

Vavilov's Law of Homologous Series of Variation – Its Relevance in the Genomics Era

Parimalan Rangan

¹*Division of Genomic Resources, ICAR-National Bureau of Plant Genetic Resources, New Delhi-110012, India*

²*Queensland Alliance for Agriculture and Food Innovation, University of Queensland, St Lucia, QLD 4072, Australia*

ABSTRACT

Genetics, the study of inheritance, has a long history, but was still a nascent science in the last half of the nineteenth century, becoming a well-established one in the early part of the twentieth century. The focus of genetics is especially on traits and their heritability, and the science uses variation within a species to understand modes of inheritance and the genes underlying the traits. Taxonomy, a very old discipline, uses variation across species to classify and understand biological diversity. Vavilov (1922) studied variation within species (Jordanans) and its parallelism across closely related species (Linneons). He documented patterns of such parallel variation within and across crop species and their wild relatives, and his insights led to a new discipline, plant genetic resources. The importance of these remarkable insights has not been fully explored, even a hundred years later. This review briefly discusses Vavilov's law and its relevance in genomic sciences today.

Keywords: C₄ photosynthesis trait, crop wild relatives, domestication trait, Jordanons, Linneons, parallelism, rice, transcriptomics, wheat

Author for correspondence: Parimalan Rangan; e-mail: r.parimalan@icar.gov.in, p.rangan@uq.edu.au; ORCID: 0000-0003-1660-8072

During its history, biological science has become diversified into various specialized disciplines such as botany, zoology, microbiology, breeding and genetics, physiology, biochemistry, and so on. Mendel's law in 1865 (law of dominance, law of segregation, and law of independent assortment), Quetelet's law in 1871 (law of individual variability), Morgan's law in 1919 (chromosomal theory of linkage), and Vavilov's law in 1920 (law of homologous series of variation) were, at one time, considered to be the four fundamental laws (or pillars) of genetics (Roemer, 1936). Interestingly, most of these laws were framed based on studies that were focused on the variability at the infra-specific level, within units that at time were often called "Jordanons". Shape (its three-dimensional representation is 'form'), size, and colour, were the three dimensions at which the Jordanons within a "Linneon" (=species) were distinguished. Taxonomically, Linneons were the fundamental units of classification and the scientific naming of plants, while in genetics, Jordanons played a significant role in both academic understanding and also in applications for crop improvement programmes. In spite of this significant role, Jordanons were well studied only in few selected crops, with special reference to agriculture and crop wild relatives (CWRs).

It is equally likely that there is similar variability in unstudied species too. Genomics tools are especially helpful in such unstudied species where no research on Jordanons were made, and has potential applications in crop improvement using appropriate biotechnological tools.

Most phenotypic variability is not accidental but is expressed within certain limits and directions (Kupzow, 1975), depending on genetic factors and the surrounding environment. Such variability in nature is studied and arranged systematically in an organized manner with dichotomous keys for easier identification and understanding (Walter and Winterton, 2007; Griffing, 2011). While organs used for the study of such variability traits are commonly present in all the organisms of study (unity), they exhibit variable forms in different species (diversity). The flower, for example, is an organ commonly present in all angiosperms that exhibits discontinuous variability in number and arrangement of floral parts (Coen and Meyerowitz, 1991). Generally, floral parts are arranged in the following order (from the outermost whorl), calyx, corolla, androecium, and gynoecium. In spite of the general uniformity in embryo-sac formation and

double fertilization events, variability in the megagametogenesis and mature embryo-sac formation with variable genome dosage between $1n$ to $14n$ in the angiosperms reflects this unity and diversity (Friedman et al., 2008). Such patterns of unity and diversity are used to classify species at family or order levels (e.g., Cronquist, 1965; 1968; Takhtajan, 1980).

Morphological Variability Associated with the Law of Homologous Series in Variation

Vavilov (1922) suggested that morphological and physiological methods used in classifying plants should be applied below the level of the Linnaean species, in subspecies or varieties or races or genotypes. This is possible when we observe the presence of similar series of variation between closely related genera or Linneons. Such similarity can be extrapolated to other genera within the family and accordingly the variable genotypes can be predicted and would be of much use in exploration trip planning and execution. This was Vavilov's law of homologous series in variation. For example, pumpkin fruits are commonly ridged, but smooth fruit without ridges also occur. Vavilov's law was helpful in discovering a ridged phenotype in the commonly smooth-fruited muskmelon.

Vavilov's law provided insights in identifying traits that could be potentially useful for taxonomical classification of intraspecific variability. Combinations of different traits or characters (e.g., flower colour, pericarp color, etc.) along with the variable expression forms (eg: flower colour – pink, white, etc.; pericarp colour – pink and green) are utilized for intraspecific classification and such useful trait complexes (eg: pink flower with green pericarp, pink flower with red pericarp, white flower with green pericarp) are termed as 'Radicals'. Radicals can be identified using novel approaches like karyology, genetics, molecular cytogenetics, genes associated with radicals, and phytogeography (Rodionov et al., 2020). Radicals are sets of distinct characters (shape, size, and colour of organs like the leaf, flower, fruit) that differentiate closely related genera or species; Linneons contain multitudinal discontinuous variants that become the basis to recognize and categorize "Jordanons" at the intraspecific level (Vavilov, 1922; Rodionov et al., 2020). Although hundreds of thousands of Linneons representing the biodiversity in plant kingdom are quantifiable, it is the Jordanons that define the dimensions of diversity within Linneons at the genotypic level, visible only when

they are closely observed and studied. Such diversity is on par among the self- or cross-pollinated crops or non-crops and represents in a scale of hundreds of millions – 1000 times higher than Linneons (Vavilov, 1922). However, the diversity or variability within Linneons (= Jordanons) are generally studied in detail only in agricultural crops and its nearest wild relatives, even though such diversity exists in each and every Linneon. Shape, size, and colour (of different organs like leaf, flower, fruit) are the three important dimensions of diversity that further differentiate and categorize Jordanons within Linneons (Vavilov, 1922). Studying such Jordanons is important to have a complete understanding of the extent of variability, especially discontinuous variability that lead to Jordanons within Linneons, and its extension to other closely-related Linneons within a family. Such understanding can be used to predict the diversity pattern of Jordanons in other closely-related Linneons (parallelism) – a major component of Vavilov's law.

Homologous Series of Variation in the Genomics Era

Genomic visualization of the limits of representation of variability at genome level within a Linneon is called the pan-genome. The reference genome (single genotype sequence) is being replaced with the reference pan-genome (Bayer et al., 2020; Zhao et al., 2020). Probably, the importance of diversity at genome-scale, especially for genes associated with agronomically important traits, has been realized in recent years and resulted in the surge of pan-genomes in important crop plants (Gao et al., 2019; Li et al., 2022; Montenegro et al., 2017). The core genes or genomic regions are part of the core-genome, and variable "dispensable" genes or genomic regions (whose presence or absence depends upon the genotype) becomes part of the pan-genome. This categorisation is helpful in identifying the novel genes associated with traits of interest and adds value to the genotype possessing those genes. This helps in the genome-scale understanding of a Linneon and the extent of variability among a set of Jordanons or genotypes within a species.

Such genome scale data are also useful in understanding the crop domestication processes to overcome the cost of domestication through genomic insights on the genetics of linkage drag (Huang et al., 2023; Rangan et al., 2023; Moyers et al., 2018). For example, genome-scale analysis led to the understanding

of domestication of Asian and African rice, based on identified mutations in homologous genic regions. Genome information makes it possible to recognize parallelism (Vavilov's law) in genes associated with the domestication process in the Asian rice (*indica* and *japonica*), and also in Asian and African rice species (Callaway, 2014; Wing, 2014).

At the transcriptome level, it is a well-known fact that the evolution of C_4 photosynthetic pathway is a neo-functionalization event, that co-opts the same gene lineages independently in different sets of species (Christin et al., 2015; Aubry et al., 2011). Transcriptomic evidence helped identify the possibility for a non-Kranz C_4 photosynthesis in developing wheat grains, while the leaves of wheat are known to accomplish C_3 type photosynthesis (Rangan et al., 2016; Henry et al., 2017). Based on syntenic relationships (Vavilov's law of parallelism) between non-foliar photosynthetic organs of wheat and sorghum, it was hypothesized that a less-efficient non-Kranz NAD-ME type C_4 photosynthesis occurs in sorghum panicles (AuBuchon-Elder et al., 2020; Rangan et al., 2022 and citations therein). Similarly, at the chromosome level, parallelism is observed in the endoreduplication and variable ploidy levels in the endosperm tissues that undergo double fusion (Friedman et al., 2008; Rangan, 2020 and citations therein).

Of the four fundamental laws of genetics, most were postulated utilizing Jordanons and were validated in independent Linneons. So, understanding of variability at the intraspecific level has contributed significantly to our scientific understanding of variation between species, from the 19th century till date. This was especially the case when Gregor Mendel's findings in *Pisum* and *Hieracium* were found to be contradictory with special reference to the law of independent assortment (Nogler, 2006; Smykal, 2014; Scheid, 2022).

Genome scale information is helpful to achieve greater clarifications and better understanding in biology, especially when morphological variability fails to distinguish, or there is extensive parallelism among the sets of species studied. Such parallelism is observed especially between the Jordanons of wild relatives and cultivated forms of crop plants. A few sets of known chloroplast (*rbcL* and *matK*) and nuclear (internal transcribed spacers – ITS) based markers have been predominantly used in the consortium for the barcode of life (CBOL) project (Hollingsworth, 2011; Stoeckle, 2003). Additionally, genes associated with flowering

and regulation, like number and arrangement of petals, number of stamen and pistil, and other regulatory genes that modulate flowering could also be tested for their potential application in angiosperms (Rangan et al., 2005 and citations therein).

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