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The plant breeding industry after pure line theory: Lessons from the National Institute of Agricultural Botany

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ABSTRACT

In the early twentieth century, Wilhelm Johannsen proposed his pure line theory and the genotype/phenotype distinction, work that is prized as one of the most important founding contributions to genetics and Mendelian plant breeding. Most historians have already concluded that pure line theory did not change breeding practices directly. Instead, breeding became more orderly as a consequence of pure line theory, which structured breeding programmes and eliminated external heritable influences. This incremental change then explains how and why the large multi-national seed companies that we know today were created; pure lines invited standardisation and economies of scale that the latter were designed to exploit. Rather than focus on breeding practice, this paper examines the plant varietal market itself. It focusses upon work conducted by the National Institute of Agricultural Botany (NIAB) during the interwar years, and in doing so demonstrates that, on the contrary, the pure line was actually only partially accepted by the industry. Moreover, claims that contradicted the logic of the pure line were not merely tolerated by the agricultural geneticists affiliated with NIAB, but were acknowledged and legitimised by them. The history of how and why the plant breeding industry was transformed remains to be written.

1. Johannsen's beans: Revisiting a classic tale of pure lines and applied science

Wilhelm Johannsen (1857–1927) was a Danish botanist who has come to be recognised as one of the most significant early Mendelians, one whose work had wide ranging implications throughout biology.[1] In Johannsen's now classic 'pure line' experiments, first published in 1903, he looked to show that there were two types of variation. The first were the kind of stark variations that exist between varieties and which are also displayed by mutants. These variations are heritable. The second were due to some change in the plant's environment and, significantly, were not heritable. To demonstrate this, Johannsen took some plants from what was a well-known—and presumed stable—variety of bean. Single plants were selected, within which there was the usual amount of variation for the character that interested him, in this instance seed size. Some plants had larger seeds than others, some smaller and so on. Single seeds from each plant were then grown on, and the resulting plants self-fertilized over a number of generations. Johannsen found that seeds from the larger producing plants tended to remain larger. This led him to think that the supposedly stable variety he was working with was actually made up of several different lines. Here then was evidence of his first kind of variation. Johannsen now turned to the seeds of each of these 'pure lines' as he called them. Each had a constant mean seed size, some of which you can find in Fig. 1, a table of Johannsen's results taken from the textbook upon which the present explanation is based. In the far left column can be found the various seed sizes that all plants continued to produce, from 70 centigrams

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Abbreviations: NIAB, National Institute of Agricultural Botany; PBI, Plant Breeding Institute.

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[1] For an account that brings out the position of Johannsen's work in the history of evolutionary theory, see Gayon (1998, pp. 260–271).

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to 20 centigrams. It was these variations within pure lines that Johannsen now wanted to prove formed a second type of variation, one that was not heritable. On the pre-Johannsenian view, selecting the larger and smaller seeds from pure lines—as he then did—should yield plants that continued to increase or decrease in size accordingly. Famously, this was not what he found. Rather, if you took the very largest seeds found in pure line number II (see Fig. 1), those of 70 centigrams, and grew them on, you produced plants with a smaller average seed size, of 55.5 centigrams, closer to the pure line mean. Similarly, if you took the smallest seeds from pure line number 18, a mere 20 centigrams, you ended up producing plants with an average seed size of 41, again much closer to its pure line mean, and crucially, still distinct from the means of the other pure lines. It was this persuasive evidence for there being two types of variation, one internal to the plant and the other external, and his eventual formulation of these as genotype and phenotype, that helped make Johannsen an international celebrity. It is work that has been considered transformative for the plant breeding industry.[2]

Popular histories of breeding and genetics remain largely linear accounts of theoretical progress and technical refinement from the rediscovery of Mendel onwards, within which Johannsen features as important for founding and clarifying core principles.[3] Historians of science have already done much to revise this otherwise attractive, simple and cumulative story.[4] Nevertheless, these two schools—traditional and revisionist—share a common and important feature. In virtually all existing accounts, the pure line concept and Wilhelm Johannsen's distinction between genotype and phenotype are held in peculiarly high regard. While some historians have already emphasised that professional plant breeders were *initially* sceptical towards the pure line during its early reception, the long term implications of Johannsen's contributions have not been doubted.[5] It is not the aim of this paper to question the value of Johannsen's theoretical achievements within the history of genetics.[6] Nor does it seek to undermine the significance of the pure line concept as a discipline building tool for geneticists.[7] Rather it has two complementary aims. Firstly, to situate Johannsen and his theories in what might be called the 'working world' of agricultural botany, replete with seed testers, farmers, and traditions all of its own.[8] This contextualisation can be achieved most persuasively with the aid of Fig. 2. Here Johannsen sits at the centre of a group of conference attendees, the majority of them agricultural leading lights from around the world, and all in Cambridge for the 1924 Fourth International Seed Testing Congress, hosted by the National Institute of Agricultural Botany (NIAB).[9] Seeing Johannsen within this photograph helps to emphasise the distance between his research programme and the global agricultural industry at large. At the same time this image also thereby helps to achieve a second aim. The distance between Johannsen's research and the agricultural industry at large can also be rendered historiographically. At present it is not known if, how, or why certain genetic principles came to first unmake and then reconstitute the global plant breeding industry, though a great deal of assumption leans in this direction. This paper constitutes an effort to expose this problem (which on a quick reading of the existing historiography, might not be thought to exist) while laying the groundwork for its solution.

Historians of science concerned with plant breeding and genetics have largely focussed upon particular geneticists and plant breeders while exploring the agricultural context as an important location for their work.[10] This historiography is diverse, complex, and currently experiencing a period of intense interest. However, there are still important parts of this picture that remain largely unexplored, the most conspicuous being the history of the plant breeding industry in the twentieth century. An important factor that has helped obscure this industry has been a dearth of easily recognised and collated primary source materials, a problem besetting investigations of twentieth-century industry more generally.[11] The closest that existing accounts typically get to discussing the industrial implications of genetics has been their assessment of purported changes in breeding practice, often in particular plant breeding stations and breeding houses.[12] As explained above, the majority of historians have already rejected the hypothesis that pure line theory led to direct changes in breeding practice. However, many of these same accounts subsequently reflect upon the changes in the plant breeding industry that they know to have taken place within the twentieth century (expansion of the varietal market, contraction of the number of professional breeding establishments, consolidation around a small number of very large multi-national corporations, changes in global intellectual property regimes, etc.) finding room for Johannsen's pure line theory as an important causal factor. There is therefore a gap between the early reception and implications of pure line theory within breeding practice, and the changes that may or may not have actually taken place in that industry over time. In this gap has been left an assumption; that with the rise of genetics came a plant breeding industry that was not only more commercially viable, but one which was reorganised according to the logic of that science. With the stability of pure lines, it is said, came mass production, economies of scale and the rapid shift towards a small number of large multinational corporations controlling seed. It is rare to find this gap and assumption fully articulated, though fortunately Tiago Saraiva has summarised the contemporary historiographical view most eloquently, stating that "By instituting a hard genetic identity of the living organism independent of place and

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[2] See in particular Johannsen (1903, 1907, 1911). The explanation in this opening paragraph is based upon Walter (1922, pp. 122–127).

[3] Kingsbury (2009) and Murphy (2007) both differentiate between pre-scientific plant selection and truly scientific plant breeding. Blaxter & Robertson (1995) are determinedly on the side of genetics as a contributor to their twentieth century 'agricultural revolution'. Somewhat puzzlingly though, they see this contribution as emerging only in the mid-1930s. "Plant breeding, which in 1936 was a simple art depending on serendipity and the breeder's instinct, had become, by the end of our fifty-year period, a highly sophisticated application of the science of botany to the manipulation of the plants genetic capacity." p. 120. This passage can either be interpreted as demonstrating sensitivity to precisely the kind of culture described in the present paper (though with little respect for the state of knowledge at this time), or merely an artefact of their focussing solely upon the period 1936–1986.

[4] Charnley & Radick (2013), Gayon & Zallen (1998), Harwood (1997, 2000), Kevles (1980), Kimmelman (1983, 1987, 1992, 1997), Müller-Wille (2007), Palladino (1993, 1994, 1997), and Theunissen (2008, 2012).

[5] On early scepticism regarding the pure line see Harwood (1997), Vicedo (1997), and Wieland (2006).

[6] Balen (1986), Churchill (1974), Kim (1991), Müller-Wille (2007), and Roll-Hansen (1980, 1989, 2009).

[7] Sapp (1983, p. 313).

[8] Agar (2012).

[9] NIAB and its archives have been the subject of a recently completed PhD thesis. Berry (2014). The archive codes referred to throughout correspond to the archive handlist, which can be accessed on the dedicated website niabarchive.org.

[10] Luca Iori's recently completed PhD thesis, on agricultural genetics and plant breeding in Italy in the early twentieth-century, is largely focussed on the life of the Italian plant breeder Nazareno Strampelli, though the thesis encompasses much more in the process; Iori (2013). On the Americans William Jasper Spillman, R. A. Emerson and Luther Burbank see Carlson (2005), Kimmleman (1992) and Palladino (1994) respectively. On generations of the Vilmorins in France see Gayon & Zallen (1998), on Nilsson-Ehle in Sweden see Åkerberg (1986), on Willhelm Johannsen in Denmark see Churchill (1974) and Roll-Hansen (1989, 2009). On Wilhelm Rimpau and Ferdinand von Lochow in Germany see Wieland (2006).

[11] Edgerton & Horrocks (1994).

[12] Elina et al. (2005), Maat (2001), Müller-Wille (2005, 2008), and Olby (1989).