

Plant Phenotypes as Distributions: Johannsen's Beans Revisited

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ABSTRACT: In the early twentieth century, Wilhelm Johannsen's breeding experiments on pure lines of beans provided empirical support for his groundbreaking distinction between phenotype and genotype, the foundation stone of classical genetics. In contrast with the controversial history of the genotype concept, the notion of phenotype has remained essentially unrevised since then. The application of the Johannsenian concept of phenotype to modularly built, nonunitary plants, however, needs reexamination. In the first part of this article it is shown that Johannsen's appealing solution for dealing with the multiplicity of nonidentical organs produced by plant individuals (representing individual plant phenotypes by arithmetic means), which has persisted to this day, reflected his intellectual commitment to nineteenth-century typological thinking. Revisitation of Johannsen's results using current statistical tools upholds his major conclusion about the nature of heredity but at the same time falsifies two important ancillary conclusions of his experiments—namely, the alleged homogeneity of pure lines (genotypes) regarding seed weight variability and the lack of transgenerational effects of within-line (within-genotype) seed weight variation. The canonical notion of individual plant phenotypes as arithmetic means should therefore be superseded by a concept of phenotype as a dual property, consisting of central tendency and variability components of organ trait distribution. Phenotype duality offers a unifying framework applicable to all nonunitary organisms.

Keywords: genotype, intraplant variation, *Phaseolus vulgaris*, phenotype, subindividual variation, Wilhelm Johannsen.

Each of the kingdoms has its own evolutionary peculiarities and these must be worked out separately before a balanced synthesis can be attempted. (Ernst Mayr 1963, p. v)

Introduction

Wilhelm Johannsen's (1857–1927) discrimination between the level of appearance (“phenotype”) and the level of inheritance (“genotype”) forms part of a group of major concepts that decisively shaped the science of genetics (Falk 2008). The phenotype-genotype distinction, crafted for the first

time by Johannsen (1909; for an English version, see Johannsen 1911), has been considered “one of the major accomplishments in the history of biology” (Churchill 1974, p. 5), “the foundation stone of classical genetics” (Roll-Hansen 2009, p. 458), and a “conceptual pillar of twentieth century genetics” (Peirson 2021, p. 1), and it has warranted its own entry in dictionaries of the history of science (Bynum et al. 1981).

Ever since their initial introduction, the concept of genotype and the closely related concept of “gene,” also proposed by Johannsen, have been the subject of countless debates and controversies about their meaning and biological reality, as well as their relations with heredity, quantitative genetics, and evolutionary biology (e.g., Churchill 1974; Wanscher 1975; Mayr 1982; Roll-Hansen 2009, 2014, 2022; Baverstock 2021). Johannsen himself contributed to the earlier revisions of these concepts (Churchill 1974; Wanscher 1975). Such controversy-laden history of the genotype and gene concepts is hardly surprising, as next to nothing was known about the material basis of heredity by the time Johannsen devised his conceptual breakthrough. Subsequent advances in cytology and molecular genetics that unveiled the material basis of heredity demanded revisions and redefinitions of Johannsen's purely abstract concepts of genes and genotypes (Churchill 1974; Wanscher 1975; Mayr 1982). I will not be concerned here with the gene and genotype concepts. My focus will instead be on the less scrutinized concept of phenotype and, more specifically, on how it applies to plants.

In contrast with the controversial history of the gene and genotype concepts, the notion of phenotype has been undebated and unrevised, persisting essentially unaltered since its inception (Wanscher 1975). As originally defined, phenotypes of organisms are “appearance types” consisting of their “intrinsically measurable realities, just what can be observed” (Johannsen 1909, p. 123) and are “real things . . . distinguishable by direct inspection” (Johannsen 1911, p. 134). This original idea of the phenotype as an appearance is the same found now in contemporary textbooks, which refer, for instance, to “the observable attributes of

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an organism” (Tamarin 2001, p. 21), “a measurable trait of an organism” (Templeton 2006, p. 6), “the physical or biochemical attributes of the organism” (Hart and Clark 1997, p. 10), or “the morphological, biochemical, physiological, and behavioral attributes of an individual” (Hamilton 2009, p. 13). This steady continuity over more than one century of the phenotype concept most likely reflects the fact that by referring to the purely observable features of organisms, the reality of a given phenotype seems obvious and can hardly be disputed. After all, there is little room for discussing whether the eye color of a *Drosophila* fruit fly, the bill length of a bird, the wing color of a peppered moth, or the banding pattern of a *Cepaea* snail can be interpreted in ways other than as simple phenotypes fitting equally well the Johannsenian and contemporary usages. In these and similar instances there is an immediate, obvious link between observable features (appearance) and a named (e.g., banded shell) or measured (e.g., bill length = 7.5 mm) phenotype. Nevertheless, this appealing simplicity holds only for unitary, nonmodular organisms with determinate growth such as most animals.

Johannsen’s Phenotype Concept as Applied to Plants

Defining an individual’s phenotype is not so straightforward in the case of nonunitary, modularly built organisms with indeterminate growth as typically happens in plants, each of which bears nonidentical repetitions of different kinds of homologous vegetative (buds, leaves) and reproductive organs (inflorescences, flowers, fruits, seeds). Assessing the leaf, flower, fruit, or seed phenotype of an individual plant that can bear up to thousands of nonidentical copies of each of these kinds of homologous, reiterated structures poses a conceptual challenge. Although the quintessentially modular plants account for a substantial fraction of total planetary biodiversity and represent the dominant life form on Earth (Christenhusz and Byng 2016), the specific complications associated with the definition of phenotypes in this dominant group of organisms have been rarely addressed or acknowledged (but see Herrera 2009, 2017; Harder et al. 2019). This represents a significant knowledge gap for understanding plant evolution, since it is actually the phenotype that is “visible” to, and filtered out by, natural selection, and it is the evolution of phenotypes that is ultimately of interest in evolutionary biology (Lewontin 1974, 2000). Because of these implications, the application of the Johannsenian concept of phenotype to modularly built, nonunitary plants deserves reexamination.

Johannsen himself had to deal with the problem of defining the seed weight phenotype of his experimental bean plants (*reinen Linien*, or “pure lines,” as he termed them; “isogenic lines” in current terminology), each of which pro-

duced hundreds of seeds each season that differed widely in individual weight (Johannsen 1903, pp. 21–25). His appealingly simple solution was to define the seed weight phenotype of a pure line as the arithmetic mean of all seed weights from the same line (Johannsen 1909, 1911). On one side, the adoption of this data aggregation procedure was probably decisive for Johannsen’s successful creation and posterior acceptance by the scientific community of his phenotype concept. But on the other side, as I will show below, Johannsen’s dismissal of the extensive variability in weights of the beans produced by each of his pure lines, along with his failure to recognize that the magnitude of within-line variability differed across lines, marked the beginning of a persistent tradition in plant biology that lasts to this day. At the heart of this tradition is the practice of systematically sweeping under the rug of arithmetic means all phenotypic heterogeneity exhibited by the set of homologous organs produced by individual plants (i.e., genotypes) and implicitly considering individual means as the single biologically meaningful representation of individual plants’ phenotypes (Herrera 2009).

In this article I will first show that Johannsen’s solution for dealing with the multiplicity of nonidentical seeds produced by plant individuals reflected the intellectual influence of the nineteenth-century fathers of the “average man” concept—namely, Belgian astronomer and statistician Adolphe Quetelet (1796–1874) and British statistician and anthropologist Francis Galton (1822–1911). Consequently, the ongoing tradition of identifying individual plant phenotypes with average values is ultimately rooted in a long bygone typological thinking. In the second part I will present a statistical reevaluation of results of Johannsen’s experiments with beans that ultimately inspired his phenotype concept (Johannsen 1911; Roll-Hansen 2009). Johannsen used statistical procedures that were perhaps primitive by the standards of his time (Roll-Hansen 1989), and some contemporary biometricians criticized his experiments because the analyses were of “an amateurish simplicity that could not be taken seriously” (Roll-Hansen 2009, p. 486). Others, however, considered that his methods were sufficient for the immediate purpose (Yule 1904). Revisitation here of Johannsen’s results using current statistical tools will uphold his major conclusion about the nature of heredity but at the same time will reveal that his disregard for seed weight variability within pure lines led to the neglect of important aspects of his results whose incorporation to the phenotype concept could have enriched the scope and generality of his classical “crucial experiment” (Roll-Hansen 1989). In particular, reanalyses of Johannsen’s results presented below will highlight the conceptual value of treating plant phenotypes with regard to features of reiterated organs as observable distributions rather than single

abstract values, as it is still often done nowadays following Johannsen's initial lead.

Plant Phenotypes as Arithmetic Means: Historical Roots and Lasting Sequels

In the mid-nineteenth century, Quetelet (1869) pioneered the application of statistical methods to social data, his work being a significant step toward measuring uncertainty (Stigler 1986). He was “fascinated by the appearance of the normal distribution in human data” (Raper 2022, p. 33) and used the arithmetic mean to identify the “typical” specimen of a group (the “average man” concept). Particular individuals were treated as instances of naturally occurring “errors” around the mean (Donnelly 2016). Galton (1883, 1889) subsequently borrowed from the core of Quetelet typological work, elaborating on biological (heredity) and social (eugenics) implications of the normal distribution of sets of measurements on objects of the same kind (Raper 2022). From Johannsen's (1909, p. 102) viewpoint, “Galton must always be revered as one of the founding fathers of the scientific theory of heredity, while Quetelet's research formed the first basis of an exact research of the variability question” (my translation).

There is no need to engage in historical conjectures to trace back the intellectual roots of Johannsen's practice of reducing the seed weight phenotypes of his pure lines to their respective arithmetic means, as he was quite explicit in this regard from the first mention of the phenotype concept (for a thorough analysis of the historical roots of Johannsen's work, see Roll-Hansen 2009). Johannsen (1909, p. 123) wrote, “The ‘type’ in Quetelet's sense [*Der Typus im Quetelet'schen Sinne*] is only a phenomenon of a superficial nature . . . one could statistically aptly call the emerging type an appearance type, or, short and clear, a ‘phenotype.’ Such phenotypes are intrinsically measurable realities: just what can be observed as typical; thus in the case of variation series, the centers around which the variants are grouped” (my translation). In its origin, the arithmetic mean of several observations was a statistical device aimed to cope with the errors arising from the imperfection of instruments and the organs of sense (Raper 2017). Under Quetelet's typological views, and also Galton's some years later, the arithmetic mean of a trait-value distribution (the “type”) was interpreted as “nature's true intention” (Raper 2022), and observed variations around the type were disregarded as nature's error, just imperfect deviations arising from the influence of “*causes accidentelles*” (Quetelet 1869) or the expression of imperfections caused by an “incalculable number of petty accidents” (Galton 1889, p. 16). Johannsen's decision to use the mean seed weights of pure lines as the representation of their appearances (phenotypes) and his disregard of variations around these means

as unimportant were just the implementation of Quetelet's and Galton's typological framework that he admired (Johannsen 1909, p. 5).

Johannsen also initiated a tradition in plant phenotype assessment that has outlived the typological current of thought that inspired it in the first place. The aggregative solution to deal with multiple phenotypic values per genotype by considering the arithmetic mean as representative is still embodied in contemporary plant studies that assess individual phenotypes for reiterated, homologous structures. This holds true, for example, in phenotypic selection research where relationships have been sought between phenotype and individual fitness in plant populations. Studies of phenotypic selection on animals and plants proliferated following the development of analytical tools for estimating the strength and direction of selection on quantitative traits (Lande and Arnold 1983; Arnold and Wade 1984; Endler 1986; Kingsolver and Schemske 1991). Phenotypic selection studies on plants have often considered organ traits with a multiplicity of values per individual (Herrera 2009, table 10.1 therein; for reviews of phenotypic selection research, see also Kingsolver and Diamond 2011; Siepielski et al. 2013; Caruso et al. 2019). The intraplant multiplicity of organ trait values had to be shoehorned into selection models that were originally devised for single-figure phenotypic characters of animal individuals. By “shoehorning” I mean that some tinkering had to be made with the original selection model to accommodate the reality that in plants many phenotypic traits of interest actually refer to reiterated organs (e.g., seed weight, flower size, leaf area) rather than to the whole plant itself (e.g., height, biomass). The solution routinely implemented has been to adopt Johannsen's “[pheno] type in Quetelet's sense” (Johannsen 1909, p. 113)—namely, taking individual arithmetic means as descriptors of individual phenotypes. This procedure of representing individual plant phenotypes by arithmetic means alone would be justified if intraindividual phenotypic variation in organ traits did not exist, or if, although existing, its magnitude was roughly similar in all individuals (Herrera 2009). These premises, however, did not hold in the case of Johannsen's beans, as shown in the section below.

Johannsen's Beans Revisited

Johannsen's famous experiments with beans (*Phaseolus vulgaris*) were planned as a test to discriminate between major competing hypotheses on the nature of heredity, the continuity of evolution, and the efficacy of natural selection as a creative force, which were at the center of the genetic debate at the time, later known as the biometrician-Mendelian controversy (Provine 1971; Olby 1989; Roll-Hansen 1989). More specifically, Johannsen's experiments intended to distinguish between the discontinuous evolution supported

by the Mendelians and the continuous evolutionary change envisaged by biometricians, which denied the truth of Mendelism, adhered to Galton's theory of ancestral heredity, and believed that selection could change a population almost indefinitely (Olby 1989; Roll-Hansen 1989). In addition to the original descriptions in German (Johannsen 1903, 1909), the experiments have been summarized many times in English (Provine 1971; Churchill 1974; Wanscher 1975; Mayr 1982; Roll-Hansen 1989; Bulmer 2003; Falk 2009). In the section below I will provide a succinct summary of the experiments conducted between 1900 and 1902 that are most directly relevant to this article and the only ones for which numerical results amenable to statistical reanalysis are available.

Methods

In the spring of 1901 Johannsen bought a lot of brown "Princess" beans, a self-fertilizing cultivar of *Phaseolus vulgaris*, from the previous year's crop. He chose 150 seeds whose individual weights collectively encompassed the full range of weights represented in the original sample. Seeds were individually weighed and sown in numbered plots in an experimental garden. Seed crops produced by self-fertilization were harvested in the fall of 1901, and seeds from the different mother plants (= pure lines) were kept separately. Each pure line was descended by spontaneous self-fertilization from a single bean from the purchased lot, and the original sample of 150 seeds (and the 19 plants he selected from among the 150 progenies) must have included multiple inbred, completely homozygous lines from the original population. Johannsen considered that the original population of beans was composed of a large number of "pure lines," each with its own type, which he later called a genotype (Bulmer 2003). In the spring of 1902 he sowed seeds from 19 selected lines from the 1901 crop (F_1 hereafter), keeping a record of their weights. The seed crops of the resulting plants were collected in the fall of 1902 (F_2 hereafter), and every seed was weighed individually (for full details, see Johannsen 1903, pp. 15–21). Detailed summaries of the results of the 1902 experiments were presented in tabular form. These included, on one side, separate tables for each pure line showing the mean and standard deviation of seed weight, broken down by the weight class of the initial mother seeds (*Muttersamen* 1901 crop; Johannsen 1903, p. 21–24, tables A–T; "dataset 1" hereafter, available on figshare [https://doi.org/10.6084/m9.figshare.22639861; Herrera 2023]) and, on the other, the distribution of seeds among weight classes, separately for each pure line (Johannsen 1903, p. 25; "dataset 2" hereafter, available on figshare [https://doi.org/10.6084/m9.figshare.22639861; Herrera 2023]). My reanalyses will consist of applying simple linear

models and variance partitioning methods to these datasets using the R environment (R Core Team 2022) and functions `lm` and `lmer` from the `stats` and `lme4` (Bates et al. 2015) packages, respectively. Model comparisons by likelihood ratio tests will be performed with the function `lrtest` from the `lmerTest` package (Zeileis and Hothorn 2002). R code used in the analyses is available on figshare (https://doi.org/10.6084/m9.figshare.22639861; Herrera 2023).

The following two questions will be specifically addressed in the reanalysis of Johannsen's results for the 1900–1902 experiments. First, did Johannsen's experimental results actually support his claim that fluctuations about the average value within the pure lines (i.e., the phenotype) "show no characteristic difference" (Johannsen 1911, p. 136) or, as it was phrased much later by Mayr (1982, p. 783), that "the variation within each group of descendants was virtually identical"? In other words, were pure lines similar with regard to the extent of intraline variation in seed weight? And second, does variation within pure lines in maternal seed weight (F_1) have some predictive value for the weight of seeds in the following generation (F_2)? This possibility was negated by Johannsen and by every author who has subsequently reviewed his work (e.g., "in a pure line all the variations are consequently purely somatic and therefore non-heritable" [Yule 1903, p. 238]; "beans grown from a small bean were exactly the same size as those grown from a large bean of the same plant" [Vernon 1909, p. 424]; "within each pure line he found no statistically significant difference in average weight of offspring from beans of quite different weights" [Roll-Hansen 2022, p. 85]).

Results

Analysis of dataset 2 (distribution of seeds among weight classes for each pure line) revealed that when the 5,494 F_2 seeds from the 19 pure lines are considered, weight differences among individual seeds from the same pure line accounted for as much as 78.7% of total sample variance, while differences among pure lines accounted for only 21.3% of total variance. A simple linear model with the standard deviation of F_2 seed weight (computed for each combination of pure line \times F_1 maternal seed weight class; dataset 1) as response variable and the mean F_2 seed weight as single predictor was statistically significant ($F_{1,63} = 18.68$, $P = 5.6e-05$, adjusted $R^2 = 0.22$). When the identity of the pure line was added to the model as one further predictor, the model was considerably improved (adjusted $R^2 = 0.46$), and the improvement was statistically significant ($\chi^2 = 46.16$, $P = .00028$, likelihood ratio test). After statistically accounting for their differences in mean seed weight, therefore, pure lines also differed widely in the magnitude of the variability around the mean (fig. 1).

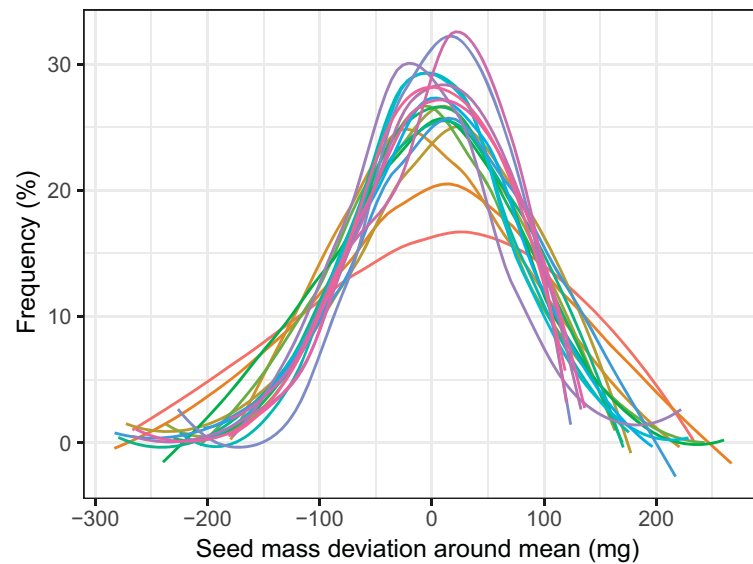


Figure 1: Smoothed frequency distributions of F_2 seed weights from the 19 pure lines in Johanssen's 1900–1902 experiments (coded with colors). To facilitate comparisons of within-line variabilities, the original seed weights from each pure line were transformed to deviations around the line's arithmetic mean.

The second question above was addressed by fitting a simple linear model to dataset 1 (mean seed weight by pure line and maternal weight class) with the mean seed weight of F_2 for each combination of line and maternal weight class as response variable. When pure line was the single predictor, the model was highly significant ($F_{18,46} = 28.73$, $P < 2.2e-16$) and accounted for a high proportion of observed variance (adjusted $R^2 = 0.88$). This result corroborated the central role of pure lines as a determinant of observed variation in bean weight, a key conclusion of Johanssen's work. When the maternal seed weight class was added to the model as a further predictor (nested within pure line), the model was significantly improved (adjusted $R^2 = 0.93$). Even though quantitatively small, the improvement resulting from including the maternal seed weight class was statistically significant ($\chi^2 = 64.45$, $P = 7.5e-07$, likelihood ratio test). This demonstrates an effect of intraline variation on seed mass of the progeny after differences among pure lines were statistically accounted for. Such significant effect reflects a prevailing inverse relationship linking maternal (F_1) and offspring (F_2) seed weight within pure lines (fig. 2; 14 of the 19 within-line regressions shown have negative slopes; mean regression coefficient \pm SE = -0.043 ± 0.037).

Discussion

Reanalysis of Johanssen's 1900–1902 classical experiments on variation and inheritance of bean weights in pure lines

has furnished contrasting results. On one side, it has provided unambiguous corroboration of Johanssen's central pioneering claim on the crucial explanatory power of pure lines (i.e., genotypes). But on the other side, two important ancillary conclusions of the experiments have been falsified—namely, the alleged homogeneity of pure lines with regard to seed weight variability and the lack of transgenerational significance of within-line variation in seed weight. The canonical notion of individual plant phenotypes as arithmetic means of organ trait values and the traditional neglect of intraplant variation as biologically nonsignificant seem therefore to have been rooted for more than one century in an erroneous, or at least incomplete, interpretation of some of Johanssen's results. Some significant implications of this finding are considered in the following sections. Before proceeding to these most conceptually laden aspects, however, it must be stressed that the extensive within-genotype variance in seed size shown by Johanssen's beans (~79% of total) was not an extraordinary biological circumstance. In wild plant populations, intraplant variance in traits of reiterated organs tends to be so large that it often exceeds among-individual variance (Herrera 2009). In a total of 227 partitions of population-wide trait variance into its within- and among-individual components, intraplant variance exceeded among-plant variance in 27% of flower-related, 71% of seed-related, 80% of fruit-related, and 87% of leaf-related estimates (Herrera 2017). Extensive intraplant variance is thus commonplace in nature and should be taken into consideration in plant selection

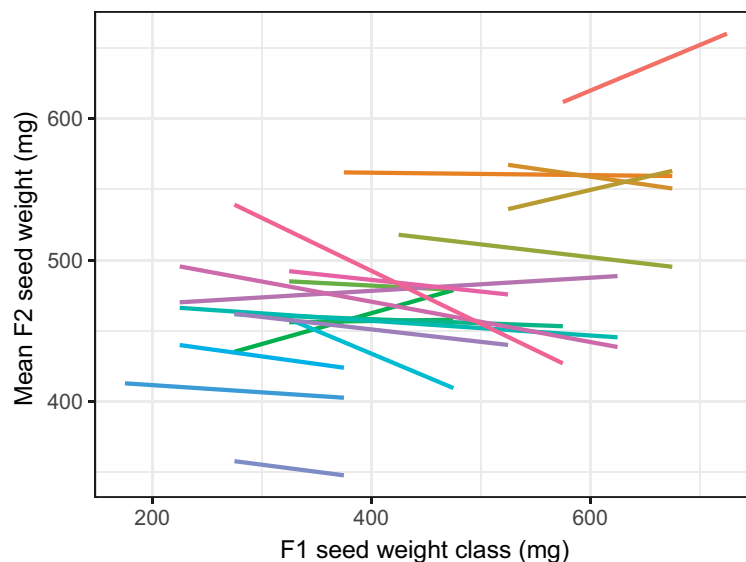


Figure 2: Fitted linear relationships between maternal (F_1) seed weight class and offspring (F_2) mean seed weight within pure lines in Johanssen's 1900–1902 experiments, separately for each of the 19 pure lines (coded with colors). Individual regressions shown are based on two to seven maternal seed weight classes per line (mean \pm SE = 3.4 ± 0.3).

studies or, at least, preliminarily evaluated rather than disregarded a priori as unimportant.

The Plant Phenotype as a Distribution

The preceding reanalyses reveal a greater biological significance of within-line variation in bean weight than Johanssen and others following his lead have historically recognized. On one side, when grown under homogeneous environmental conditions, pure lines not only differed in mean bean weight but also in their variabilities around the respective means. The degree of internal heterogeneity of each pure line actually formed part of its measurable “appearance,” thus properly qualifying as an element of its phenotype as well. Since seed weights within lines were normally or quasi-normally distributed (fig. 1; Johanssen 1903, 1909) and normal distributions are completely described by two parameters (mean and standard deviation), the corollary follows that describing pure lines by a combination of mean and standard deviation actually amounts to recognizing their phenotypes as statistical distributions rather than single figures, as derived from Johanssen's pioneering typological view.

In wild plant populations, intraplant variability of a given quantitative character of a reiterated structure should likewise provide a descriptive property of the “appearance” of the individual. As illustrated in figure 3, plants with identical Johanssenian phenotypes (arithmetic means) can still display contrasting “appearances” because of differences in variability alone. Haldane's (1957, p. 312) terse contention

that “individual plants not only have their characteristic means, but their characteristic standard deviations” (see also Roy 1959), although neglected at the time, has recently been confirmed in wild plant populations whenever it has been explicitly investigated. Irrespective of species, kind of reiterated organ, or quantitative trait involved, plant populations are characteristically made up of individuals that differ in the magnitude of intraplant trait variability, and such variation among individuals in internal variability does also persist when plants are grown under similar controlled conditions (Seburn et al. 1990; Herrera 2009, table 7.1 therein; Herrera et al. 2015; Shimada et al. 2015; Arceo-Gómez et al. 2017; March-Salas et al. 2021; Proß et al. 2021; Møller et al. 2023; Paglia et al. 2023). For the “appearance” of an individual plant to be properly described, therefore, its phenotype should be treated as a dual property consisting of the mean (= central tendency component) and standard deviation (= variability component) attributes of the trait distribution. In cases where trait values' distributions within plants depart substantially from normality, the higher moments of the statistical distribution (skew, kurtosis) could be added to obtain a complete description of the phenotype.

This heterodox (i.e., nonconformant to the predominant typological notion introduced by Johanssen) definition of plant phenotypes is reinforced by the findings that not only the individual means of organ trait values but also their intraindividual variabilities can be heritable and “visible” to natural selection. First, studies in classical population genetics have often found that intraplant variability is heritable. This was found, for instance, by Paxman (1956) for

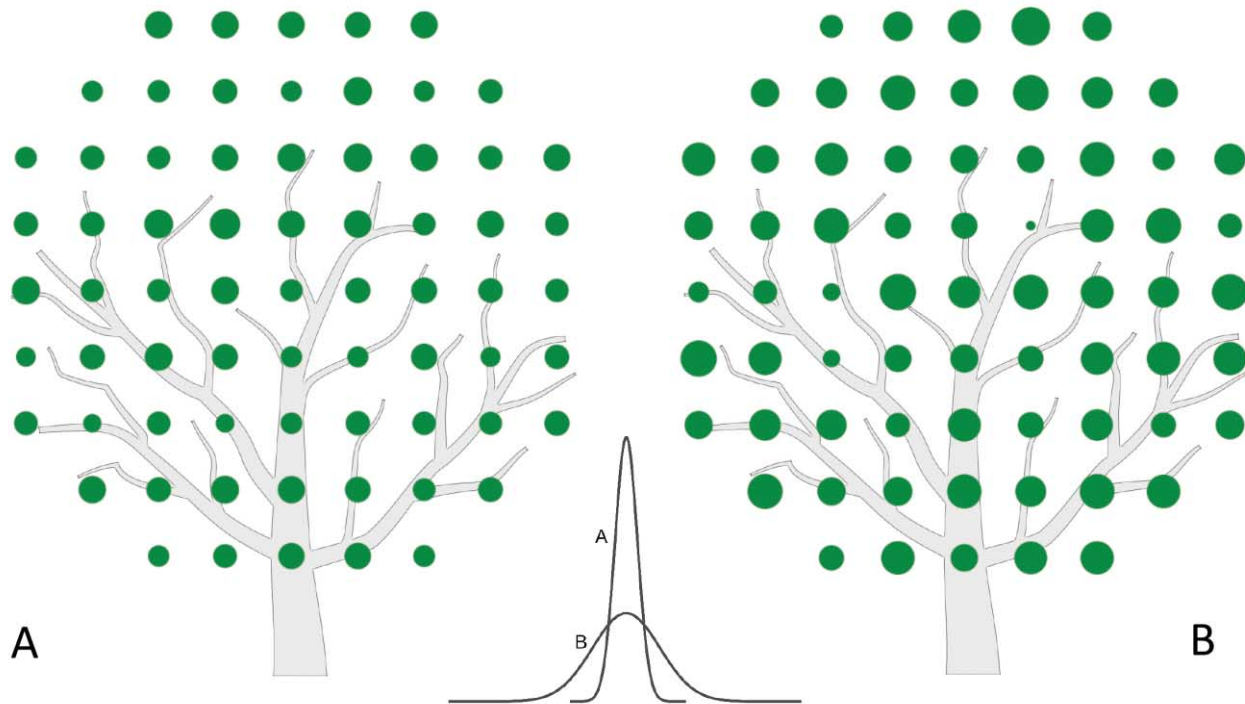


Figure 3: Trait variability within individual plants is a component of their measurable “appearance” and qualifies as an element of the phenotype in addition to the trait mean. These graphs depict two random number samples drawn from normal distributions with the same mean but different standard deviations (standard deviation in *A* is one-third of that in *B*), simulating two hypothetical plants with different variabilities in a quantitative trait of a reiterated organ without differing in the means. Each circle represents a single random value, and the circle size has been mapped to “trait values” so that variability can be visually appreciated. The location of circles in the graphs reflects only their order in the random sample. Inset depicts the two normal distributions from which random values were drawn.

intraplant variability in leaf and flower traits of *Nicotiana rustica*, by Seyffert (1983) for intraplant variation in floral anthocyanin content in the flowers of *Matthiola incana*, and by Bagchi et al. (1989) for leaf venation in *Tectona grandis* (for similar results, see also, e.g., Drennan et al. 1986; Seburn et al. 1990; Biere 1991; Winn 1996). In the same vein, individual differences in intraplant leaf variability have been found to be associated with genetic markers in *Helleborus foetidus* (Herrera et al. 2015). And second, phenotypic selection studies on wild plant populations that have modeled fitness as a function of trait mean plus variance, including some measurement of intraindividual variability in organ traits as predictors of individual fitness (e.g., coefficient of variation), have found significant selection on intraplant variability irrespective of whether selection on trait means did also occur or not (Herrera 2009, table 10.2 therein; Benitez-Vieyra et al. 2014; Sobral et al. 2014; Austen et al. 2015; Schreiber et al. 2015; Shimada et al. 2015; Dai et al. 2016; Arceo-Gómez et al. 2017; Kulbaba et al. 2017; Palacio et al. 2017; Harder et al. 2019). For example, in the hermaphroditic tree *Ipomoea wolcottiana*, individual fitness was inversely related to intraplant variability in anther-

stigma separation (Arceo-Gómez et al. 2017), and in the bird-dispersed tree *Psychotria carthagenensis*, there existed disruptive selection gradients on intraindividual variation in fruit traits (Palacio et al. 2017). The two preceding complementary lines of evidence (inheritance of and selection on intraindividual variance) emphasize that the variability components of a plant phenotype—rather than reflecting “nature’s errors” devoid of interest, as embodied in Johannsen’s typological notion of the phenotype concept—are the realized expression of the intrinsic capability of individual genotypes to produce adaptive, fitness-enhancing arrays of nonidentical homologous organs. Depending on features of the biotic and abiotic selective environments, an individual’s ability to produce more or less phenotypically variable arrays will itself become a target of selection through diversifying bet hedging, resource partitioning, or division of labor mechanisms (Herrera 2009, 2017; Herrera et al. 2022).

Transgenerational Significance of Intraplant Variation

Another relevant result of the reanalysis of Johannsen’s 1900–1902 experiments is that, contrary to his claims and

those of authors quoting him, within-line seed variation did have a measurable, predictable effect on the weight of seeds produced by the next generation of the pure line. The predominantly inverse relationship found here indicates that within pure lines, the larger seeds tended to produce plants that eventually yielded smaller seeds on average. This result does not challenge Johannsen's conclusion about the lack of heritability of within-line variation, since inheritance of within-line variation would have produced a predominantly positive relationship. Nevertheless, the finding that within-line variation had some effect on the next generation's seed weight distribution does challenge the long tradition of disregarding intraplant variability as ecologically and evolutionarily irrelevant (Haldane 1932; Mayr 1982). Early in the twentieth century, influential authors were aware of the variability of properties within individual plants and named it variously ("individual variability" [Pearson 1900]; *partielle Variabilität* [De Vries 1901]; "fluctuations" [Johannsen 1909]). They attempted to incorporate that particular level of variation into their views of inheritance and evolution (e.g., Pearson 1901, 1903). The disinterest in the phenomenon of intraindividual variability in organ traits that prevailed for most of the twentieth century was mostly a consequence of Johannsen's experiments contributing to the dismissal of a particular theory of selection and inheritance (Galton's and Pearson's side in the biometrician-Mendelian controversy) with which such variability had been circumstantially associated (Mayr 1982; Roll-Hansen 1989). As shown here, however, Johannsen's experiments actually revealed that a transgenerational effect of seed weight variation did exist within pure lines, although this aspect went unnoticed because of the lack of an adequate statistical methodology. The insistent emphasis over the years on the specific part of Johannsen's results that negated the inheritance of variation within pure lines (or "soft inheritance" sensu Mayr 1982), combined with the lack of knowledge on the possible mechanistic basis of such variation (but for recent research on epigenetic mosaicism in plants, see, e.g., Alonso et al. 2018; Herrera et al. 2021, 2022; Yao et al. 2021), has so far hindered the exploration of the various pathways whereby intraplant variability can eventually impinge on individual fitness irrespective of whether it is inherited or not.

Concluding Remarks

Aggregation, or the combination of observations to obtain a statistical summary, has been deemed one of the "seven pillars of statistical wisdom" (Stigler 2016). Nevertheless, statistical considerations alone are insufficient to solve biological problems, as explicitly emphasized by Johannsen (1903, p. 9, my translation: "statistical theory certainly cannot do it alone to clarify the basic biological problems!")

and exemplified by his work. The central tenet of this article is that aggregation of trait values of reiterated homologous structures of individual plants misses an important component of their phenotypes. Although I have focused only on plants, the phenotypic heterogeneity of genotypes also occurs in nonunitary organisms from other kingdoms and also, but less frequently, in certain traits of some unitary organisms. In yeasts and filamentous fungi, cells within clonally derived populations that have a uniform genetic background often display differences in phenotype (Hewitt et al. 2016). In corals, colonies consisting of a single genotype are often internally heterogeneous in chemical, physiological, and morphological traits (Ulstrup et al. 2006; Menezes et al. 2013; Conlan et al. 2018; García-Cárdenas et al. 2023). Among insects, phenotypic variation within aphid clones produced parthenogenetically from a single stem mother (equivalent to "evolutionary individuals"; Janzen 1977) has been extensively reported (Andrade and Roitberg 1995 and references therein). In some birds, within-clutch variance in egg size is comparable to among-clutch variance (Christians 2002). The dual concept of phenotype advocated here for plants should therefore be applied in all of these instances as well.

Studies of phenotypic selection in nonunitary organisms, particularly plants, have traditionally adopted the typological, Johannsenian view of the phenotype, as noted earlier. Beyond the practical implications, the adoption of the dual phenotype concept in these organisms creates an extended conceptual framework where new hitherto unexplored evolutionary questions can be addressed. In nonunitary organisms, for instance, it may be asked whether coupled (e.g., positive directional selection on both the mean and the variance) and uncoupled (e.g., stabilizing selection on mean and directional selection on variance) selection on within-genotype mean and variance should produce contrasting trajectories of phenotypic evolution. More generally, and more importantly too, the key question arising is whether adaptive phenotypic evolution proceeds in inherently different ways in unitary and nonunitary organisms because of the duality of the latter's phenotypes. Were this the case, recognizing phenotypic duality as an evolutionary peculiarity of nonunitary organisms could furnish a key to unlock the rather cryptic statement of Ernst Mayr (1963) used as an epigraph in this article.

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Data and Code Availability

All data and code used in the analyses are available on figshare (<https://doi.org/10.6084/m9.figshare.22639861>; Herrera 2023).

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