of these scientists' sponsoring institutions.

Numerous centennial and celebratory volumes document the achievements of the USDA, state experiment stations, and agricultural colleges. However, these institutions have generally been given short shrift by historians of biology. Their attention has focused on the elite colleges and laboratories dedicated to the ideal of pure research.

From the perspective of researchers at Johns Hopkins, Columbia, or Woods Hole, agricultural colleges and experiment stations were doubtless at the periphery of the new biology. However, we see no reason to privilege their standpoint. It certainly does not accord with the self-conception of those employed at agricultural institutions. They were generally proud of their mandate: to serve the public interest. As we have seen, that goal did not exclude a commitment to basic research. On the contrary, much fundamental work in biology, especially genetics, emerged from these institutions. For this reason alone, they deserve greater attention from historians of biology. Of further interest is the fact that their research agendas reflected, in a particularly blunt way, political and economic interests. To consider these institutions is thus to broaden our understanding both of American culture and American science.

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Notes

1. Willet M. Hays, "Address by Chairman of Organization Committee," *Proceedings of the American Breeders Association*, 1905, 1: 9-15.
2. William Bateson, "Hybridisation and Cross-breeding as a Method of Scientific Investigation," *Journal of the Royal Horticultural Society*, 1900, 24: 59-66.

3. Charles B. Davenport, "Report of the Committee on Eugenics," *The American Breeders Magazine*, 1910, 1: 126-129. See also Barbara A. Kimmelman, "The American Breeders Association: Genetics and Eugenics in an Agricultural Context," *Social Studies of Science*, 1983, 13: 163-204.

4. Deborah K. Fitzgerald, "The Business of Breeding: Public and Private Development of Hybrid Corn in Illinois, 1890-1940" (Ph.D. dissertation, University of Pennsylvania, 1985).

5. During this period, investigators generally used the terms hybridization, crossbreeding, and cross-fertilization to mean, respectively, interspecific crosses, intervarietal crosses, and intraspecific crosses between male and female of different plants. Darwin based his crucial analogy between interspecific hybrids and intervarietal mongrels on such distinctions. In practice, the analogy proved more powerful than the distinction, and many investigators used the terms interchangeably. We will see that, after 1910, hybrids came to acquire a more precise, technical meaning.

6. Walter A. Cannon, "Review of Proceedings: International Conference on Plant Breeding and Hybridization," *Torrey*, 1905, 1: 12-14.

7. C. W. Ward, "Improvement of Carnations," *Memoirs of the Horticultural Society of New York*, 1904, 1: 151-155.

8. William Bateson, "Practical Aspects of the New Discoveries in Heredity," *Mems. Hort. Soc. N.Y.*, 1904, 1: 1-8.

9. William Bateson, *Mendel's Principles of Heredity: A Defence* (Cambridge: Cambridge University Press; New York: Macmillan Co.; 1902). Alan Cook notes that the book was published on 3 or 4 June 1902 in Britain and must have appeared almost simultaneously in the United States (private communication).

10. Liberty Hyde Bailey, "Comments," *Mems. Hort. Soc. N.Y.*, 1904, 1: 8.

11. William Bateson to Beatrice Bateson, 3 October 1902, William Bateson papers, University of Cambridge Library, letter G-3D-05; typed transcript at G8G01D. We gratefully acknowledge the Library's permission to quote from Bateson's letter. The originals of the collection prefaced G have recently been transferred to the Library from the John Innes Institute, which now has photocopies. Mrs. Rosemary Harvey, archivist at the John Innes, kindly supplied copies of Bateson's 1902 letters from America.

12. Garland Allen, *Life Science in the Twentieth Century* (New York: John Wiley and Sons, 1975), p. 52.

13. *Ibid.*

14. "Seedsmen," or "practical breeders," were primarily farmers who also bred particular varieties of seed/grain for purpose of sale. A few of these farmers (such as the Funks) engaged in breeding for sale as a major enterprise but for most it was minor activity. Some seedsmen (mostly urban horticulturalists) were businessnessmen *simpliciter*.

15. Barbara A. Kimmelman examines the founding and early years of research departments in genetics within the agricultural colleges at Ithaca, N.Y., Madison Wis., and Berkeley, Calif., in "A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1890-1920" (Ph.D. dissertation, University of Pennsylvania, 1987).

16. Bateson, "Practical Aspects," p. 3.

17. C. C. Hurst, "Notes on Mendel's Methods of Cross Breeding," *Mems. Hort.*

Sec. N.Y., 1904, 1: 11-16; Hugo de Vries, "On Artificial Auivism," *Mems. Hort. Soc. N.Y.*, 1904, 1: 16-23.

18. This point is illustrated by the diverse character of articles on Mendelism published in American journals between 1901 and 1903. The first to appear was Charles Davenport's "Mendel's Law of Dichotomy," in the *Biological Bulletin*, 1901, 2: 307-310. It was quickly followed by E. B. Wilson, "Mendel's Principles of Heredity and the Maturation of the Germ-cells," *Science*, 1902, 16: 991-992; Walter Sutton, "On the Morphology of the Chromosome Group in *Brachystola magna*," *Biol. Bull.*, 1902, 3: 24-39; W. J. Spillman, "Exceptions to Mendel's Law," *Sci.*, 1902, 16: 709-710 and 784-796; R. A. Emerson, "Preliminary Account of Variation in Bean Hybrids," *15th Annual Report of the Nebraska Experiment Station*, 1902; and Walter A. Cannon, "A Cytological Basis for the Mendelian Cases," *Bulletin of the Torrey Botanical Club*, 1902. Other early accounts include Liberty Hyde Bailey, "A Discussion of Mendel's Law and its Bearings," Address before the Society for Plant Morphology and Physiology, Washington, D.C., 29 Dec. 1902, published as "Some Recent Ideas on the Evolution of Plants," *Sci.*, 1903, 17: 441-454; Walter Sutton, "The Chromosomes in Heredity," *Biol. Bull.*, 1902, 4: 231-251; and William Castle, "The Laws of Heredity of Galton and Mendel and some Laws Governing Race Improvement by Selection," *Proceedings of the American Academy of Arts and Sciences*, 1903, 38: 535-548; reprinted as "Mendel's Law of Heredity," in *Sci.*, 1903, 18: 396-406. Compare with the lack of interest expressed by the *Botanical Gazette*. The first mention of Mendel is a dismissive comment by the editor, John Merle Coulter, in a review of the third edition of Liberty Hyde Bailey's *Plant Breeding* (*Botanical Gazette*, 1904, 37: 471-472). The *American Naturalist* was also unimpressed. Other than a passing reference in a Botanical Note of 1902, there is no mention of Mendelism until 1904, and then only in Charles Davenport's book reviews. Editorial notes and articles first appear in 1907.
19. Jan Sapp, "The Struggle for Authority in the Field of Heredity, 1900-1932: New Perspectives on the Rise of Genetics," *Journal of the History of Biology*, 1983, 16: 311-342.
20. Willet M. Hays, "Address by Chairman of Organization Committee," p. 10.
21. W. J. Spillman, "Mendel's Law in Relation to Animal Breeding," *Proc. ABA*, 1905, 1: 171-176; H. J. Webber, "Explanation of Mendel's Law of Hybrids," *Proc. ABA*, 1905, 1: 138-143.
22. William Bateson, "G. Mendel: Experiments in Plant Hybridisation," *J. Royal Hort. Soc.*, 1901, 26: 1-32.
23. U.S. Department of Agriculture, Office of Experiment Stations, Abstract of G. Mendel, "Experiments in Plant Hybridization," *Experiment Station Record*, 1901-1902, vol. 13 (Washington, D.C.: Government Printing Office, 1902), p. 744.
24. *Ibid.*, p. 745.
25. *Ibid.*, p. 1004.
26. See, for example, U.S. Department of Agriculture, Office of Experiment Stations, Abstracts of W. F. R. Weldon, "Mendel's Law of Alternative Inheritance in Peas," C. C. Hurst, "Mendel's Law Applied to Orchid Hybrids," and Carl Correns, "Apparent Exceptions to Mendel's Law of Dissociation in Hybrids," *Experiment Station Record*, 1902-1903, vol. 14 (Washington, D.C.: Government Printing Office, 1903), pp. 466-467, 569. Also see U.S. Department of Agriculture, Office of Ex-

periment Stations, Abstracts of A. D. Darbishire, "On the Bearing of Mendelian Principles of Heredity on Current Theories of the Origin of Species," Erich von Tschernak, "Further Studies in Crossing Peas, Stocks, and Beans," and David Starr Jordan, "Some Experiments of Luther Burbank," *Experiment Station Record*, 1904-1905, vol. 16 (Washington, D.C.: Government Printing Office, 1905), pp. 232, 263, 773-774. Jordan's study indicated that Burbank's results did not generally conform to Mendel's laws.

27. Bailey, "A Discussion of Mendel's Law," pp. 445-446.
28. Margaret Kossiter, "The Organization of the Agricultural Sciences," in Alexandra Olsson and John Voss, eds., *The Organization of Knowledge in Modern America, 1860-1920* (Baltimore: Johns Hopkins University Press, 1979), pp. 211-248.
29. Our interpretation of the Progressive Era accords with the work of Sidney Fine, *Laissez Faire and the General Welfare State: A Study of Conflict in American Thought 1865-1901* (Ann Arbor: University of Michigan Press, 1956); Samuel P. Hays, *The Response to Industrialism 1885-1914* (Chicago: University of Chicago Press, 1947); Harold U. Faulkner, *Politics, Reform, and Expansion 1890-1900* (New York: Harper and Row, 1959); Robert H. Wiebe, *The Search for Order 1877-1920* (New York: Hill and Wang, 1967); and James Weinstein, *The Corporate Ideal in the Liberal State 1890-1918* (Boston: Beacon Press, 1968). See also Samuel P. Hays, "Introduction: The New Organizational Society," in Jerry Israel, ed., *Building the Organizational Society* (New York: The Free Press, 1972), pp. 1-15.
30. U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1885*, "Report of the Statistician," by J. R. Dodge (Washington, D.C.: Government Printing Office, 1885), p. 372.
31. For example, see U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1880*, "Report of the Statistician," by Charles Worthington (Washington, D.C.: Government Printing Office, 1880), p. 210; Dodge, "Report of the Statistician," pp. 372-376; and U.S. Department of Agriculture, *First Report of the Secretary of Agriculture, 1889*, "Report of the Secretary of Agriculture" by J. M. Rusk (Washington, D.C.: Government Printing Office, 1889), p. 14.
32. Dodge, "Report of the Statistician," pp. 379-380.
33. *Ibid.*, p. 373.
34. A valuable discussion of the growing importance of U.S. international markets (although, like its subjects, it disparages the significance of the agricultural sector) is Walter LeFebvre, *The New Empire: An Interpretation of American Expansion 1860-1898* (Ithaca: Cornell University Press, 1967). Works addressing this theme in agriculture include Fred A. Shannon, *The Farmer's Last Frontier: Agriculture, 1860-1897* (New York: Farrar and Rinehart, 1945); Alan I. Marcus, *Agricultural Science and the Quest for Legitimacy: Farmers, Agricultural Colleges, and Experiment Stations, 1870-1890* (Ames: Iowa State University Press, 1985); and David Danbom, *The Re-sisted Revolution: Urban America and the Industrialization of Agriculture, 1900-1930* (Ames: Iowa State University Press, 1979), although it deals with a slightly later period.
35. U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1887*, "Report of the Commissioner of Agriculture," by Norman J. Colman (Washington, D.C.: Government Printing Office, 1888), p. 8.
36. U.S. Department of Agriculture, *Report of the Secretary of Agriculture for*

- the year 1888. "Report of the Statistician," by J. R. Dodge (Washington, D.C.: Government Printing Office, 1889), p. 201.
37. *Ibid.*, pp. 201-202. See also U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1891*, "Report of the Statistician," by J. R. Dodge (Washington, D.C.: Government Printing Office, 1892), pp. 301-306.
38. U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1892*, "Report of the Secretary of Agriculture," by J. M. Rusk (Washington, D.C.: Government Printing Office, 1893), p. 10; also U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1893*, "Report of the Secretary of Agriculture," by J. Sterling Morton (Washington, D.C.: Government Printing Office), p. 16.
39. The agricultural appropriation act of 1881 statutorily established a divisional organization for the USDA, at which time the divisions of Seed, Gardens and Grounds and of Botany were founded. The Division of Pomology was established in 1886; the Division of Vegetable Pathology achieved independence from the Division of Botany in 1891, and became the Division of Vegetable Physiology and Pathology in 1895; in that year, the Division of Agrostology was also founded. The Section Foreign Seed and Plant Introduction was established in 1897. See U.S. Department of Agriculture, *Division of Publications, Historical Sketch of the U.S. Department of Agriculture: Its Objects and Present Organization*, by Charles H. Greathouse, Bulletin no. 3 (Washington, D.C.: Government Printing Office, 1898), pp. 33-40; Fred Wilbur Powell, *The Bureau of Plant Industry, Its History, Activities and Organizations*, Institute for Government Research, Service Monographs of the United States Government no. 47 (Baltimore: Johns Hopkins University Press, 1927), pp. 1-9; and David Fairchild, *The World Was My Garden, Travels of a Plant Explorer* (New York: Charles Scribner's Sons, 1939), pp. 105-107.
40. U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1885*, "Report of the Chief of the Seed Division," by William M. King (Washington, D.C.: Government Printing Office, 1885), p. 47.
41. *Ibid.*, p. 51.
42. *Ibid.*, p. 53.
43. U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1886*, "Report of the Pomologist," by H. E. Van Denna (Washington, D.C.: Government Printing Office, 1886), p. 260.
44. U.S. Department of Agriculture, *Report of the Commissioner of Agriculture for the year 1887*, "Report of the Pomologist," by H. E. Van Denna (Washington, D.C.: Government Printing Office, 1888), pp. 627-628.
45. U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1892*, "Report of the Superintendent of Gardens and Grounds," by William Saunders (Washington, D.C.: Government Printing Office, 1893).
46. U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1892*, "Report of the Chief of the Division of Vegetable Pathology," by B. T. Galloway (Washington, D.C.: Government Printing Office, 1893), p. 246.
47. B. T. Galloway, "Division of Vegetable Physiology and Pathology," *Yearbook U.S.D.A. 1897* (Washington, D.C.: Government Printing Office, 1898), p. 104.
48. *Ibid.*, p. 106.
49. Albert F. Woods, "Work in Vegetable Physiology and Pathology," *Yearbook U.S.D.A. 1898* (Washington, D.C.: Government Printing Office, 1899), pp. 264-266. See also U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1899*, "Report of the Secretary of Agriculture," by James Wilson (Washington, D.C.: Government Printing Office, 1899), p. 15.
50. An illustration of the division's work during this period and of the intellectual problems addressed by its researchers, see Walter T. Swingle and Herbert J. Webber, "Hybrids and Their Utilization in Plant Breeding," *Yearbook U.S.D.A. 1897*, pp. 383-421.
51. For example, see U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1889*, "Report of the Botanist," by George Vasey (Washington, D.C.: Government Printing Office, 1889), pp. 377-381; and U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1890*, "Special Report of the Assistant Secretary: the Scientific Work of the Department in its Relations to Practical Agriculture," by Edwin Willis (Washington, D.C.: Government Printing Office, 1890), pp. 59-73.
52. Rossiter, "The Organization of the Agricultural Sciences," pp. 213-215.
53. U.S. Department of Agriculture, *Report of the Secretary of Agriculture for the year 1898*, "Report of the Secretary of Agriculture," by James Wilson (Washington, D.C.: Government Printing Office 1898), p. 47.
54. U.S. Department of Agriculture, Office of Experiment Stations, *Organization of the Agricultural Experiment Stations of the United States*, Norman J. Colman, Bulletin no. 1 (Washington, D.C.: Government Printing Office, 1884).
55. See Charles E. Rosenberg, "The Adams Act: Politics and the Cause of Scientific Research," in Charles E. Rosenberg, *No Other Gods: On Science and American Social Thought* (Baltimore: Johns Hopkins University Press, 1976), pp. 174-175.
56. This group included William James Beal, Charles E. Bessey, and Liberty Hyde Bailey. On their efforts, see Andrew Denny Rodgers, *John Merle Coulter, Missionary in Science* (Princeton: Princeton University Press, 1944), esp. pp. 52-64, and idem, *Liberty Hyde Bailey, A Story of American Plant Sciences* (Princeton: Princeton University Press, 1949), esp. pp. 22-181, 242-247. See also Richard Overfield, "Charles E. Bessey: The Impact of the 'New Botany' in American Agriculture, 1880-1910," *Technology and Culture*, 1975, 16: 162-181.
57. See U.S. Department of Agriculture, Office of Experiment Stations, *Digest of the Annual Reports of the Agricultural Experiment Stations in the United States for 1888*, Bulletin no. 2, pt. 1 (Washington, D.C.: Government Printing Office, 1884). For a discussion of constraints on scientific work at the stations during this period, see Rosenber, "Science, Technology, and Economic Growth: The Case of the Agricultural Experiment Station Scientist, 1875-1914," in Rosenber, *No Other Gods*, pp. 153-172.
58. The stations were South Dakota, Maryland, Massachusetts, and Mississippi. See U.S. Department of Agriculture, Office of Experiment Stations, *List of Horticulturalists of the Agricultural Experiment Stations in the United States, with an Outline of Work in Horticulture at the Several Stations*, by W. B. Alwood, Bulletin no. 4 (Washington, D.C.: Government Printing Office, 1889).
59. *Ibid.* The stations were Colorado, Florida, Kansas, Michigan, New York (Geneva), Missouri, New Jersey, and Ohio.
60. U.S. Department of Agriculture, Office of Experiment Stations, *List of Horti-*

nists of the Agricultural Experiment Stations in the United States, with an Outline of the Work in Botany at the Several Stations, Bulletin no. 6 (Washington, D.C.: Government Printing Office, 1890), p. 6.

61. *Ibid.*, pp. 7-23, for responses from the stations in alphabetical order by state. The states with strong programs planned in crossbreeding were Illinois, Indiana, Kansas, Michigan, New Jersey, and Ohio.

62. See H. J. Webber and E. A. Bessey, "The Progress of Plant Breeding in the United States," *Yearbook U.S.D.A. 1899* (Washington, D.C.: Government Printing Office, 1899), esp. pp. 478, 480-481, 487-488.

63. Office of Experiment Stations, *List of Botanists*, p. 6.

64. The Illinois and Kansas stations' corn work is summarized in the U.S. Department of Agriculture, Office of Experiment Stations, *Handbook of Experiment Station Work: A Popular Digest of the Agricultural Experiment Stations in the United States*, Bulletin no. 15 (Washington, D.C.: Government Printing Office, 1893), pp. 81-89 (entry under "Corn, crossing").

65. William Bateson, *Materials for the Study of Variation* (London: 1894); the culmination of the Vries' late-nineteenth-century work was his *Die Mutationstheorie*, vol. 1 (Leipzig: 1901) and vol. 2 (Leipzig: 1903).

66. Wilfred Mark Webb, "The International Conference on Hybridisation and Cross-breeding," *Nature*, 1899, 60: 305-307. Others invited but not present (in addition to Bailey) were David Fairchild of the USDA, Luther Burbank, and J. M. MacFarlane of the University of Pennsylvania.

67. William Bateson, "Hybridisation and Cross-breeding as a Method of Scientific Investigation."

68. Hugo de Vries, "Hybridisation as a Means of Pangenetic Infection," *J. Royal Hort. Soc.*, 1900, 24: 69-75.

69. C. C. Hurst, "Experiments in Hybridisation and Cross-breeding," *J. Royal Hort. Soc.*, 1900, 24: 90-127. "Prepotency" suggests a sire's ability to impress his traits on his progeny. It generally referred to an overall "type," rather than single characters.

70. *Ibid.*, p. 90.

71. Herbert J. Webber, "Work of the United States Department of Agriculture in Plant Hybridisation," *J. Royal Hort. Soc.*, 1900, 24: 128-145; see also L. H. Bailey, "Progress of Hybridisation in the United States of America," *J. Royal Hort. Soc.*, 1900, 24: 209-213.

72. Willet M. Hays, "Breeding Staple Food Plants," *J. Royal Hort. Soc.*, 1900, 24: 257-265.

73. See Webb, "International Conference on Hybridisation and Cross-breeding," p. 307.

74. Office of Experiment Stations, *Experiment Station Record* (1902), p. 205.

75. W. M. Hays, "Address by Chairman of Organization Committee."

76. W. J. Spillman, *Memoirs N.Y. Hort. Soc.*, 1904, 1: 155.

77. Bailey, "A Discussion of Mendel's Law," p. 450.

78. Bateson, "Practical Aspects," p. 2.

79. Bailey, "A Discussion of Mendel's Law," p. 450.

80. L. C. Dunn, *A Short History of Genetics* (New York: McGraw-Hill, 1965), p. 125. The following list provides a few representative comments: Paul Mangelsdorf

writes that the increased yields resulting from hybrids "contributed not only to this country's war effort but also the rehabilitation of Europe after the war," in "George Harrison Shull," *Genetics*, 1955, 60: 2-3. L. J. Stadler claims that "It is . . . no exaggeration to say, speaking in terms of the over-all national economy, that the dividend on our research investment in hybrid corn, during the war years alone, was enough to pay the money cost of the development of the atomic bomb," quoted in G. Shull, "Hybrid Seed Corn," *Sci.*, 1946, 103: 547-550. Bentley Glass states that the increase in yield was "enough to pay for the Manhattan Project" and even "most significantly, increased production [which] permitted the United States to ship vast quantities of food abroad after the war, thus preventing famine and pestilence," in "Shull, George Harrison," *Dictionary of American Biography*, suppl. 5 (New York: Scribners, 1977), p. 629. Richard Crabb writes that hybrid corn helped "tip the scales in our favor in a war to the finish," in Richard Crabb, *The Hybrid-Corn Makers: Prophets of Plenty* (New Brunswick, N.J.: Rutgers University Press, 1948), p. 13.

81. Jean-Pierre Berlan and Richard Lewontin, "The Political Economy of Hybrid Corn," *Monthly Review*, 1986, 38: 35-47; and Berlan and Lewontin, "Breeder's Rights and Patenting Life Forms," *Nat.*, 1986, 322: 785-788, esp. pp. 787-788.

82. They should do better, rather than equally well, because of the ubiquity of partial dominance (discussed below).

83. G. H. Shull, "Beginnings of the Heterosis Concept," in John Gowan, ed., *Heterosis* (Ames: Iowa State College Press, 1952), pp. 14-48.

84. Shull, "A Pure-line Method of Corn Breeding," *Proc. ABA*, 1909, 5: 51-59.

85. Edward M. East and Donald F. Jones, *Inbreeding and Outbreeding: Their Genetic and Sociological Significance* (Philadelphia: J. B. Lippincott, 1919), p. 168.

86. Shull, "A Pure-line Method of Corn Breeding," p. 52.

87. Charles Darwin, *The Effects of Cross and Self-fertilization in the Vegetable Kingdom* (London: John Murray, 1876).

88. E. M. East, "The Distinction between Development and Heredity in Inbreeding," *Am. Nat.*, 1909, 43: 173-181.

89. *Ibid.*, p. 177.

90. John Farley, *Gametes and Spores* (Baltimore: Johns Hopkins University Press, 1982), pp. 203-208.

91. G. H. Shull, "Duplicate Genes for Capsule Form in *Bursa bursa-pastoris*," *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, 1914, 12: 97-149, on p. 127.

92. *Ibid.*, p. 126; also quoted in G. H. Shull, "What is Heterosis?" *Genetics*, 1948, 33: 439-446, on p. 440.

93. G. H. Shull, "The Composition of a Field of Maize," *Proc. ABA*, 1908, 4: 296-301, on p. 301.

94. Shull, "Hybrid Seed Corn," p. 549.

95. Conway Zirkle, "Early Ideas of Inbreeding and Crossbreeding," in Gowen, *Heterosis*, pp. 1-13.

96. See Frederick D. Richey, "Hybrid Vigor and Corn Breeding," *Journal of the American Society of Agronomists*, 1946, 38: 833-841, and G. F. Sprague, "Heterosis in Maize: Theory and Practice," in R. Frankel, ed., *Heterosis: Reappraisal of Theory and Practice*, (New York: Springer-Verlag, 1982), p. 50.

97. E. M. East, "Heterosis," *Genet.*, 1936, 21: 375-397, on p. 375.

98. E. M. East and D. F. Jones, *Inbreeding and Outbreeding*.
99. The inbred plants used to produce hybrids were so depressed that they generated little (hence expensive) seed. In the double-cross, the plants that produce the seed are themselves hybrids.
100. "Homozygosity, when obtained with the combination of all the most favorable characters, is the most effective condition for the purpose of growth and reproduction." East and Jones, *Inbreeding and Outbreeding*, p. 187.
101. Fred Hull, "Recurrent Selection for Specific Combining Ability in Corn," *J. Am. Soc. Agron.*, 1945, 37: 134-145.
102. J. L. Lush, *Animal Breeding Plans*, 3rd ed. (Ames, Iowa: The Collegiate Press, 1945). Lush's influence is noted in James F. Crow, "Muller, Dobzhansky, and Overdominance," *J. Hist. Biol.*, 1987, 20: 351-380.
103. By 1945, 99.9 percent of corn acreage in Iowa and 98.1 percent in Illinois and Indiana had been planted in hybrids. USDA, *Agricultural Statistics, 1947* (Washington, D.C.: Government Printing Office, 1949), table 48, p. 43.
104. East and Jones, *Inbreeding and Outbreeding*, p. 182.
105. Such a response occurs when there are large numbers of *already existing* inbred lines, maximizing the chance of finding a favorable cross.
106. East and Jones, *Inbreeding and Outbreeding*, pp. 177-178.
107. *Ibid.*, p. 182.
108. *Ibid.*, pp. 169, 181. Jones characterizes hybrids as a "makeshift measure" in "Selection in Self-Fertilized Lines as the Basis of Corn Improvement," *J. Am. Soc. Agron.*, 1920, 12: 77-100, on p. 95.
109. East and Jones, *Inbreeding and Outbreeding*, p. 224.
110. George S. Carter to Henry A. Wallace, 12 May 1925, quoted in Jack Kloppenburg, *First the Seed: The Political Economy of Plant Biotechnology* (Cambridge: Cambridge University Press, 1988). The Wallace papers are deposited at the University of Iowa Library and are available on microfilm.
111. Compare Jones, "Selection in Self-fertilized Lines," p. 87 and Willet Hays, "Distributing Valuable New Varieties and Breeds," *Proc. AHA*, 1905, 1: 58-65.
112. See Fitzgerald, "The Business of Breeding," esp. chap. 5 and conclusion.
113. See Kloppenburg, *First the Seed*, and Fitzgerald, "The Business of Breeding."

Scott F. Gilbert

10 Cellular Politics: Ernest Everett Just, Richard B. Goldschmidt, and the Attempt to Reconcile Embryology and Genetics

Reflecting on embryology in the 1930s, Johannes Holtfreter stated:

We managed more or less successfully to keep our work undisturbed by humanity's strife and struggle around us and proceeded to study the plants and animals, and particularly, the secrets of amphibian development. Here, at least, in the realm of undespoiled Nature, everything seemed peaceful and in perfect order. It was from our growing intimacy with the inner harmony, the meaningfulness, the integration, and the interdependence of the structures and functions as we observed them in dumb creatures that we derived our own philosophy of life. It has served us well in this continuously troublesome world.¹

The attempts to reintegrate embryology and genetics during the last years of the 1930s represent the last chapter in the emergence of American biology. When had American biology finished "emerging"? I suspect that stage was reached when it had successfully resisted the last attempts to reintegrate it into European-dominated traditions of inquiry. For genetics, this occurred in the late 1930s when Richard B. Goldschmidt and Ernest Everett Just separately countered the American school of genetics with European alternatives. Goldschmidt and Just both attempted to place genetics into a physiological framework. Goldschmidt was the director of the genetics section of the Kaiser Wilhelm Institute before fleeing the Nazis and coming to America in 1936. For Goldschmidt, the "static genetics" of T. H. Morgan, centered on individual particulate genes, was to be replaced by "physiological genetics" wherein the gene did not exist as an individual unit, and its activity, not its location, was the focus of research.