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***Mendelism, plant breeding and experimental cultures:
Agriculture and the development of genetics in France***

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Abstract

The article reevaluates the reception of Mendelism in France, and more generally considers the complex relationship between Mendelism and plant breeding in the first half of the twentieth century. It shows on the one side that agricultural research and higher education institutions have played a key role in the development and institutionalization of genetics in France, whereas university biologists remained reluctant to accept this approach on heredity. But on the other side, plant breeders and agricultural researchers, despite an interest in Mendelism, never came to see it as the breeders' panacea, and regarded it instead as of only limited value for plant breeding. I account for this judgment in showing that the plant breeders and Mendelism designed two contrasting kinds of experimental systems and inhabited distinct experimental cultures. While Mendelian geneticists designed experimental systems that allowed the production of definite ratios of different forms that varied in relation to a few characters, plant breeders' experimental systems produced a wide range of variation, featuring combinations between hundreds of traits. Rather than breaking this multiple variation down into simple elements, breeders designed and monitored a genetic lottery. The gene was a unit in a Mendelian experimental culture, an "epistemic thing" as H.-J. Rheinberger put it, that could be grasped by means of statistical regularities, but it remained of secondary importance for French plant breeders, for whom the strain or the variety –not the gene– was the fundamental unit of analysis and manipulation.

Keywords : History of genetics, Mendelism, plant breeding, experimental system, plant breeders rights, France, agriculture

Mendelism, plant breeding and experimental cultures: Agriculture and the development of genetics in France

Introduction

France played a very modest role in the international development of genetics during the first half of the 20th century. Scholars who have studied the development of genetics in France, like Ernst Mayr, Denis Buican, Jean Gayon, Richard Burian, Doris Zallen, and Marion Thomas all agree that Mendelian genetics did not establish itself to any great degree in the French scientific landscape during the first half of the century¹. Although Mendelism was widely diffused and discussed in scholarly journals, it was rarely taught in the universities and only a few isolated French biologists, like L. Cuénot and E. Guyenot, contributed to the international field of Mendelian research.

Denis Buican has proposed a straightforward explanation for this situation: “*the influence of neo-Lamarckism, in the period from 1900 to 1945, had a negative impact, because the hypothesis of the heredity of acquired characters was a dogma that slowed down the normal development of the science of heredity*”². For him, the hegemony of neo-Lamarckism in French biology accounts both for a stubborn rejection of Mendelism in the first half of the 20th century and for several biologists’ sympathy for Lysenkoism after WW2. Burian, Gayon, and Zallen have revised this manichaeic presentation of a “*forty-five year fight of the forces of light against those of darkness, with a small number of enlightened individuals battling against massive retrograde forces*”³ They have shown that besides the influence of neo-Lamarckism, researchers following traditions inherited from Louis Pasteur and Claude Bernard approached heredity in ways that made them unsatisfied with Mendelism, and that these very sources of reluctance for adopting Mendelism generated fertile ground for the growth of molecular genetics in France after 1940, especially at the Pasteur Institute with the work of Jacob, Monod and Lwoff⁴.

Another serious limitation in most studies on the reception of genetics in France is a narrow focus on university biologists and the lack of attention paid to the role of horticultural and agricultural professionals (tradesmen, horticulturists, breeders, agricultural scientists, etc). Pioneering historical works have established the key role played by such communities of

¹ Buican, 1984 ; Burian, Gayon and Zallen., 1988; Gayon and Burian, 2000; Thomas, 2004

² Buican, 1984, p. 193.

³ Burian, Gayon and Zallen., 1988, p. 360.

⁴ See also Sapp, 1983.

professionals, often involved in eugenics movements and/or the “modernization” of agriculture, in the reception of Mendelism and the development of genetics in the US, UK and Germany⁵. But only a few exploratory studies have looked into the interface between genetics and agriculture in France and this work has not led to a revision of the “French Mendelian desert” thesis. Jean-Louis Fischer rightly pointed out the need to investigate the reception of genetics in horticultural and agricultural circles, but focused in his own research on the priest Germain Vieules, a rather peripheral figure in these circles⁶. Marion Thomas has looked at the work of the biologist Louis Blaringhem who visited Hjalmar Nilsson in Svalöf in 1904 and applied his pure sort selection method for barley breeding as well as promoting Johannsen’s concept of the pure line⁷. Blaringhem tried to reconcile Mendel with a neo-Lamarckian reading of De Vries’s mutation theory, an approach shared by Thomas H. Morgan at that time. But in contrast to Morgan’s encounter with drosophila mutants, Blaringhem’s encounter with pure-line plant breeding did not lead him to change his neo-Lamarckian “experimental evolution” perspective, which led him to study the inheritance of anomalies caused by traumatic action rather than in Mendelian studies of crosses⁸. Finally, Gayon and Zallen note that, even if Philippe de Vilmorin, the director of Vilmorin-Andrieux, the foremost French breeding and seed trade company, became a Mendelian and published Mendelian research, the rediscovery of Mendel’s laws did not modify the breeding schemes used by his company⁹.

Thus the standard picture is of a French “Mendelian desert” and a general failure to integrate Mendelism into plant breeding. Although this picture captures part of the reality, it is partial and based on two implicit assumptions typical for a “history from above”. First, the deployment of genetics among agricultural and horticultural scientists and breeders remains underestimated. It seems probable that the “pre-academic phase” of genetics, that Paul and Kimmelman situate during the period 1900-1915 in the USA, lasted right up until 1945 in France. Nevertheless, this phase, and the role of agricultural scientists and breeders more generally, deserves deeper enquiry and should not simply be dismissed on the basis of a narrow academic definition of genetics. Second, the standard picture, in lamenting that Mendelism did not restructure plant breeding schemes, implicitly assumes that it should have done so. It takes the worldview of the promoters of Mendelism for granted, claiming that they

⁵ See Kevles, 1980; Paul and Kimmelman, 1988 ; Palladino, 1993 and 1994, Olby, 1987. On Germany, see Harwood, 1997 and Wieland, 2004.

⁶ Fischer 1990 ; For a contrast with the ‘mendelization’ of the powerful Royal Horticultural Society see Olby 2000.

⁷ Thomas, 2004.

⁸ Kohler 1994, pp. 37-46.

⁹ Gayon and Zallen, 1998, p. 260 and 244.

were shifting breeding out of the obscurity of empiricism and into the light and predictability of science.¹⁰

Several studies have, however, started to challenge this kind of Mendel-centered view of plant breeding, and have instead documented much more complex, locally situated, reciprocal relationships between academic studies of heredity and breeding activity.¹¹ They are consistent with an important trend in the history of technology, which views technological research as a distinct sphere of knowledge rather than as a practical “application” of scientific knowledge.¹² These studies also echo a “history from below” perspective that emerged in the 1960s’ in social history. This approach aims at a shift in viewpoint, from writing history from the perspective of elites, to writing history from the perspective of social groups who had previously been largely hidden from history.¹³ Applied to the relation of Mendelism and plant breeding, such a perspective implies to escape the standard narrative of (Mendelian) *theory* reshaping (breeding) *practice*, or its failure to do so, and to consider instead plant breeders’ sphere of knowledge seriously, to explore both the experimental practices and cognitive mindsets of both Mendelians and plant breeders, and study how the two spheres interacted and borrowed elements from each other while remaining largely distinct right up until the middle of the twentieth century.

Such a deeper examination, “from below”, of academic and private plant breeders’ practices, institutions and attitudes towards Mendel’s laws of heredity might help us to revise our views both on the claim that Mendelian genetics was not well established in France and on the question of why this was the case. The first section of this article shows how the milieu of agricultural scientists, horticulturists, and breeders played a much more important role in the development and institutionalization of genetics in France than has previously been recognized. The second section explores some of the reasons why state-sponsored and private plant breeders, despite an initial interest in –and a fairly good knowledge of– Mendel’s laws and Johannsen’s pure-line theory never came to see them as the breeder’s panacea, and regarded them instead as being of only limited value. The third section accounts for the limited importance breeders’ gave to Mendelism by using Hans-Jörg Rheinberger’s notions of “experimental system” and “epistemic thing”, as well as Giovanni Dosi’s concept of “technological paradigm.”

Experimental systems are set ups of living and non-living objects, devices and skills that “*cogenerate the phenomena and material entities and the concepts they come to*

¹⁰ A paradigmatic example of such an assumption is Roll-Hansen, 1997

¹¹ Paul and Kimmelman, 1988; Palladino, 1993 and 1994; Harwood, 1997 and Wieland, 2006: this volume

¹² For one influential work among many other of this kind, see Vincenti, 1990.

¹³ Such a perspective was imported into the field of history of science as “History of science from below” by Cooter and Pumfrey, 1994. Regarding the relation of Mendelism and plant breeding, such an approach was pioneered by Paolo Palladino 1993, 1994.

embody”¹⁴. Early twentieth-century Mendelian geneticists’ and plant breeders’ experimental systems were part of the same world of combinatory relations, a world quite different from that of nineteenth-century breeders and hybridizers more familiar with notions of historical (atavism, regression) or mechanical (force) relations. Nevertheless, while Mendelian geneticists designed experimental systems that allowed the production of definite ratios of different forms that varied in relation to a few characters, plant breeders designed experimental systems that produced and explored a wide range of variation, featuring combinations between hundreds of traits. Rather than breaking this multiple variation down into simple elements, breeders’ experimental culture designed and monitored a wide genetic lottery. The gene was a unit in a Mendelian experimental culture, an “epistemic thing” that could be grasped by means of statistical regularities, but it remained of secondary importance, and did not become a primary object of knowledge and manipulation –an “epistemic thing”– in breeders’ experimental systems. I also situate such an un-Mendelian experimental system within early twentieth century’s plant breeding “technological paradigm,” a concept forged by historians and economists of technology to acknowledge the cognitive dimension in technological research¹⁵. In conclusion I show that the international plant breeders’ rights system established in 1961, in which the gene or the trait was not a relevant unit of appropriation, reflected this un-Mendelian experimental culture and technological paradigm at a profound level.

Breeders, agricultural scientists and the development of genetics in France

At the Fourth International conference on Genetics in Paris in 1911, more than 83% of the participants were breeders and agricultural or horticultural professionals and only 13% were academic biologists. Far from reflecting a passing pre-academic phase of French genetics, this situation persisted right up until the middle of the twentieth century¹⁶. In 1953, the International Union of Biological Sciences published an index of geneticists, featuring about 2000 scientists, 124 of whom were French. Although this list was not exhaustive, it is quite revealing, when one sees that among the French geneticists, 69% belonged to agricultural research and teaching institutions, whereas basic research institutions and universities

¹⁴ Rheinberger, 1997, p. 28.

¹⁵ Dosi, 1982 ; see also Vincenti’s view of engineering as knowledge: Vincenti, 1990, pp. 3-7

¹⁶ Fischer, 1990, p. 41.

accounted for only 23%. Moreover, no less than 28% of the French geneticists were based in French overseas colonies¹⁷.

Investigating the (slow) development of genetics in France therefore requires situating it in relation to agriculture and horticulture. Together with the university zoologist Lucien Cuénot, it was a plant breeder and seed trader, Philippe de Vilmorin (1872-1917), who contributed most to the introduction of Mendelism in France before 1914. De Vilmorin headed a seed company established in the eighteenth century. He was the grandson of Louis de Vilmorin (1816-1860), who invented the technique of pedigree selection (“sélection généalogique”) and the son of Henry de Vilmorin (1843-1899) whose hybrid wheat variety had fuelled the growth of the Company, which, by 1889, boasted no less than 400 employees. At the 3rd International Conference on Genetics held in London in 1906, Philippe de Vilmorin declared : “*When I came to this conference to hear Mendelian theories I was rather doubtful, but I have been so much with you, and have heard all that has been said (...), I am and I will ever be an apostle of the theory*”¹⁸. As a result he obtained that the next conference would be held in Paris in 1911, and launched Mendelian studies concerning several species that led him to collaborate with William Bateson¹⁹. **[here insert photo 1]**

In 1910, He established a “laboratory of botany and genetics” at the Company’s headquarters and selection station in Verrières, near Paris. This laboratory was the first ever explicitly designated “genetics” laboratory in France. Here, researchers turned not only cultivated plants (peas, wheat, rye, barley, beet, beans, potatoes...) into objects of Mendelian research, but also dogs (studies of the inheritance of the size of the tail and legs), boars (body color) and rats. Remarks such as “*rats are an excellent material for Mendelian studies*” and that potatoes were “*a very bad material for Mendelian crosses*” also indicate the shift from concerns of plant improvement to a more speculative research orientation and the wide-ranging adoption of Mendelian experimental strategies.²⁰ Headed by the horticultural engineer Auguste Meunissier (1876-1947), the laboratory welcomed foreign geneticists recommended by Bateson or Punnett, such as A. Hagedoorn and W. Backhouse. Together with Cuenot’s group in Nancy, Vilmorin’s laboratory was the main research center for Mendelian genetics in France, and published several Mendelian articles between 1910 and 1914²¹. **[Here insert photos 2 and 3]** Thanks to various Mendelian crosses, Meunissier and Vilmorin had by 1911

¹⁷ Union Internationale des Sciences Biologiques, *Index des généticiens*, Paris, 1953

¹⁸ 3rd International Conference on hybridization, p. 74

¹⁹ Gayon and Zallen, pp. 258-59.

²⁰ Meunissier 1918, p. 121 and 115.

²¹ The first of them being : P. de Vilmorin, “Recherches sur l’hérédité mendélienne.” *C.R.A.S.*, vol. 151 (1910), pp. 548-551

identified twenty characters in wheat whose inheritance could be accounted for by Mendelian “genetic factors.”²²

Before the 1911 conference, P. de Vilmorin undertook the task of convincing French biologists, and the agricultural and horticultural communities to work on Mendelian genetics.

He remained at first rather ecumenical and broad in his definition of genetics as,

*“encompassing all questions related to the physiology of inheritance, heredity, atavism, fluctuating variation, selection, natural or provoked mutation, inheritance of acquired characters, telegony, etc.”*²³ He presented a version of Mendelism linked to De Vries

mutationism, a theory much better accepted among French biologists than Mendelism thanks to the neo-Lamarckian mutationist synthesis proposed by Louis Blaringhem. Vilmorin framed

mutationism, and Mendelism as new approaches that could help to overcome the old debate

between neo-Lamarckism and neo-Darwinism, a debate depicted as sterile and “*closed in a vicious circle*”²⁴. But soon after, P. de Vilmorin began to oppose vigorously neolamarckism

and experimental transformism that dominated French biology.²⁵ At the 1911 conference, de

Vilmorin rejected the acclimatization theory in the case of wheat: “*if the climate has any evolutionary role, it is through the elimination of unfit plants, and not by conferring aptitudes,*

in other words, acclimatization, as a slowly acquired habit under the influence of external conditions, does not exist.”²⁶ In 1913, he and Meunissier claimed that “*we consider as proven*

[the position] that the external factors have no hereditary influence, that is to say that there exists no ‘inheritance of acquired characters’ as hypothesized by Lamarckism”²⁷.

P. de Vilmorin died while still young in 1917, but the Vilmorin Company continued to

support the development of genetics in France. In a context when French biologists ignored or

rejected the chromosome theory, Auguste Meunissier reported on the 1927 international

conference on Genetics as “*the crowning of the chromosome theory*”²⁸ and the company

developed cytological research, a domain that remained underdeveloped in French plant

biology between the wars.

Besides private horticulturalists and plant breeders, public institutions for agricultural research and higher education became major sites for the development of genetics in France.

At the end of the nineteenth century, agricultural sciences were already experiencing a

²² *IVe Conférence internationale de Génétique –Paris 1911. Comptes-rendus et rapport édités par Philippe de Vilmorin*, Masson, Paris, 1913, pp. 17 and 20

²³ Vilmorin, 1910, p. 12

²⁴ Vilmorin, 1910, p. 8

²⁵ On experimental transformism in plant biology and the influence of Gaston Bonnier, see Tirard, 2003.

²⁶ Vilmorin, 1913, p. 312

²⁷ Vilmorin et Meunissier 1913,p. 2

²⁸ Meunissier, 1928, p. 209.

biological turn, moving away from the domination of agricultural chemistry towards the affirmation of biological approaches, such as plant breeding and genetics, and also soil biology, microbiology, plant pathology, and economic entomology²⁹. In 1884, Emile Schribaux created a seed testing station (Station d'Essai des Semences), and in a new chapter on plant breeding written for the second edition of his textbook on "agricultural botany" in 1906, he presented the farmer as a type of mechanical engineer who operates on plants, described as "living machines", and harnesses the "force" of variation in the same ways the engineer harnesses mechanical forces³⁰. As the "force" metaphor indicates, Schribaux was not yet well-versed in Mendelism, but in a subsequent article, which appeared in 1908, he presented a much fuller version of Mendel's laws. At this time, Schribaux had started to teach some principles of Mendelian genetics in his course on plant breeding at the *Institut National de la Recherche Agronomique* in Paris, introducing this subject into the most highly reputed and most theoretically oriented of all the *Ecoles Nationales d'Agriculture* that were run by the Ministry of Agriculture.

In 1907, Louis Blaringhem was appointed lecturer in economic botany at the Faculty of Science of the Sorbonne, thanks to the sponsorship of SECOBRA, a brewers' association, and he too had integrated Mendelian genetics into his course on plant breeding by 1910.³¹ By this time, Félicien Bœuf (1874-1961), professor of botany at the *Ecole Coloniale d'Agriculture de Tunis* and head of Tunisia's principal plant breeding station had also introduced Mendel's laws into his teaching, and in the early 1920s, a chair of "Genetics, crop sciences, and applied botany" was created for Bœuf at this same school. Thus, the first chair of genetics ever created in the French higher education was created not in the metropolitan center of France, but in its colonial periphery, and in an agricultural institution.

This innovation was later followed by the creation of the following positions: a chair in genetics and horticultural breeding in 1935 for Auguste Meunissier at the *Ecole Nationale d'Horticulture* in Versailles; a chair of genetics in 1936 for F. Bœuf at the *Institut National Agronomique* in Paris; the appointment of Luc Alabouvette (one of Schribaux's students) at the chair of agriculture of the *Ecole Nationale d'Agriculture* in Montpellier; a training center on genetics in 1943 for F. Bœuf at the *Office de la Recherche Scientifique Coloniale* (the forerunner of today's *Institut de Recherche pour le Développement*, a research agency operating in less developed countries). Following the spread of the teaching of genetics at the

²⁹ Jas, 2001; Castonguay, 2005

³⁰ Schribaux and Nanot, 1906, p. 347

³¹ Blaringhem, 1913.

university level, several textbooks on plant breeding were published that constituted a collection of valuable (although still rare) presentations of classical genetics in France: Blaringhem's *Le perfectionnement des plantes* in 1913, Bœuf's *L'amélioration des plantes cultivées* in 1927, and his *Les bases scientifiques de l'amélioration des plantes* in 1936, and Coquidé's *Amélioration des plantes cultivées et du bétail* in 1920, among others. Although Bœuf depicted the chromosome theory as a mere hypothesis in 1927, by 1936, he was presenting it as "well founded"³². In a context where most French biologist were still skeptical about or indifferent to the chromosome theory, and where cytology was poorly developed, Bœuf's 1936 textbook represented –together with M. Caullery's 1935 book – one of the best presentations of the genetic mapping of Morgan's school, as well as the work of Emerson's maize-genetics school, Painter, Belling, etc³³. As for the rediscovery and dissemination of Mendel's laws in the 1900s, these "agricultural connections" constituted a major pathway for the wider reception of the chromosome theory in the interwar years in France.

Research laboratories and stations for genetics research also emerged in the context of the growth of agricultural research. The laboratory for "genetics and seed selection" was founded in 1918 in the *Institut Scientifique de Saïgon* (French Indochina) by the botanist Auguste Chevalier, a friend of P. de Vilmorin.³⁴ In the metropolis, a department for "phyto-genetics" was created in 1923 within the *Institut des Recherches Agronomiques* (IRA), a state agency for agricultural research established in 1920.³⁵ Nevertheless, this institute was placed under the authority of the Ministry of Agriculture (rather than the Ministry of Education) and was created in a context where the modernization of agriculture was not yet the high priority policy that it was to become after WW2. Thus, academic agricultural science's moves towards autonomy remained tentative and fragile, as is borne out by the closing of the IRA in 1934. The nucleus of plant breeders from the IRA nevertheless remained active, although now under the more direct authority of the administration, and soon came to form the core of the *Institut National de la Recherche Agronomique* (INRA) established in 1946. The number of scientists and engineers in plant genetics and plant breeding at INRA increased from 47 in 1946 to 68 in 1955³⁶.

This means that long before the first chair of genetics was created in a French university in 1946, several such chairs existed in agricultural institutions along with genetics

³² Bœuf, 1936, p. 169.

³³ Caullery, 1935.

³⁴ Bonneuil, 1997.

³⁵ Castonguay, 2005

³⁶ Bonneuil and Thomas, 2006.

research laboratories. It comes as no surprise then that, even at the Sorbonne in the late 1940s and 1950s, most of the students attending the course on genetics were agricultural engineers, and two-thirds of French geneticist registered by the International Union of Biological Sciences in 1953 belonged to agricultural research and teaching institutions.

Now that we have established the key role public and private agricultural institutions and networks played in the reception and development of genetics in France, we can address the question as to why the reception of Mendelism among plant breeding professionals did not have any significant effect in terms of the general pattern of the late and slow development of modern genetics in France as a whole. A first answer can be found in institutional and socio-economic factors. It is only after 1944 that domestic agriculture became a policy target to be “modernized”, so as to obtain mass-produced food as well as freeing up the manpower needed for industry and the service sectors. Before WW2 the issue of agriculture as a policy problem was framed within a “stability frame”: the small farmer was seen as stabilizing the regime of the third Republic in response to the political dangers of the urban working class³⁷. Prior to 1944, the government’s efforts to “modernize” the national agriculture were modest, which explains the limited investments in agricultural research before 1945 (in sharp contrast to its steady expansion in the USA at the same time). Moreover, agricultural higher education (under the direction of the Ministry of Agriculture) and the University (Ministry of Education) were poorly interconnected in the first half of the twentieth century, impeding much cross-fertilization between academic biology and agricultural research.³⁸

Despite the interest that the French agricultural institutions showed in Mendelism from the start, the slow development and institutional autonomization of agricultural research as well as its separation from the university system prevented the growth of a boundary community of “scientific” plant breeders well established in the genetics international community, that could promote the Mendelian theory of heredity as the emblem of their institutional independence. Such a boundary community flourished in the USA at the USDA and at the new land-grant universities, in Germany at E. Baur’s Institute for Plant Breeding in Berlin, and in the UK at the Agricultural College at Cambridge University³⁹. These boundary communities asserted their identity of “scientific breeders” by praising the revolutionary role for science in agriculture, the revolutionary role of Mendel’s laws of inheritance in plant breeding, and by spending a considerable amount of experimental effort to align breeding

³⁷ Muller, 2000 ; Gervais et al., 1976.

³⁸ Castonguay, 2005; Gayon and Burian, 2000.

³⁹ For similar arguments linking the reception of genetics and agricultural-institutional factors in the UK, USA and Germany, see Kevles, 1980; Palladino, 1994; Harwood, 1997 and 2005.

concepts and practices with Mendelian and Morganian concepts and practices. But such an institutional niche was almost unoccupied in France, and the next section explores the consequences of this situation for the ways in which plant breeders used and assessed Mendelism.

Was Mendelism useful for plant breeding?

While it is clear that agricultural higher education and research provided a major niche for genetics in France prior to 1945, we can ask whether these institutions were a major ground for Mendelian research. What did really change in the experimental practices of these researchers and to what extent did private and public plant breeders apply or develop Mendelian strategies? Let us first explore this issue in the case of Philippe de Vilmorin. As I have explained, he did much to introduce Mendelism into France, and he and Meunissier clearly opposed neo-Lamarckism on a Mendelian basis. But did he modify his breeding strategies along Mendelian principles? Jean Gayon and Doris Zallen have proposed a negative response to this question. They argue that, in contrast to what they consider as a Mendelian approach, “*hybridization was not for [the Vilmorins] a means of fixing a character, but only a source of variation. They held to this view even when the paradigm began to be abandoned*” and they conclude that “*althought not ignoring Mendelism, the Vilmorin Company did not really succeed in integrating the Mendelian paradigm before 1914.*”⁴⁰

Gayon and Zallen’s thesis needs to be refined and reformulated. First, a deeper examination prevents us from claiming that P. de Vilmorin and A. Meunissier did not derive and promote any new and clearer practical breeding principles from Mendelism. From the Mendel’s first law they derived the idea that breeders should not start spotting and selecting interesting plants for desired traits at the first generation F1 of crossing (when they will be fully heterozygous) but only after the second generation (F2) of inter-breeding. They also found in Mendelism the idea that it is possible to fix a pure line for certain characters within two (if desired traits are recessive) or three generations (if one desired trait is dominant, they suggested inbreeding F2 plants so as to detect – through homogeneity of their progeny– the fraction of these individuals that were homozygous). In principle, this would make breeders more efficient, transporting them from the weight and inertia of history (force, atavism, regression...) into the timeless space of combinatory calculations: “*For any given character, a pure race is not, as previously believed, the one that shows a long lineage of ancestors bearing this character; it is simply a race in which the character is produced by the*

⁴⁰ Gayon and Zallen, qotes resp. p. 260 and p. 259-60.

union of similar gametes” claimed Meunissier, a point he had taken from Mendelians like Bateson, Punnett or Davenport⁴¹. The breeding strategy for *Hybride des Alliés* – a very successful variety put on the market in 1917 which development started ten years earlier at Verrières – illustrated this emancipation from history. Knowing that the villosity of the glumes – a trait rejected by millers – was recessive, Meunissier and Vilmorin did not hesitate to use a variety, bearing this unwanted trait but interesting for others traits, as a parental material for the *Hybride des Alliés*: “*Under the influence of notions like ‘atavism’ and without a knowledge of the independence of characters, nobody would have dared to use such a variety as a parent! We did dare to do so because we knew that villosity, once eliminated, would never appear again.*”⁴²

Second, Gayon and Zallen’s implicit norm that Mendelism in breeding should mean using hybridization primarily as a means of fixing a character, and prioritizing hybridization over fixation by inbreeding, may be a misleading view. This view derives from considering the hybrid corn’s success story as the model of a truly Mendelian breeding strategy. In the case of F1 hybrids of pure (homozygous) lines developed by Shull and East after 1909 in the USA, hybridization is indeed a means of obtaining a certain phenotype at an industrial scale in accordance with the first law of Mendel. F1 hybrid plants from homozygous parent lines are – not fixed but – in effect identical and predictable: they were “heterozygous clones” as J.-P. Berlan characterized them⁴³. It would nevertheless be misleading to consider hybrid corn as the model for the correct use of Mendelism in plant breeding. Hybrid corn was commercialized in the USA only starting in 1935, so it would be anachronistic to assess early twentieth-century breeding strategies against this model.⁴⁴

Furthermore, far from being a planned and predictable process guided by Mendelian theory, the strategy originally adopted in hybrid corn breeding programs was to perform all possible crossings in a group of inbred lines and then make an evaluation of the single hybrids obtained, followed by the selection of the most promising ones. This constitutes a rather empirical and routine-orientated way of screening valuable hybrids. It is only after Sprague and Tatum’s 1942 article on the combining ability that tools to help predict *ex ante* the value

⁴¹ Meunissier 1910, p. 13; Vilmorin and Meunissier 1913, p. 6

⁴² Meunissier 1918, p. 134.

⁴³ Berlan, 2005, p. 5.

⁴⁴ Moreover, several scholars have shown that hybrid corn success was helped by several historical and biological contingencies that have little to do with Mendel’s laws, including industry’s quest for seeds that farmers have to buy every year, and the existence of an inbreeding depression in corn that excluded pure lines as target varietal types, high multiplication rate (more than 500 kg harvested today for one kg corn sown, ten times higher than in wheat) that made hybrids economically viable, high prioritization of hybrid breeding option in US public research system since the 1920s, and limited knowledge concerning population and quantitative genetics at that time that could have guided other options (population breeding). See Berlan, 1987; Kloppenburg, 1988; Fitzgerald, 1990.

of inbred lines as a parent of a hybrid progressively became available⁴⁵. So from a “history from above” perspective and for historians really willing to tell the story of plant breeding along the plot of “science replacing empiricism”, mid twentieth century quantitative genetics constitutes a better “hero” than early twentieth-century Mendelism.

Rather than assaying plant breeding research against an idealized view of what should have been a scientific/Mendelian breeding approach, let us try instead to approach the question from the perspective of plant breeders. On one hand, in textbooks introductions and public lectures, Vilmorin, Meunissier, Blaringhem, Bœuf, Schribaux, Coquidé and other plant breeders often depicted the new science of genetics as a revolutionary force moving plant breeding from empiricism to a genuinely scientific endeavor, thereby establishing themselves as experts in the optimization of “living machines”. “*The obtainment of new types is [thanks to Mendel’s laws] no longer left to chance*” boasted de Vilmorin and Meunissier in 1913,⁴⁶ and Schribaux likewise proclaimed the advent of “made to order” varieties⁴⁷. But on the other hand, these same plant breeders soon came to doubt the revolutionary importance of Mendelism for the progress of plant breeding.

The first sign of discontent with Mendelism was related to Johannsen’s concept of the fixity of pure lines and his thesis that further selection in a pure line was useless⁴⁸. Breeders like P. de Vilmorin and F. Bœuf promoted this view at the 1911 international conference, using this line of argument to combat neo-Lamarckism. Although some breeders, including Bœuf, did not exclude the heredity of acquired characters as definitively as P. de Vilmorin, most annual crops breeders considered pragmatically considered that this option for plant improvement “*is so slow that the breeder should not rely on acquired characters (...) to improve varieties*”⁴⁹ or that “*the variations caused by external factors [are] considered for the moment as non-hereditary, at least in the crops we are interested in.*”⁵⁰ Johannsen’s pure line concept also helped disqualify past breeders’ methods of continuous selection (characterized as unscientific) as well as farmers’ mass selection practices. Defining true scientific wheat breeding as resting upon artificial hybridization and then inbreeding to obtain “pure lines” was a way to professionalize and distinguish plant breeding from farming, as well as a way to

⁴⁵ Sprague and Tatum, 1942

⁴⁶ Vilmorin and Meunissier 1913, p. 5.

⁴⁷ Schribaux, 1908, p. 614

⁴⁸ Johannsen, 1903

⁴⁹ Schribaux, 1906, pp. 353-54

⁵⁰ Bormans 1927, p. 38

expand the seed business⁵¹. In 1925, a decree for the wheat seed trade drafted by E. Schribaux limited the use of the term “selection” exclusively to the seeds obtained from varieties fixed by inbreeding: breeders who used other breeding strategies such as mass selection were not allowed to claim that their variety had been “selected”⁵².

Nevertheless, on the basis of their familiarity with and thorough observation of large numbers of plants from many inbred pure line varieties, breeders were not convinced of their absolute fixity. “Pure lines” were seen as being pure, homozygous, for only a few traits, and at each generation new “sports” were observed among the large number of individuals that the breeders obtained in their breeding plots. A simple calculation proposed by a plant breeder helps understand this: if one considers 10 loci and two alleles for each locus, the frequency of getting a homozygous individual for ten given alleles is only about 10^{-6} ($= (1/4)^{10}$)⁵³. If the ten desired alleles are recessive, with enough crosses and descendants (over one million) under study, one gets a “pure” homozygous line for these 10 traits already in F2. But if several or most of the desired traits are dominant, then –unless one had a tester line bearing the 10 recessive traits and did millions of artificial crosses between F2 individuals and this tester (while this was doable in *Drosophila*, it was out of reach with cereals) – one could not isolate the desired homozygous line even after 10 years of pedigree selection (and meanwhile the populations composing the lines might well be subjected not only to a small rate of mutation and to chromosomal translocation events). This explains why French plant breeders – including the Vilmorins, like most of their German and English colleagues⁵⁴, even if they occasionally waxed lyrical about Mendelism and the pure line concept, went on selecting within “pure line” commercial varieties, even though this did not agree with Johannsen’s precepts.

Plant breeders had a second reason to doubt the importance of Mendelism, which had to do with the alleged predictability of the results from crosses. Mendelian enthusiasts emphasized that plant breeding was, thanks to Mendel’s laws abandoning empiricism in favor of planned design as in chemical synthesis. Thus, stacking genes would be as easy for plant breeders as assembling molecules was for the chemist. This impression of operating within a finite, known and predictable combinatorial territory was reinforced by the idea, popularized by Svalöf geneticists, by Johannsen and also in France by Louis Blaringhem and Félicien

⁵¹ For similar strategies used by plant breeders to disqualify other breeding practices in the UK and Germany see Harwood 1997, Rangnekar 2000 and Palladino 1993.

⁵² Décret du 26 mars 1925 (*Journal Officiel*, 29 mars 1925, 3189).

⁵³ Bormans, 1927, p. 40.

⁵⁴ Wieland 2006; Palladino, 1993, p. 316-7.

Bœuf, that all possible combinations could be put in a table by the geneticist. Having obtained all the possible combinations, the scientific breeder would know that his work was finished and that he just had to screen the best combination.

Such a table was obtainable if one considered only a small number of characters such as the smoothness or wrinkles of Mendel's celebrated peas, but was indeed impossible for cereal breeding where hundreds of genes were involved in numerous agronomic (often quantitative) characters. So even if breeders sometimes talked the talk of "planned" and "made to order" breeding (stories of wheat varieties harmoniously combining traits of their two parents are numerous⁵⁵), they designed their experimental space so as to let a wide range of variations emerge, leaving space for new combinations, new "sports". Individuals displaying characters beyond the range of their parents were named "transgressive hybrids." In principle, these were accounted for in terms of several Mendelian traits, but in practice, several agriculturally significant characters (precocity, yield, strength, resistance to the cold...) were dependent on dozens of genes: it was impossible to conduct any Mendelian analysis or to identify the exact number of genes involved. This left the breeders with the impression that simple Mendelian formulas were useless to them. The fact that wheat was a hexaploid plant (up to 3 interacting loci for a single monogenic character instead of one as in diploids!) complicated even further any Mendelian study. In 1906, Schribaux expressed the Mendelian hope that the complexity of the genetic lottery would be disentangled by a careful study of hereditary traits: *"It was up until now impossible to predict the characters that would appear in a hybrid (...) In the near future – as promised by the recent experiments from Mendel, Tschermak, de Vries and Correns – we will certainly know the general laws behind such phenomena."*⁵⁶ But twenty years later, instead of "saving Mendel" with ad hoc hypotheses involving a growing number of Mendelian factors like some plant geneticists who followed Bateson, Schribaux overtly abandoned the Mendelian dream. *"These transgressive variations, in particular the most interesting, escape any theoretical prediction (...) Despite much real progress in our knowledge, hybridization remains a lottery, a game of hazard between man and nature. To win at the lottery, or at least to increase the chances of winning, the best way is to buy a lot of tickets. Similarly in cereal breeding, the best way is to operate a great number of crosses and in each cross, to study a large number of types before choosing"*⁵⁷.

⁵⁵ Schribaux 1908; Maylin 1926, p. 15

⁵⁶ Schribaux and Nanot, 1906, p. 356

⁵⁷ Schribaux preface for Maylin, 1926, p. IX-X. This quote reminds us of a similar judgement made by Karl Fruwirth, a German public breeder who belonged to the sceptics with respect to the importance of Mendelism for plant breeding: "Breeding is still an art even today, for despite an education in the techniques and a familiarity

Reflecting on this “lottery” in a less pessimistic way than Schribaux, Paul Bormans, a plant geneticist working for a farmers’ cooperative wrote: “*it is precisely the infinite number of combinations that one gets with only a few hereditary characters that allows us these possibilities [to obtain ever higher yields lines] and a fertile ground for research where valuable combinations are far from being exhausted*”⁵⁸.

The contrasting experimental systems of Mendelism and plant breeding

Plant breeders did not limit their interests to Mendelian studies of a few well-defined traits, but instead, whether in the fatalistic terms of Schribaux, or in line with the more promethean vision of Bormans, they stressed the key importance of large number. They emphasized the multiplicity of factors involved in the quantitative characters that determined the agronomic value of a variety, the need for a large number of crosses, and the necessity of keeping a large number of plants under the experimenter’s gaze so that rare individuals could be spotted and assessed. A deeper understanding of the relationship between genetics and plant breeding needs, therefore, to escape the standard narrative of (Mendelian) *theory* reshaping (breeding) *practice*, or its failure to do so, and explore instead both the experimental practices and cognitive mindsets of both Mendelians and French plant breeders.

This is where the notions of “experimental systems” and “epistemic things” become extremely useful. In Hans-Jörg Rheinberger’s framework for understanding research dynamics, “*the experimental conditions ‘contain’ the scientific objects in the double sense of the expression: they embed them, and through that very embracement, they restrict and constrain them*”⁵⁹. This framework helps us to understand how the different purposes and different experimental systems of Mendelian genetics and plant breeding generated different scientific objects, different units of analysis and different modes of manipulation. In contrast to the classical Mendelian experimental system and strategy, plant breeders designed an experimental space that was populated by millions of individuals and hundreds of traits which they could study and upon which they could intervene. For breeders, the aim of experimenting was not to account for ratios of individuals based on hypotheses concerning a few Mendelian traits (as in Bateson’s Mendelian experimental program). Instead what these breeders aimed

with the laws of genetics, one still requires a breeder’s eye in order to be able to spot valuable plants during selection and varietal testing”, quoted by Harwood, 2005, p. 166.

⁵⁸ Bormans, 1927, p. 41.

⁵⁹ Rheinberger, 1997, p. 29.

to do was to harness a vast genetic lottery and then sort it out, thereby assessing hundreds of potentially interesting new combinations.

Designing an experimental system that would handle this vast genetic lottery implied five key elements. First of all gathering the greatest genetic diversity for the greatest number of characters in one space. By 1911, the Vilmorin Company possessed one of the largest wheat collections in Europe, containing some 1200 varieties, accumulated through voyages of exploration, participation in international fairs, and a dense network of correspondents who gathered and dispatched landraces (ie, those varieties traditionally planted in a region over many generations).

Gathering a huge diversity of varieties was not enough in itself, however, as this collection of genetic diversity could produce novelties only when properly “shaken up”. Thus, the knowledge and techniques needed to optimize the intermixing of genomes and the continuous production of new combinations constitute a second key step. Just as the experimental system of Morgan’s group, the drosophila mutations breeders, was designed to produce hundreds of new forms from single mutations that could be isolated (and their loci “mapped”), the plant breeders experimental system was designed to produce hundreds of new forms by continuous flows and infinite combinations of alleles. It is for this reason that some breeders studied the biology of cereals reproduction as a way to improve the rate of success of artificial crosses, and that the better equipped among them conducted artificial crosses on a large scale.

Improvements in the efficiency of the methods for screening such large and intermixed populations represent a third key element of the breeders’ experimental culture. Efficient breeding meant improving the means for identifying potentially interesting individual plants among large populations, a task similar to finding the proverbial needle in the haystack. For this job, the “art” or “good eye” of the breeder – consistently identified by breeders as being crucial to their practice – was the key element. The skill was initially developed by wandering through the selection plots and spotting valuable plants,⁶⁰ and this traditional practice was maintained although simultaneously being redefined in terms of new tools and methods that emerged in the late nineteenth century. New tools became available, along with new ways of organizing the work more systematically; performing large scale biometrical analyses, the systematic inscription of observations in “breeding notebooks”, and the refinement of the

⁶⁰ One can see the “good eye” of the breeder, ‘in action’ while wandering in a plot, in a film on the Vilmorin Company: Henry L. de Vilmorin, *Obtention et sélection des blés*, Gaumont (série enseignement, recueil agriculture), 1923.

taxonomical gaze capable of subdividing a population of a variety into many smaller and purer varieties, a technique pioneered at the Svalöf station in Sweden. A history of these micro-techniques remains to be written, but my guess is that the new alignments of tacit knowledge, discipline of the breeder's expert body, and the use of inscription and description devices might have been as crucial to the success of plant breeding in the late nineteenth and early twentieth centuries as the introduction of Mendel's laws.⁶¹

Fourth, once candidate plants (numbering in their hundreds) had been spotted as potentially interesting, they were subjected to inbreeding (pedigree selection) and became fairly pure lines. The "purity" of these lines was not checked through a direct estimation of their homozygosity but rather at the phenotypic level on the basis of taxonomical, biometrical and agronomic data. For breeders, a satisfying pure line was an entity that was stable and uniform enough to produce robust results in properly conducted agronomic experiments and convince farmers to buy "improved seeds".

Assessing and comparing hundreds of lines to select a few of them as commercial products was the final key element of the breeders' experimental system. This belonged to the long tradition of the "agricultural assay". Since the late nineteenth century, this activity had been improved through a systematic homogenization of nature and of human operations, which went hand in hand with new forms of discipline demanded of the workforce (leveling soil disparities in experimental plots, standardizing germination rates of seeds, sowing at a standard spacing, weeding, artificial inoculation of strains of plant pathogens, etc.). Improvements were also obtained through an increased use of the statistical methods and methodologies of experimentation advanced by Ronald A. Fisher and Theodor Roemer in the interwar years (repetition, analysis of variance and probable error, tests of significance, etc.). Far removed from Mendel's own monastic garden, this fifth element of breeders' experimental culture was a decisive force in producing robust data on the agronomic value of various varieties, allowing researchers to offer more consistent advice to farmers and establish trust in a growing seed market.

In interwar France, as in many other countries, the function of screening and comparing existing varieties fell to publicly funded research stations. Whereas the public plant breeding stations of the late nineteenth century focused on assessing purity and identity to protect against fraud, Schribaux's successors at the *Institut de Recherches Agronomique*, like Luc Alabouvette, Charles Crépin and Jean Bustarret, turned to the task of assessing the

⁶¹ For a detailed study on how register inscription practices constrained Nilsson-Ehle's mode of thinking at Svalöf, see Müller-Wille, 2005.

“agronomic and technological value” of varieties (yield, resistance to cold and rusting, strength, etc.). They headed an expanding network of agricultural stations, and collaborated on technical and regulatory issues with private breeders under the aegis of the *Association Internationale des Sélectionneurs de Grandes Cultures* (Major Crops Breeders’ International Association) founded in 1927, and headed by Schribaux and Meunisser. They established a new gold standard in the assessment of varieties in France; the multi-site, replicated plot field trial. On the basis of their data, they sought to draw up lists of recommended and forbidden varieties for each region. Bœuf, Alabouvette, Crépin and Bustarret dreamed of a geneticist state that would consider its task to be the elevation of the genetic value of seeds sown in farmers’ fields.

With the advent of new agricultural and seed *dirigisme* during and after the Second World War, this dream of a new kind of biopower became reality: all varieties had to pass a thorough battery of analyses and field trials before being put on the market. Furthermore, the advisory committee (the “*Comité Technique Permanent de la Sélection*”, established in 1942) that set the norms for these tests was dominated by Bœuf, Alabouvette, Crépin and Bustarret. Being in command of the flow of “genetic progress” injected into the farms, they decreed the elimination of most landraces and older commercial lines from the seed market, to the great satisfaction of advanced private breeders who co-managed the new regulatory system. Furthermore, when the *Institut National de la Recherche Agronomique* was established in 1946 as a powerful research agency for agricultural research, it was plant breeders, rather than other groups with stronger academic links to the University, the CNRS or the Pasteur Institute, who were chosen to lead it, with Crépin serving as the first executive director⁶².

Given the different features of breeders’ experimental system, it is not surprising that they did not see the gene as a fundamental unit. Jean Bustarret, head of the department of plant breeding and genetics, and later executive officer at the INRA, played a leading role in organizing agricultural research as well as the internal seed market in France. Like his teacher, E. Schribaux, and like all French public and private plant breeders of his time, he did not view the variety primarily in Mendelian terms. Uniformity was much more relevant for him than homozygosity. He categorized varietal forms into two groups: the population varieties (heterogeneous and unstable) and the uniform and stable varieties (whether pure lines from inbreeding, clones from asexual multiplication, or heterozygous F1 hybrids). Rather than an issue of combination of Mendelian genetic traits, purity was an experimental

⁶² On the rise of state plant breeders as a social group, the creation of INRA and the construction of the varieties assessment and regulatory system, see Bonneuil and Thomas, 2006.

predicate – the variety was seen as being primarily a stable parameter that could be fixed and then manipulated within the experimental system of the network of experimental stations.

The uniform and stable variety was also an industrial predicate – being regarded as a predictable and standardized factor in an industrialized form of agriculture and food production system. In the context of Bustarret’s experimental culture, his industrial vision of agriculture, and the mission he assigned to the state of managing genetic progress, Mendelian traits or “genes” appeared neither as the relevant scientific unit nor as the right target for intervention and regulation. He viewed the variety, not the gene, as the “natural unit” and considered that *“A gene does not directly determine the appearance of a given character, but only a certain cellular function that eventually results in the appearance of the character. One says currently that a gene ‘commands’ one character (...) but in fact the action of any given gene has an impact on the whole physiology of the plant.”*⁶³

Conclusion: an un-Mendelian system of property rights for an un-Mendelian experimental culture

This stance, expressed as late as 1944 sharply contrasts with the discourse of “gene action”, depicted by Evelyn Fox-Keller (2000) as having invaded biological discourse in the twentieth century. Was Bustarret’s un-Mendelian view of the plant variety just a symptom of a physiologically oriented, specifically French, approach to heredity? Was it the expression of the national idiosyncrasy of a French plant-breeding community that had developed too slowly to produce niches for academic plant breeders –as in Cambridge or in E. Baur’s plant breeding institute in Berlin– well integrated into the international academic genetics community? Paolo Palladino, Jonathan Harwood and Thomas Wieland’s work reveals that many German and British plant breeders also assessed rather critically the importance of Mendelism in plant breeding.⁶⁴ A recent study of the Swedish plant breeder and geneticist Nillson-Ehle, traditionally depicted as a hero of the integration of Mendelism in plant breeding, hints towards a similar conclusion. Staffan Müller-Wille provides indeed a very fine analysis of the gap between a Mendelian way of thinking and the particular way of handling and describing strains as “epistemic things” at the station of Svalöf, which he calls the “taxonomic gaze”.⁶⁵

I would therefore argue that Bustarret’s view, even if erased from top-down Mendel-centered histories of plant genetics, was shared by many breeders up until the middle of the twentieth century because their experimental culture, even if it had adopted its combinatory gaze, was profoundly

⁶³ Bustarret, 1944, p. 342; A detailed analysis of Bustarret’s vision of the variety is provided in Bonneuil and Thomas, 2006.

⁶⁴ Harwood, 1997, 2005 ; Palladino 1993, 1994; Wieland, 2004

⁶⁵ Müller-Wille, 2005.

different from a Mendelian one. The gene was the essential unit in this Mendelian experimental culture, although not a material unit but a symbolic entity that could be grasped by statistic regularities in proportions. Thus, genes were also units in Morgan's and Emerson's schools of genetic mapping, as they could measure their relative position on the chromosome being, and genes became a molecular reality with the advent of molecular biology. But, until the 1970's, the gene remained of secondary importance, rather than primary object of knowledge and manipulation, in breeders' experimental culture. Striking evidence of this is provided by the small place given to repeated backcrossing among the breeders' strategies. Before the 1960s, almost no wheat breeders in the world used repeated backcrossing as a strategy to try to add one gene (and not much more) from one variety to another variety, even with the identification of genes responsible for dwarfism or resistance to rusting. Most of them knew the importance of such repeated backcrossing in Morgan's school for constructing tester lines, but they considered this strategy less valuable for them than the broader intermixing of genomes that constituted their standard experimental breeding practice.⁶⁶

Breeders' indifference to the gene as a unit is also evident in the kind of international system of intellectual property they put into place. A Treaty establishing the International Union for the Protection of New Varieties of Plants (UPOV) was signed in Paris in 1961 by Belgium, the Federal Republic of Germany, France, Italy and the Netherlands, which were soon followed by Denmark, Sweden and the United Kingdom (about 60 states are parties of the UPOV today). Under the supervision of Jean Bustarret, who chaired the international technical negotiations towards the treaty between 1957 and 1961, this treaty took into account the specificity of plant breeding experimental culture and the innovation process⁶⁷.

First, the treaty considered that it was possible to create varieties, considered as new technological artifacts, using common techniques (such as artificial crossing and inbreeding) and hence considered it necessary to grant the inventors rights over such varieties. This would have been impossible under the regular patent system, considering the lack of "inventive activity" in the process. Breeders rejected the idea of patenting breeding techniques or requiring the publication of a full description of the process of invention, as was required for getting a patent, because they considered that the techniques were common to all breeders and that their description was insufficient to specify their inventions. Bustarret commented that "*the laws of genetics show us that it is highly unlikely that two breeders making the same cross will obtain the same variety*"⁶⁸. Breeders sought to protect not only varieties obtained by artifice but also

⁶⁶ A. Gallais, personal communication.

⁶⁷ For an analysis of the UPOV, see Joly and Ducos, 1993; Rangnekar, 2000; Hermitte, 2004.

⁶⁸ Bustarret, 1961, p. 188.

those resulting from “natural” processes, such as accidental cross-fertilization or spontaneous mutation in breeders’ plots that were captured by the breeders’ experimental system. Protecting “varieties” as distinctive products –with much negotiation between breeders and countries concerning the level of uniformity and distinctiveness required for protection – rather than as inventive processes as in the standard patent systems, hence constituted a recognition of the role played by chance and tacit skills in breeding. A new valuable variety was seen as the product of an interaction between the genetic resources to hand, the breeding methods employed, chance, and the skill of the breeder. This choice reflected an agreement among breeders about the nature of their work of innovation.

The second important feature of plant breeders’ rights under UPOV, is that it granted protection to varieties, not to genes or traits, and that it made it gave the breeder free use of a variety (independently of the holder of the rights) as parental material from which to develop a new variety. This meant that all the genes in any protected variety were freely accessible to all breeders. The intellectual property rights did not concern any specific new functionality improved by one gene, but only the variety as a balanced combination of characters, as a physiological or agricultural whole, very much in accordance with Bustarret’s view. In principle, a breeder could “mine” an interesting major gene from another variety and introduce it into one of his own varieties though repeated backcrossing. In practice, however, this strategy was very seldom adopted, since breeders expected to obtain a faster rate of genetic progress from the multiplicity of forms produced by the first crossing. Rather than loosing time in trying to stack genes one by one, breeders preferred to produce millions of combinations featuring hundreds of different traits and screen within the resulting diversity. So, once again, the breeders’ system of intellectual property rights reflected their experimental culture and technological paradigm at a profound level.

Even sixty to seventy years after the rediscovery of Mendel’s laws, the Mendelian trait – the gene – was neither an experimental unit of manipulation nor a unit of regulation and appropriation for plant breeders’. The UPOV operated according to an un-Mendelian regime designed for an un-Mendelian experimental system and technological paradigm. It is only in the last 25 years, with the synergic advent of genetic engineering and the possibility of patenting genes, that this coherent system has become destabilized following the emergence of genes as the dominant units of manipulation and appropriation within new experimental systems appropriate to the epistemic cultures of molecular biology and biotechnology.

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